Psyche

Advances in Neotropical Myrmecology

Guest Editors: Jacques Hubert Charles Delabie,
Fernando Fernández, and Jonathan Majer

Advances in Neotropical Myrmecology

Psyche

Advances in Neotropical Myrmecology

Guest Editors: Jacques Hubert Charles Delabie,
Fernando Fernández, and Jonathan Majer

Editorial Board

Contents

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 286273, 3 pages
doi:10.1155/2012/286273

Editorial

Advances in Neotropical Myrmecology

Jacques Hubert Charles Delabie,[1] Fernando Fernández,[2] and Jonathan Majer[3]

[1] *Laboratório de Mirmecologia, Convênio CEPLAC-UESC, Centro de Pesquisa do Cacau, CP 7, 45500-000 Itabuna, BA, Brazil*
[2] *Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Carrera 30 No. 45-03, Bogotá, Colombia*
[3] *Curtin Institute for Biodiversity and Climate, Curtin University, P.O. Box U1987, Perth, WA 6845, Australia*

Correspondence should be addressed to Jacques Hubert Charles Delabie, jacques.delabie@gmail.com

Received 30 November 2011; Accepted 30 November 2011

> *. . . I believe Myrmecology is even more significant for tropical ecology than Ornithology, because the impact of ants in tropical habitats is tremendous. In addition ants served for many disciplines as model systems, for example, Sociobiology, Communication Biology, Chemical Ecology, and in recent years ants and other social insects have become model organisms for the study of Epigenetics . . .* (Bert Hölldobler in a message sent to the organizers of the XX Simpósio de Mirmecologia (2011) which was held at Petrópolis, Brazil)

Knowledge about Neotropical ants began to accumulate ever since European colonization, when the Portuguese owner of a sugarcane factory in the Reconcavo region of Bahia, Brazil, Gabriel Soares de Souza in 1587 [1] and the Spaniard José Celestino Mutis in 1780s [2, 3] made the first observations about ants in their American habitats. These observations were soon followed by more texts published by naturalist travelers in the XIX Century reporting ant behavior, among whom Bates [4] is one between the best known. Myrmecology as a discipline of entomology took its roots when these travelers and a myriad of correspondents distributed throughout the American continent sent biological material to European collections where taxonomists such as Auguste Forel, Carlo Emery, or Felix Santschi could study and describe considerable amounts of new ant material [5]. In the meantime, Forel, Santschi (as Forel's secretary), and Edouard Bugnion (Forel's brother-in-law) made a memorable travel (1896) through the Sierra Nevada de Santa Marta region in the northeast of Colombia, where they subsequently accumulated ant observations and experiences which they will use throughout their lives. Interestingly, all the three produced independent memories of the Colombian expedition ([6, 7], Santschi's notes in [8]). Other important contributors to earlier Neotropical myrmecology in the XIX and XX centuries were the German mycologist Alfred Möller in southern Brazil and Franciscan priests Thomas Borgmeier and Walter Kempf; the Brazilians Herman Luederwaldt, Karol Lenko, Mario Autuori, Elpídio Amante, and Cincinnato Rory Gonçalves; the Argentineans Carlos Bruch, Angel Gallardo, and Nicolas Kusnezov; and the North Americans William M. Mann, Neal Albert Weber, and William Morton Wheeler [9–14]. Research output from the Neotropical Region still remained modest until the Second World War. This began to change with the rapid development of national infrastructures that started to occur in the 1960s and the burgeoning of new universities in the 1970s and 1980s. Most of the older scientific contributions were historically devoted to taxonomy and leaf-cutter ant damage and control, but the topics which have called the attention of myrmecologists in recent years have been much more diverse and concerned essentially with ant communities, ant-plant relations, mutualisms, biomonitoring, biogeography, morphology and anatomy, genetics and cytogenetics, and taxonomy.

Selection of exculsive identifiers for publications from the Neotropics makes it difficult to measure output from publication databases, but taking leaf cutter ants as a surrogate, and using key words *Acromyrmex*, *Atta*, or Attini, as search identifiers in the ant database *Formis 2011* [15],

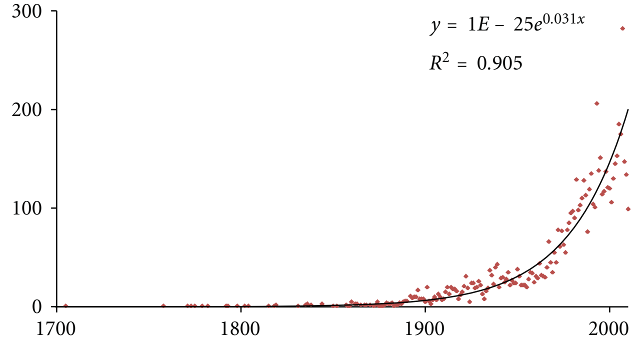


Figure 1: The exponential spread of papers containing the words *Acromyrmex*, *Atta,* or Attini in the title, abstract, or key words ($n = 6,561$). The regression is calculated for the period from 1850–2010. Although the tribe is not exclusively Neotropical, we estimate an annual output of 300 leaf-cutter ants papers by 2020. *Formis 2011* [15].

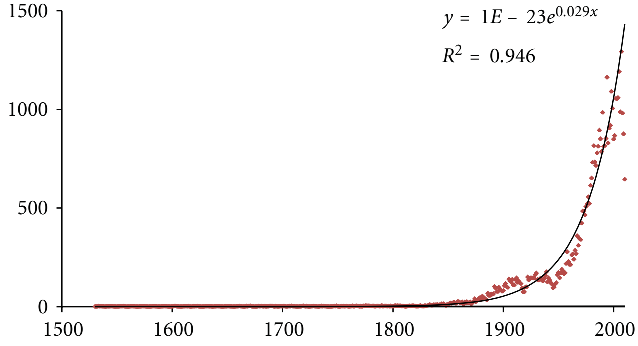


Figure 2: The exponential spread of World ant literature ($n = 46,182$). The regression is based on annual production and is calculated for the period between 1800 and 2010. An extrapolation estimates to 1,700 for the number of projected papers on ant biology for 2020. *Formis 2011* [15].

indicates an almost exponential increase in output from Latin America during the latter part of the last century through to the present time (Figure 1). This pattern closely follows World trends (Figure 2) and, assuming that for every paper published on leaf cutter ants, another four to six papers are currently produced on other Neotropical ant species, the Latin American ant literature could soon account for one third of annual World ant literature. So great is this increase, that extrapolation suggests an annual output of 1700 papers (World lower estimation) per year by the time of 2020. This enthusiasm for ants is matched by the existence of a Latin American Sections of the International Union for the Study of Social Insects, and also by a very attractive biennual Simpósio de Mirmecologia, which is traditionally attended by hundreds of scientists and students from Brazil and, in the recent years, by an increasing number of scientists from elsewhere in the Americas, Europe, and Australia.

This volume brings together some of the recent research on ants in the Neotropical Region and includes contributions by authors from Argentina, Australia, Belgium, Brazil, Colombia, Costa Rica, Ecuador, France, French Guiana, Mexico, Venezuela, and USA. Six of the contributions are concerned with taxonomy and systematics of the ant fauna and reflect the spread of interest in ant taxonomy and the new integrative taxonomy approach [16]. One is concerned with ant morphology and continues the long tradition in Brazil of identifying special features within local ants. A further three papers address aspects of ant biology, including division of labour, chemical recruitment, and behavioural differentiation between castes, with emphasis on reproduction.

Three of the papers are concerned with the ecology of individual species, while a further five take a community ecology approach to the fauna. In addition, since the Neotropics contain some of the World's biodiversity hotspots, five other papers describe various aspects of the interactions between ants and some of the unique plant species which occur in this region. There is one paper on leaf cutter ants which, interestingly, indicates that leaf cutting activity can influence the local spread of fire in Amazon ecosystems.

The influence of the ALL protocol [17] and the use of Winkler sampling in studies of community ecology are evident in some of the papers, although one contribution discusses the potential for a new sampling method, subterranean trapping, to augment existing techniques. Finally, the use of ants as bioindicators, originally pioneered in Australia [18], has escalated throughout countries in the Neotropical Region, and one paper reviews such studies in Brazil, presenting ideas for improvements to the procedure.

Perusal of the papers in this volume, and those elsewhere, indicates that a sizeable proportion of Neotropical ant species have yet to be described, and researchers in these groups tend to assign ants to morphospecies; they may even use morphospecies codes for described species if they do not have ready access to the main museums where reference collections are held. This unsatisfactory situation is confounded by the fact that each research group tends to adopt its own morphospecies coding system, or even a separate coding system for each individual study! Thus we have endless papers featuring *Pheidole* sp. 1, *Pheidole* sp. 2, and *Pheidole* sp. 3, but we have no idea whether they are the same species or not.

This imposes serious limitations for the making of comparisons between studies—a lost opportunity indeed. It is a relatively simple matter to determine an ant to genus level and assign codes to perceptibly different morphospecies, but obtaining determinations requires access to keys, museums, or specialists, and producing a uniform morphospecies coding system requires a system of voucher specimens, deposited in secure and accessible locations, which is a requirment to be inserted in "material and methods" by many of the entomological journals. All of this takes time and money.

What can we do to overcome this impediment? We suggest that each of the major countries have at least one, and preferably more, central reference collections, comprising formally determined material plus vouchers of coded morphospecies, all compiled using a standardised numbering and data-based system. Attempts should be made to "clone" these collections, or at least regional subsets of the material, and placing the subcollections in strategic regions of the country where they are accessible to local research groups. As an adjunct to this, keys to the material should be produced, illustrated with line drawings or photographs, and rapidly made available on the internet. The existence of undescribed "morphospecies" need be no bar to the production of keys. Heterick's [19] recent book *A guide to the Ants of South-Western Australia* features keys and line diagrams of the 500 or so species which exist there, of which almost half are only known by morphospecies codes. We admit that coordination of collections from the various research groups would be an enormous task, especially if cross-national coordination was involved. At the very least, integrated collections for each country could be assembled, with each having a prefix letter before the code number (e.g., *Pheidole* sp. B1, *Pheidole* sp. B2, and *Pheidole sp.* B3, etc. for Brazil, e.g.). Subsequent integration of the national collections, at least for individual genera, could then be undertaken as specialist projects or could be coordinated through organized groups, possibly under the direction of the International Union for the Study of Social Insects (IUSSI).

To assemble these "national" collections and keys would require dedicated staff, a committed and guaranteed amount of resources, with security of tenure. However, considering the importance of ants in our natural and cultural landscapes, and their increasing importance in the disciplines linked to Neotropical entomology as a whole, this might well be a good investment. Major research organisations, governments, and national or international philanthropic funding bodies should seriously consider this option. An embryo of this effort is the site http://www.antweb.org/ maintained by the Californian Academy of Sciences, which has the explicit mission of documenting, through high-quality imagery, the whole ant diversity of the Planet, beginning with the types. Besides offering the option of "digital curation" for countries or areas, initiatives like this can encourage taxonomists to have consensus on the delimitation of morphospecies of large or problematic genera, together with the well-known genera with broad morphological variation. It is critical that the few researchers with access to types can offer high-quality photos of them, in order to assist those who have to rely less on loans and risky mail.

The numerous internet sites which currently exist about ants, specialized symposia, ant field courses, and many other activities clearly show that the tropical myrmecology lives a golden era with a very promising future.

Acknowledgments

The authors would like to thank Donat Agosti, Joe Cora, Jacques Forel, Norm Johnson, Bert Hölldobler, and Sanford Porter who assisted in various ways, along with the numerous anonymous referees. J. Delabie is supported by the FAPESB/CNPq project PNX001/2009 and a research grant by CNPq.

Jacques Hubert Charles Delabie
Fernando Fernández
Jonathan Majer

References

[1] K. Lenko and N. Papavero, *Insetos no Folclore*, Plêiade e FAPESB, São Paulo, Brazil, 2nd edition, 1996.

[2] F. Fernández and E. O. Wilson, "José Celestino Mutis, the ants and *Pheidole mutisi* sp nov.," *Revista Colombiana de Entomología*, vol. 34, no. 2, pp. 203–208, 2008.

[3] E. O. Wilson and J. M. Gómez Durán, *Kingdom of Ants, José Celestino Mutis and the Dawn of Natural History in the New World*, The Johns Hopkins University Press, Baltimore, Md, USA, 2010.

[4] H. W. Bates, *The Naturalist on the River Amazons*, vol. 2, John Murray, London, UK, 1863.

[5] D. Agosti and N. F. Johnson, "La nueva taxonomía de hormigas," in *Introducción a las Hormigas de la Región Neotropical*, F. Fernández, Ed., pp. 45–48, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia, 2003.

[6] E. Bugnion, "A. Forel. Souvenirs myrmécologiques recueillis," *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, vol. 15, pp. 156–193, 1931.

[7] A. Forel, *Mémoires*, Neuchatel, 1941.

[8] D. Chérix and M. Sartori, "A propos de Félix Santschi (1872–1940)," *Bulletin Romand d'Entomologie*, vol. 6, pp. 45–86, 1986.

[9] A. Möller, "As hortas de fungo de algumas formigas sul-americanas," *Revista de Entomologia*, supplement 1, pp. 1–122, 1941, translated by A. P. Viégas & E. M. Zink from the German 1893 original edition in *Botanische Mitteilungen aus den Tropen*, Jena.

[10] W. W. Kempf, "Father Thomas Borgmeier, O. F. M. (1892–1975) *in memoriam*," *Studia Entomologica*, vol. 19, pp. 1–37, 1976.

[11] N. Kusnezov, *Hormigas Argentinas—Claves para su Identificación*, vol. 2, Fundación Miguel Lillo, Tucuman, Argentina, 1978.

[12] H. S. Lopes, "Frei Walter entomólogo," *Studia Entomologica*, vol. 20, pp. 3–15, 1978.

[13] A. Neiva, *Esboço Histórico Sobre a Botânica e Zoologia no Brasil*, UNB, Brasília, Brazil, 1989.

[14] C. R. F. Brandão, "Avanços da mirmecologia no Brasil," *O Biológico*, vol. 69, pp. 1–3, 2007.

[15] FORMIS, "FORMIS: A Master Bibliography of Ant Literature," EndNote Versions 8–13, compilation by D. P. Wojcik & S. D. Porter, 2011, http://www.ars.usda.gov/saa/cmave/ifahi/formis.

[16] B. C. Schlick-Steiner, F. M. Steiner, B. Seifert, C. Stauffer, E. Christian, and R. H. Crozier, "Integrative taxonomy: a multisource approach to exploring biodiversity," *Annual Review of Entomology*, vol. 55, pp. 421–438, 2010.

[17] D. Agosti, J. Majer, E. Alonso, and T. Schultz, *Ants: Standard Methods for Measuring and Monitoring Diversity*, Biological Diversity Handbook Series, Smithsonian Institution Press, Washington, DC, USA, 2000.

[18] A. N. Andersen and J. D. Majer, "Ants show the way down under: invertebrates as indicators in land management," *Frontiers in Ecology and the Environment*, vol. 2, pp. 291–298, 2004.

[19] B. E. Heterick, "A guide to the ants of South-western Australia," *Records of the Western Australian Museum*, supplement 76, pp. 1–206, 2009.

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 926089, 6 pages
doi:10.1155/2012/926089

Research Article

Tatuidris kapasi sp. nov.: A New Armadillo Ant from French Guiana (Formicidae: Agroecomyrmecinae)

Sébastien Lacau,[1,2,3] Sarah Groc,[4] Alain Dejean,[4,5]
Muriel L. de Oliveira,[1,3,6] and Jacques H. C. Delabie[3,6]

[1] *Laboratório de Biossistemática Animal, Universidade Estadual do Sudoeste da Bahia, UESB/DEBI, 45700-000 Itapetinga, BA, Brazil*
[2] *Département Systématique & Evolution, UMR 5202 CNRS-MNHN, Muséum National d'Histoire Naturelle, 75005 Paris, France*
[3] *Programa de Pós-Graduação em Zoologia, Universidade Estadual de Santa Cruz, UESC/DCB, 45662-000 Ilhéus, BA, Brazil*
[4] *Écologie des Forêts de Guyane, UMR-CNRS 8172 (UMR EcoFoG), Campus Agronomique, BP 319,*
97379 Kourou Cedex, French Guiana
[5] *Université de Toulouse, UPS (Ecolab), 118 Route de Narbonne, 31062 Toulouse Cedex 9, France*
[6] *Laboratório de Mirmecologia, CEPLAC/CEPEC/SECEN, CP 07, km 22, Rodovia, Ilhéus-Itabuna, 45600-970 Itabuna, BA, Brazil*

Correspondence should be addressed to Sébastien Lacau, slacau@cepec.gov.br

Received 11 September 2011; Revised 3 November 2011; Accepted 21 November 2011

Academic Editor: Fernando Fernández

Tatuidris kapasi sp. nov. (Formicidae: Agroecomyrmecinae), the second known species of "armadillo ant", is described after a remarkable specimen collected in French Guiana. This species can be easily distinguished from *Tatuidris tatusia* by characters related to the shape of the mesosoma and petiole as well as to the pilosity, the sculpture, and the color.

1. Introduction

As a result of the constant acquisition of new morphological and molecular data, combined with a big increase in the collection of biological material, the last decades have seen a true revolution in ant systematics and phylogeny [1, 2]. In spite of this, some rare genera of ants still remain unusually mysterious. A long time after their original description, they continue to reveal a low taxonomical diversity and are rarely collected in the field. Frequently, their phylogenetic relationships also remain poorly understood. The Neotropical genus *Tatuidris* (Formicidae: Agroecomyrmecinae) was described by Brown and Kempf in the 1967 issue of Psyche [3] after a peculiar new species collected in El Salvador. Until now, this genus has remained monotypic and very isolated in the Family Formicidae. The type species, *Tatuidris tatusia*, is known only from the very distinctive morphology of the worker that combines some primitive and derived characters, while its biology is completely unknown [4]. In addition, morphological and molecular studies have caused some authors to hold differing points of view regarding the phylogenetic position of *Tatuidris* in the family Formicidae. Thus, based on its morphology, the genus was initially placed in the subfamily Myrmicinae [3], within the tribe Agroecomyrmecini. The genus was then transferred to the Agroecomyrmecinae [5], a new subfamily proposed by Bolton, who has suggested that this taxon might be the sister group to all Myrmicinae. More recently, the genus was again combined in the Myrmicinae [6] and then returned to the Agroecomyrmecinae as a poneroid [7] and more latterly as a poneromorph [8]. However, based on morphological characters, in a very recent paper, Keller [9] corroborated Bolton's former proposal [5] in considering that *Tatuidris* is the sister group to the Myrmicinae. Recently, some new molecular data have led other authors to argument that *Tatuidris* may be the sister group to the subfamily Paraponerinae in some rooted trees but placed it next to Amblyoponinae in some other analyses [10–12].

In such a context, the search for new species of *Tatuidris* and the study of their morphology represents an important challenge for better understanding the phylogenetic relationships of this genus within the Formicidae. Here we report the recent finding in French Guiana of a remarkable single specimen of *Tatuidris* that differs from *T. tatusia* in several distinctive morphological characters, and this paper aims to describe it.

2. Material and Methods

Morphological examination of specimens was completed at various magnifications using a light stereomicroscope Olympus SZX7. Morphometric measures were made with a Carl Zeiss measuring microscope and recorded to the nearest 0.01 mm. All measurements are given in millimeters, using the following definitions and abbreviations:

CI: Cephalic Index: HW 100/HL,

EL: Eye Length: the maximum diameter of the eye,

GL: Gaster length: the length of the gaster in lateral view from the anteriormost point of first gastral segment (fourth abdominal segment) to the posterior most point (sting omitted),

HFL: Hind Femur Length: maximum length of hind femur in anterior view,

HL: Head Length: the length of the head proper, excluding the mandibles; measured in full-face view from the midpoint of the anterior clypeal margin to a line drawn across the posterior margin from its highest points,

HW: Head Width: the maximum width of the head in full face view,

LA7: Length of Antennal segment 7: maximum length of the seventh (apical) antennal segment,

ML: Mandible Length: length of a mandible measured in ventral view from its basal articulation to its apex,

PeNI: Petiole Node Index: (PeNW 100/PeNL),

PeL: Petiole Length: the maximum length of the petiole in lateral view,

PeNL: Petiolar Node Length: the maximum length of the petiole node in dorsal view,

PeNW: Petiolar Node Width: the maximum width of the petiole node in dorsal view,

PpL: Postpetiole Length: the maximum postpetiole length in lateral view,

PpNL: Postpetiolar Node Length: the maximum length of the postpetiole node in dorsal view,

PpNW: Postpetiolar Node Width: the maximum width of the postpetiole node in dorsal view,

PrW: Pronotum Width: the maximum width of the pronotum in dorsal view,

PrpW: Propodeum Width: the maximum width between the propodeum angles as seen in dorsal view,

SL: Scape Length: the maximum straight line of the antennal scape, excluding the condylar bulb,

TL: Total Length (HL + ML + WL + PL + PPL + GL),

WL: Weber's Length: diagonal length, measured in lateral view, from the anterior margin of the pronotum (excluding the collar) to the posterior extremity of the metapleural lobe.

The microphotographs were made using the following sequential process: the specimen was first filmed using a video camera (Sony Full HD 1080 AVCHD, 10.2 Mp) mounted on a light microscope (Zeiss Jena), while the resolution was continuously scanned from the top to the bottom of the holotype specimen; the videos (in format.mts) were processed using the free software ImagGrab 5.0 (available at http://paul.glagla.free.fr/imagegrab.htm) in order to extract the sharpest images referable to differing focal points, and composite pictures were then assembled using the free software Combine ZM (available at http://www.hadleyweb.pwp.blueyonder.co.uk/index.htm). Finally, each optimum microphotograph was improved using Adobe Element Photoshop software (version 6.0).

The terminology for the external morphology and the surface sculpturing follows [13–15]. In the description and the diagnosis of this new species, our terminology referring to the pilosity describes the variation in size of the setae observed in *T. tatusia* and *Tatuidris kapasi sp. nov.* Thus, we recognize four setal types depending on their length: that is, very short (about 0.016 mm), short (about 0.05 mm), intermediate (about 0.11 mm), and long (about 0.3 mm). Also, the characters of the tribe and the genus are not mentioned (for a complete summary of the taxonomic characters, see [3, 5]).

Depository of the Holotype. The unique known specimen of the taxon is deposited in the collection of the Laboratorio de Mirmecologia at the Cocoa Research Center at CEPLAC (Itabuna-BA, Brazil), referred to by the CPDC acronym [16]. Comparative data for *Tatuidris tatusia* were obtained from the literature [3] and direct observations on microphotographs of high-resolution available in AntWeb site [17].

3. Results

3.1. Tatuidris kapasi Lacau and Groc: New Species. See Figures 1, 2, 3, 4, 5, and 6.

3.2. Type Material. Holotype worker: specimen deposited at CPDC and labeled "Guyane Française, Montagne de Kaw, N04 38.21 /W052 17.36 , Alt. 260 m., ix.2008, Winkler trap, Col. S. Groc, A. Dejean, and B. Corbara".

3.3. Etymology. "kapasi" is the Wayanas' Amerindian (French Guiana, Surinam, and Brazil) word for "armadillo", a mammal belonging to the Order Cingulata. The generic and specific names of the first described species [6] referred to the same animal group.

3.4. Diagnosis. The worker of *Tatuidris kapasi* exhibits all the diagnostic characters of the tribe Agroecomyrmecini and the genus *Tatuidris*. It differs from the worker of *T. tatusia* in

Figure 1: *Tatuidris kapasi*: holotype worker. Habitus: left lateral view.

Figure 2: *Tatuidris kapasi*: holotype worker. Head: full-face view.

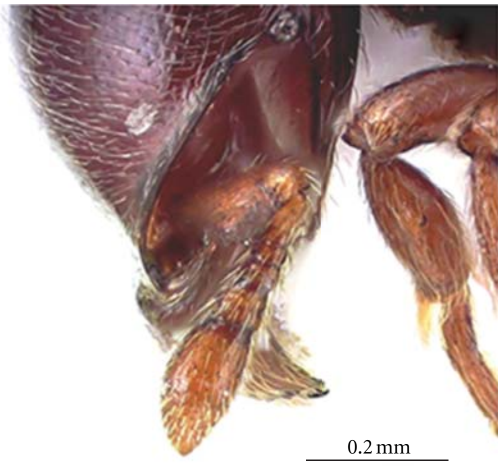


Figure 3: *Tatuidris kapasi*: holotype worker. Detail of head: left side view.

Figure 4: *Tatuidris kapasi*: holotype worker. Mesosoma: dorsal view.

the following characters (states for *T. tatusia* indicated in brackets): occipital border a little more concave (nearly straight); about 5-6 facets in each eye (about 10 facets); clypeus with the free margin medially straight and laterally concave (free margin concave overall); pronotum with the ventral sector of lateral faces smooth and shining (with longitudinal rugulae); dorsum of mesosoma mostly sculptured with concentric rugulae and carinulae (mostly smooth and shining); mesosoma as seen from above with lateral margins moderately converging backward (Propodeum width/Pronotum width = 0.55) (lateral margins more converging backward (Propodeum width/Pronotum width = 0.45)); mesopleuron with anterior crest wider and ventrally truncated (crest narrower and not truncated); mesopleuron smooth and shining, except for punctuations and areolae on its ventral margin (with longitudinal rugulae and areolations); metapleuron punctate and areolate, and with longitudinal rugulae around the metapleural gland orifice (metapleuron with areolations); the bulla of the metapleural gland (visible through the integument when observed in profile), forming a ring whose posterodorsal margin is fused with the posterolateral margin of the propodeum (the bulla of the metapleural gland forming a ring that is distinctly separated from the posterolateral margin of propodeum); propodeal declivity less concave in lateral view (more concave); propodeal spiracle separated from declivitous margin of propodeum by two diameters (separated by no more than one diameter); viewed dorsally, petiolar node twice as wide as long (viewed dorsally, shape of petiolar node subrectangular, the node no more than about 1.5 times as wide as long); viewed dorsally, shape of postpetiolar node rectangular, and not wider behind than in front (viewed dorsally, shape of postpetiolar node subrectangular, and a little wider behind than in front); and dorsum of the petiolar and postpetiolar nodes with superficial concentric rugulae and carinulae (smooth and shining). Moreover, the pilosity is markedly more dense all over the body (more scattered) and does not include any long suberect setae (long suberect setae present).

Figure 5: *Tatuidris kapasi*, holotype worker. Detail of petiole and postpetiole, left lateral view.

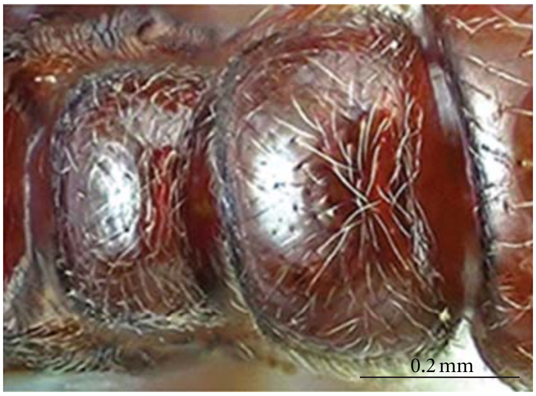


Figure 6: *Tatuidris kapasi*, holotype worker. Detail of petiole and postpetiole, dorsal view.

Furthermore, despite the fact that *T. kapasi* is known only by a single specimen and *T. tatusia* by two specimens formally described, the following comparative measurements suggest an overall size differential between the two species: the head shape is a little wider in *T. kapasi* (CI: 125,78) than in *T. tatusia* (CI: 118,2 ± 1.56, min-max: 117.07–119.28 ($n = 2$)), the scape is slightly shorter in *T. kapasi* (SL 0,32) than in *T. tatusia* (SL 0,4 ($n = 1$)), the pronotum is narrower in *T. kapasi* (PrW 0,64) than in *T. tatusia* (PrW 0,79 ($n = 1$)), and the shape of the petiole node in dorsal view is more noticeably rectangular in *T. kapasi* (PeNI 200) than in *T. tatusia* (PeNI 153.64 ($n = 1$)).

4. Description

Worker. Measurements (Holotype): TL 3.42, CI 125.80, EL 0.05, GL 1.00, HFL 0.50, HL 0.70, HW 0.93, LA7 0.27, ML 0.39, PeL 0.21, PeNI 200, PeNL 0.18, PeNW 0.36, PpL 0.28, PpNL 0.25, PpNW 0.45, PrW 0.64, SL 0.32, WL 0.80.

Except for the diagnostic characters, the external morphology of *Tatusia kapasi sp. nov.* is very similar to that of *T. tatusia*. In our discussion, the shared characters are regarded by ourselves as sufficient for the two species to be placed within the same genus. The spatial distribution and patterns of the sculpture and pilosity as well as the body color of this new species are described hereafter.

Sculpture. It includes head dorsum wholly smooth and shining, except for occipital sector covered with transverse carinulae; outer surface of mandibles smooth and shining except for longitudinal superficial striae on ventral (external) margin; ventrolateral sector of the head longitudinally carinulate; antennal scape shagreened and superficially areolate; pronotum ventrolaterally smooth and shining; dorsum of mesosoma with concentric rugulae and carinulae; mesopleuron smooth and shining except for punctuations and areolae on ventral margin; metapleuron with punctuations and areolae and longitudinal rugulae around the metapleural gland orifice; propodeal declivity mostly smooth and shining with fine striae and reticulate; petiolar and postpetiolar nodes laterally finely longitudinally carinulate.

Pilosity. It includes dorsum of head, mesosoma, petiole, and postpetiole with abundant setae, all fine, flexuous, and decumbent, varying in size and distribution as follows: some very short and relatively dense (i.e., those on clypeus and the outer surface of mandibles); others short and dense (those on dorsum of head, clypeus, mesosoma, petiolar, and postpetiolar nodes, and gaster); and others intermediate and dense (namely, setae on dorsum of head, mesosoma, petiolar, and postpetiolar nodes, dorsum of gaster and tibia). No long setae present.

Color. Body brownish-ferruginous, thick margins often appearing more blackish; legs brownish-yellowish.

Gyne and Male. They are unknown.

Geographic Range. This new species is known only from the type locality in French Guiana, situated at 260 m altitude in the Kaw Mountains, on a side exposed to the trade winds, near a great cave sheltering a big bat community. The local vegetation is typical of Amazonian lowland rainforest that is never flooded. New records of this species will probably occur in other localities of the Guiana Shield in the near future. However, the fact that no other specimen of *Tatuidris* has been recorded yet in the recent studies on ant biodiversity in the Guiana Shield, even using Winkler traps or other methods at a large scale [18, 19], suggests that this genus is genuinely rare in the Guianas, its members possibly spatially separated in small, isolated populations.

Biology. The biology of this species is unknown, but the fact that the type specimen was found in a leaf-litter sample, using a Winkler trap, suggests that it nests in some microhabitats of the leaf-litter or more or less deeply in the soil. It is also noteworthy that the leaf-litter sample (surface of 1 m^2) in which *T. kapasi* was caught was characterized by a very high specific richness: a total of 20 other ant species belonging to 12 genera was recorded (Groc et al., unpublished information). Such richness in a unique leaf-litter sample is uncommon in Neotropical forests [19].

5. Comments and Discussion

The description of this new species of *Tatuidris* is an important event for Myrmecology, since the genus has remained monotypic for over 40 years. However, as noted by Longino [4], the advent of litter sifting and Winkler extraction as a popular method of ant collecting in the last decade led to the discovery of new species belonging to genera previously considered as rare and poorly diversified. This is the case for the new species here described. This genus has been revealed to be not as rare as it was believed to be since several new specimens were recently collected in various Neotropical countries: Brazil, Colombia, Costa Rica, El Salvador, Ecuador, French Guiana, Mexico, Nicaragua, Panama, and Peru (see specimens imaged on the Websites: Ants of Costa Rica [4] and AntWeb [17]). In this context, D. Donoso is currently performing a first revision of this genus based on the new material deposited in myrmecological collections in the world.

While *T. kapasi* exhibits a distinct morphology from that of *T. tatusia*, it possesses all the diagnostic characters of Agroecomyrmecinae and Agroecomyrmecini. The next step will consist in studying the whole biology of these ants for which literature is particularly scarce. *Tatuidris kapasi* has peculiar mandibular brushes and a powerful elongated sting similar to that of *T. tatusia*. Brown and Kempf suggested that such adaptations indicates that armadillo ants might be specialist predators of active or slippery arthropod prey [3]. Also, we note that the flat pencil of stiff, curved yellow setae borne at the extensor angle on the forelegs, an apomorphy of this genus, may be used by these ants in order to clean the massive brush of heavy setae present along the inner surface near the masticatory margin of the mandible, through a movement directed forward. Thus, these characters could potentially represent an adaptation to feed on prey bearing a defensive pilosity. Moreover, the morphology of the gyne and the male of *Tatuidris* has never been described. However, microphotographs of a gyne and a male, together winged, are offered in the site Antweb, suggesting that a normal sexual reproduction by swarming occurs in this genus.

Acknowledgments

The authors thank Dr. Brian Heterick for his kind help in reviewing the English of this manuscript, and Bruno Corbara and Olivier Roux for field assistance. Financial support for this study was provided by (1) the Programme Amazonie II of the French CNRS (project 2ID), (2) the Programme Convergence 2007–2013, Region Guyane from the European Community (project DEGA), (3) the FPVI European-funded Integrated Infrastructure Initiative Grant SYNTHESYS (S. Groc), (4) the PRONEX Program FAPESB/CNPq (PNX0011/2009, Brazil), and (5) the Program CAPES/CNPq/MCT (PROTAX 52/2010, Brazil). J. H. C. Delabie acknowledges his research grant from CNPq. In accordance with Section 8.6 of the ICZN's International Code of Zoological Nomenclature, printed copies of the edition of Psyche containing this article are deposited at the following six publicly accessible libraries: Green Library (Stanford University), Bayerische Staatsbibliothek, Library—ECORC (Agriculture & Agri-Food Canada), Library—Bibliotheek (Royal Belgium Institute of Natural Sciences), Koebenhavns Universitetsbibliotek, University of Hawaii Library.

References

[1] P. S. Ward, "Phylogeny, classification, and species-level taxonomy of ants (Hymenoptera: Formicidae)," *Zootaxa*, no. 1668, pp. 549–563, 2007.

[2] P. S. Ward, "Integrating molecular phylogenetic results into ant taxonomy (Hymenoptera: Formicidae)," *Myrmecological News*, vol. 15, pp. 21–29, 2011.

[3] W. L. Brown Jr. and W. W. Kempf, "*Tatuidris,* a remarkable new genus of Formicidae (Hymenoptera)," *Psyche*, vol. 74, pp. 183–190, 1968.

[4] J. T. Longino, "Ants of Costa Rica," 2011, http://academic.evergreen.edu/projects/ants/AntsofCostaRica.html.

[5] B. Bolton, "Synopsis and classification of Formicidae," *Memoirs of the American Entomological Institute*, vol. 71, p. 370, 2003.

[6] C. Baroni-Urbani and M. L. de Andrade, "The ant tribe Dacetini: Limits and constituent genera, with descriptions of new species," *Annali del Museo Civico di Storia Naturale Giacomo Doria*, vol. 99, pp. 1–191, 2007.

[7] B. Bolton and G. D. Alpert, "Barry Bolton's Synopsis of the Formicidae and Catalogue of Ants of the World, Version 3 January 2011," http://gap.entclub.org/.

[8] B. Bolton and G. D. Alpert, "Barry Bolton's Synopsis of the Formicidae and Catalogue of Ants of the World, Version 1 July 2011," http://gap.entclub.org/.

[9] R. A. Keller, "A phylogenetic analysis of ant morphology (Hymenoptera: Formicidae) with special reference to the poneromorph subfamilies," *Bulletin of the American Museum of Natural History*, vol. 355, pp. 1–90, 2011.

[10] S. G. Brady, T. R. Schultz, B. L. Fisher, and P. S. Ward, "Evaluating alternative hypotheses for the early evolution and diversification of ants," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 103, no. 48, pp. 18172–18177, 2006.

[11] C. S. Moreau, C. D. Bell, R. Vila, S. B. Archibald, and N. E. Pierce, "Phylogeny of the ants: diversification in the age of angiosperms," *Science*, vol. 312, no. 5770, pp. 101–104, 2006.

[12] C. Rabeling, J. M. Brown, and M. Verhaagh, "Newly discovered sister lineage sheds light on early ant evolution," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 105, no. 39, pp. 14913–14917, 2008.

[13] B. Bolton, *Identification Guide to the Ant Genera of the World*, Harvard University Press, Cambridge, Mass, USA, 1994.

[14] R. D. Eady, "Some illustrations of microsculpture in the Hymenoptera," *Proceedings of the Royal Entomological Society of London*, vol. 43, pp. 66–72, 1968.

[15] R. A. Harris, "A glossary of surface sculpturing," *Occasional Papers on Systematic Entomology*, vol. 28, pp. 1–31, 1979.

[16] C. R. F. Brandão, "Major regional and type collections of ants (Formicidae) of the world and sources for the identification of ant species," in *Ants: Standard Methods for Measuring and Monitoring Biodiversity*, D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz, Eds., pp. 172–185, Smithsonian Institution Press, Washington, DC, USA, 2000.

[17] B. L. Fisher, "AntWeb," 2011, http://www.antweb.org/description.do?Subfamily=agroecomyrmecinae&genus=tatuidris&name=tatusia&rank=species&project=worldants.

[18] J. S. Lapolla, T. Suman, J. Sosa-Calvo, and T. R. Schultz, “Leaf litter ant diversity in Guyana,” *Biodiversity and Conservation*, vol. 16, no. 2, pp. 491–510, 2007.

[19] H. L. Vasconcelos and J. H. C. Delabie, “Ground ant communities from central Amazonia forest fragments,” in *Sampling Ground-Dwelling Ants: Case Studies from the World’s Rain Forests*, D. Agosti, J. D. Majer, L.T. Alonso, and T. Schultz, Eds., vol. 18, pp. 59–70, Curtin University, Perth, Australia, 2000, School of Environmental Biology Bulletin, no. 18.

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 636749, 23 pages
doi:10.1155/2012/636749

Review Article

Ants as Indicators in Brazil: A Review with Suggestions to Improve the Use of Ants in Environmental Monitoring Programs

Carla R. Ribas,[1] Renata B. F. Campos,[2] Fernando A. Schmidt,[3] and Ricardo R. C. Solar[3]

[1] *Laboratory of Ant Ecology, Sector of Ecology, Department of Biology, Federal University of Lavras, 37200-000 Lavras, MG, Brazil*
[2] *Institute of Education of Divinópolis, Educational Foundation of Divinópolis, 35501-170 Divinópolis, MG, Brazil*
[3] *Post-Graduate Program in Entomology, Department of Entomology, Federal University of Viçosa, 36570-000, Viçosa, MG, Brazil*

Correspondence should be addressed to Carla R. Ribas, crribas@gmail.com

Received 31 May 2011; Revised 11 August 2011; Accepted 16 August 2011

Academic Editor: Jonathan D. Majer

We describe the use of ants as indicators in Brazil, based on a critical review of published articles. The analysis of fifty-eight papers, encompassing a range of almost 25 years, indicates an increased number of studies using ants as indicators in the last decade. Among the parameters analyzed in the papers, species composition is the most suitable to evaluate the effect of the disturbance on ant communities. The use of other metrics that consider the specificity and fidelity (e.g., IndVal index) of ant species to a level or state of disturbance is also highly desirable. We discuss several alternative ways of overcoming many of the drawbacks related to the robustness of the results and to reduce the financial, logistic, and time costs involved with the use of ants as indicators in monitoring programs. By doing so, we expect to encourage new research on ants as bioindicators as well as to summarize current knowledge, facilitating further research.

1. Introduction

Intensive exploitation of natural resources and the resulting impacts on pristine habitats have led to calls from the scientific community and the general public to measure or monitor the level of these environmental impacts [1–3]. Bioindicators are a useful way to evaluate such impacts, since changes in their population dynamics or community parameters can indicate an environmental state more easily, quickly, and safely and with lower financial and labour inputs than direct measurements [4–6].

McGeoch [7] divided the general use of the term bioindication into three categories according to the three main applications: (i) environmental indicators: used to detect or monitor changes in the environmental state, (ii) ecological indicators: used to demonstrate the impact of an environmental stress on the biota or monitor longer-term stress-induced changes in the biota, and (iii) biodiversity indicators: used to identify the diversity of a taxa in a specified area or to monitor changes in biodiversity.

Therefore, there are several characteristics that an indicator species must have, the most notable being ease of measurement, sensitivity to environmental stress, and predictable responses to environmental stress [4, 8]. The use of certain species or groups of species as indicators of successful rehabilitation practices or for environmental monitoring has been recommended in recent years (e.g., [5, 6, 9]).

Ants have been used as a powerful tool in several ecological studies [10, 11]. This group has useful characteristics for successful indication and monitoring of environmental impacts, including widespread distribution, high abundance, importance in ecosystem functioning, ease of sampling, and relatively well-known taxonomy and ecology [12].

Thus, ants have been used as indicators of several environmental impacts, such as fire, deforestation and logging, agricultural intensification, mining, and urbanization [13, 14]. The first study suggesting the use of ants as indicators was in the early 1980s [15], and the use of ants as indicators is now widespread in Australia (e.g., [16–19]) and is becoming a major focus of myrmecological research worldwide (e.g., [20–25]).

Although ants are a simple, cheap, and powerful indicator of environmental impacts and rehabilitation (e.g., in Australia [17]), in Brazil, a country which harbours enormous diversity and complexity of habitats, the standard use of ants as indicators is still relatively new and should be evaluated in greater detail (see [26, 27]). According to Philpott et al. [14] and Gardner [6], a critical need is the selection of ant species that are affected by distinct types of disturbance in different regions, in order to guarantee their usefulness as good indicators.

Therefore, as we described above, given the international use of ants as indicators, several studies have investigated the use of ants as indicators in Brazil. In order to describe the background of bioindication with ants in Brazil, we carried out a critical review of several studies concerned directly or indirectly with the use of ants as indicators.

Using the three categories proposed by McGeoch [7], environmental, ecological, or biodiversity indicators, we describe the historical development of ants as indicators and evaluate the implications of these studies. Additionally, we highlight ways of overcoming the major challenges to the widespread use of ants as tools in environmental monitoring programs.

2. Methods

We searched for papers regarding ants as indicators, restricting our search to those carried out in Brazil. To encompass a broad time range of papers, we used the following keywords in Portuguese and English, respectively: “formiga,” “ant,” “indicador,” “bioindicador,” “indicator,” “bioindicator,” “Brasil,” “Brazil,” and the combination of the words cited above in the Scielo and in the ISI Web of Knowledge websites. We also used papers from our personal archives, gathered under several keywords.

In all papers, we accessed the following information: the language, the general idea of the paper (i.e., descriptive, a general survey, a test of correlations or hypotheses), if the paper specifically analyzed ants as indicators; the aims; the ant sampling methodology, the parameters of ant fauna which were analyzed (i.e., diversity, composition, population dynamics), the environmental parameters which were observed, the results which were obtained, and the main conclusion reached in the study.

We define the paper as specifically analyzing ants as indicators if it explicitly declared this intention in the aim or the introduction (Explicit indication papers). However, if this criteria was not clear but the article still analyzed ants as indicators, we defined these as “Implicit indication papers.” Papers in which the major aim was not the use of ants as bioindicators, but which presented results that could Potentially enable the use of ants as indicators, were considered as “Potential indication papers.” Finally, papers that did not meet any of the above criteria, that is, did not mention in any way the use of ants as indicators, or with results that could not be used to evaluate ants as indicators, were considered as “Indirect bioindication papers.”

The disturbances or aims investigated in the papers were split into the categories “Agriculture,” “Vegetation type,” and “Human land-use,” according to the habitats studied, namely: habitats with agricultural activities only, habitats with natural vegetation only, and habitats with both agricultural activities and natural habitats. Similarly, “Succession” studies were those investigating natural succession, and “Restoration” studies were those evaluating different rehabilitation techniques, such as succession following managed restoration efforts.

We used McGeoch [7] as a reference to decide if the ants were used as environmental, ecological, or biodiversity indicators in the reviewed papers (see McGeoch’s [7] definition in the introduction section). Moreover, we defined ant species as indicators when there was a species list in the paper showing the occurrence of ants in specific sites or when the author considered the ant species to be an indicator elsewhere in the paper. If the ant species occurred in just one habitat, we considered the species to be an indicator of the specific habitat.

We verified the most frequent responses of ants to disturbance, summarizing responses, and relating the most frequent responses to the most frequently used sampling methodologies to determine if there were any trends. To study this relationship, we considered only methodologies that had been used in at least three papers.

3. Results

We analyzed 58 papers, which encompassed a span of almost 25 years (from 1987 to 2010). Among the papers, only one was not classed as an “indication paper” or “Potential indication paper” [83]. The others specifically mentioned the intention to use ants as indicators (either explicitly, using the word “indicator,” or implicitly, using ants as a tool or model to indicate the ecological and environmental parameters) (38 papers) or at least have the Potential to do so (17 papers) (Table 1). Two papers [84, 85] were not included in the table because the scope of the papers was not to analyse ants as indicators but to suggest new tools to simplify their use as indicators.

From the 58 papers, exactly half (29) were published in English and the other half in Portuguese. Among the “Potential indication papers,” 11 were published in English and six in Portuguese, while among the “indication papers” the number of papers written in Portuguese (22) was higher than the papers written in English (18).

Papers directly concerned with the use of ants as bioindicators began almost 10 years after the development of “Potential indication papers”, in which the main focus was the response of ant communities to several disturbances (e.g., logging and land use). Only in the last decade has there been a positive trend of papers using ants as model organisms for bioindication in Brazil (Figure 1).

Regarding ant sampling procedures, 34 studies used only a single sampling method: 14 used two, six used three, and four opted for more than three methods. The methodologies used to capture ants were baits, beating, Berlese extraction,

Table 1: Papers reviewed regarding ants as indicators in Brazil, indicating the main disturbance investigated (Disturbance), the aim of the paper (Aim), if the paper was explicitly, implicitly or has the Potential to be used in indicator studies (Indication), the environmental parameters analyzed/sampled (Environmental parameters), the responses of ant community to disturbance that were found to be significant (Effects on ant community), the indicator type used (Indicator type) and the paper (Reference).

Disturbance	Aim	Indication	Environmental parameters	Effects on ant community	Indicator type	Reference
Agriculture	Evaluate the effect of different soil tillage and crop management systems on soil fauna groups	Yes (implicit)	Soil tillage and crop management systems	Change in species dominance (discriminant and correspondence analysis)	Environmental	Baretta et al. [28]
Agriculture	Evaluate the ant diversity in fig crops under different managements	Yes	Types of soil cover plants	Change in density of species ($P < 0.05$, Tukey test)	Environmental	Merlim et al. [29]
Agriculture (forestry practices in *Eucalyptus*)	Use the ant guild concept to evaluate changes in *Eucalyptus* plantations following control of leaf-cutting ants	Yes	Forestry practices	Change in species composition—observed frequency of species and guilds (non-statistical test)	Environmental	Lacau et al. [30]
Agriculture (preceded by deforestation and fire)	Assess the recolonization by fauna in areas cleared and burned to plant corn and beans	Yes	Human land-use and resting time	Increase in abundance in the less-disturbed areas (non-statistical test)	Environmental	Nunes et al. [31]
Agriculture (formicid granulated baits)	Evaluate the effect of different applications of formicide baits on nontarget ant community	Yes	Forms and timing of application of formicid-granulated baits	No effect of bait type on ant species richness ($P > 0.05$, ANOVA) Reduction in species richness observed only in control method, systematic application being more harmful ($P < 0.05$, ANOVA)	Environmental	Ramos et al. [32]
Anthropogenic activities	Quantify heavy metals in worker ants of *Camponotus rufipes* collected in different environments	Yes	Observed human interference	Three groups of ants with different heavy metal concentrations (PCA analyses)	Environmental	Silva et al. [33]
Conservation status	Create an inventory of epigaeic ant species that occur in vine forest and use them to indicate the level of conservation of this ecosystem	Yes	None	Inventory (nonstatistical test)	—	Carvalho et al. [34]
Conservation status	Verify the impact of human use in mangroves	Potential	Observed levels of human use	Reduction on species richness ($R^2 = 0.53$, $P = 0.007$)	Environmental	Delabie et al. [35]
Conservation status	Inventory the ant community in the Baturité hills	Yes	None	Inventory (nonstatistical test)	—	Hites et al. [36]
Conservation status	Study the ant communities in preserved and impacted savanna sites	Yes	Observed human interference	Reduction of diversity in impacted sites ($F = 101.62$, $P < 0.0001$)	Environmental	Ramos et al. [37]
Fire	Test the negative effect of fire in *Restinga* environments on the ant community	Potential	Presence of fire	Increase in species richness with presence of fire (mean and confidence intervals of estimated species richness)	Environmental	Endringer et al. [38]

Table 1: Continued.

Disturbance	Aim	Indication	Environmental parameters	Effects on ant community	Indicator type	Reference
Fire	Test the hypothesis that ant species richness and composition change after burning sand dunes	Yes	History of fire	More ant species and distinct species composition in the unburned area (non-statistical test)	Environmental	Teixeira et al. [39]
Fragmentation	Verify the responses of ants nesting in twigs in the litter layer to habitat changes associated with forest fragmentation	Potential	Distance to forest edge, remnant isolation, leaf-litter depth, density of dead twigs, and vegetation (three parameters measured)	Higher species richness ($F = 8.56$, $P = 0.006$); most ant species had greater nest densities in continuous areas than in remnants, change in species composition ($F = 8.14$, $P = 0.001$) with forest edge	Ecological	Carvalho and Vasconcelos [40]
Fragmentation	Determine the effect of forest fragmentation on ant communities	Yes	Remnant area, distance to forest edge, vegetation cover of matrix, and vegetation (three parameters measured)	No effect of many fragment characteristics on ant species richness: area ($F = 8.22$, $P = 0.77$), distance core-border ($F = 64.86$, $P = 0.42$). Only tree density had an effect ($F = 46.30$, $R^2 = 23.32$, $P = 0.02$)	Ecological	Gomes et al. [41]
Fragmentation	Know the community of ants in forest fragments	Yes	Remnant area	No change in species richness with remnant area ($R^2 = 0.02$, $F = 0.22$, $P = 0.64$)	Environmental	Santos et al. [42]
Forestry systems	Describe the epigaeic ant communities in *Eucalyptus* plantations	Yes	*Eucalyptus* age	No change in species richness with *Eucalyptus* age ($P = 0.58$)	Environmental	Fonseca and Diehl [43]
Human land-use	Compare the ant community structure between a crop and a secondary forest	Potential	Land use	Reduction of diversity and equitability and change in species composition (non-statistical test)	Environmental	Castro and Queiroz [44]
Human land-use	Compare the impact of different agroecosystems on ant species richness	Yes	Land use	Higher species richness in forest edges and pasture (non-statistical test); coffee crop presented reduced estimated richness ($h = 10.85$, $P > 0.05$)	Environmental	Dias et al. [45]
Human land-use	Survey of ant and termite fauna in four patches with different vegetation structures and in one open field	Potential	Land use	Change in species richness and composition (non-statistical test)	Environmental	Diehl et al. [46]
Human land-use	Test the effects of *Restinga* soil characteristics on ant communities	Yes (implicit)	Land use, physical and chemical soil properties, and microbial activity	Change in species richness (non-statistical test) and composition (canonical correspondence analysis)	Ecological	Gomes et al. [47]
Human land-use	Elucidate ant species richness and community structure associated with the micro basin of Sanga Caramuru-Chapecó	Yes	Habitat type, temperature, and rainfall	Change in species composition (Bray-Curtis Cluster Analysis indicated higher similarity for disturbed areas) and higher richness (observed and estimated) in the native area (sample-based accumulation curves)	Environmental	Ilha et al. [48]

Table 1: Continued.

Disturbance	Aim	Indication	Environmental parameters	Effects on ant community	Indicator type	Reference
Human land-use	Determine the level of similarity of ant communities in forest areas (three native forest remnants) and an *Eucalyptus* reforestation	Yes	Land use	Change in species composition (Jaccard index—$C_J = 0.29 \pm 0.02$ among *Eucalyptus* crops *versus* forest remnants and $C_J = 0.40 \pm 0.06$ among forest remnants)	Environmental	Lapola and Fowler [49]
Human land-use	To inventory the ant fauna in a Cerrado area and in *Eucalyptus* plantations with five classes of understory ages	Yes	Eucalypt age	Higher density of species in Cerrado areas than in *Eucalyptus* (non-statistical test) and estimated species richness similar between areas ($h = 1.6$, $P > 0.05$)	Environmental	Marinho et al. [50]
Human land-use	Investigate the effect of structural characteristics of the environment on ant communities	Yes	Habitat type	Change in species richness and composition (non-statistical test)	Environmental	Santana-Reis and Santos [51]
Human land-use	Test the hypotheses that there was a decrease in ant species richness and a change in the species composition in habitats with more intense soil use	Yes	Land use	Sites with distinct soil use host a differential ant species composition (cluster analysis-Euclidean distance)	Environmental	Schmidt and Diehl [52]
Human land-use	Evaluate the effect of collection time (day and night) on ant fauna attracted to baits in areas of *Eucalyptus cloeziana* (Myrtaceae) and Cerrado (savanna vegetation)	Potential	Land use	Collection time effect was more important to ant fauna structure than the vegetation effect (ordination analyses)	Environmental	Tavares et al. [53]
Human land-use and succession	Compare ant diversity under different land-use systems	Yes	Land use and age of succession	Change in density of species (non-statistical test), species richness (sample-based accumulation curves and $\chi 2$), and composition (cluster analysis)	Environmental	Braga et al. [54]
Inundation	Document the ant fauna in three different forest types (one annually inundated and two on terra firme)	Potential	Vegetation (several parameters measured)	Change in diversity, similarity, and proportion of different nesting and feeding habitats (non-statistical test)	Ecological	Majer and Delabie [55]
Logging	Test the hypothesis that logging affects forest ant fauna by reducing the species richness and changing the composition of ground-foraging ant communities	Yes	Canopy openness, abundance of understory vegetation, and leaf-litter depth	Change in species composition proportion of *Pheidole* was reduced from 21.4% and 26% in unlogged forest and low-impact logging, respectively, to 14.8% in high-impact logging ($F = 4.99$, $P < 0.05$)	Ecological	Kalif et al. [56]

Table 1: Continued.

Disturbance	Aim	Indication	Environmental parameters	Effects on ant community	Indicator type	Reference
Mining	Determine the levels of heavy metals in plants and identify soil organisms of the mesofauna that could be biological indicators of soil quality	Yes	Physical and chemical soil properties and heavy metal content	Decrease in abundance and increase in lead (Pb) accumulation (non-statistical test)	Environmental	Barros et al. [57]
Mining	Ant fauna survey and community structure, analyses of the ground-dwelling ants in native vegetation and areas with different inferred copper levels	Yes	Areas with different inferred copper levels	Decrease in species richness with inferred copper levels (non-statistical test)	Environmental	Diehl et al. [58]
Restoration (agriculture)	Investigate the recolonization profile of the restored Atlantic Forest	Yes	Age after planting	Increase in species richness ($P < 0.05$, ANOVA) and change in species composition (ANOSIM, $P < 0.01$)	Environmental	Pais and Varanda [59]
Restoration (anthropogenic disturbance)	Test the hypothesis that ant fauna is closely related to the structural complexity of habitat	Yes	Age of restoration	Change in species composition (non-statistical test)	Environmental	Coelho et al. [60]
Restoration (dredging disturbance)	Evaluating ant bioindication of impacted habitats	Yes	Time since restoration, distance from the impact, and physical properties of soil	Change in species richness: higher in cerrado than in the restoration habitats, and also higher in the ecotone and intermediate zones than on the beach ($F = 3.95$, $P < 0.05$) and change in abundance ($F = 1.9$, $P < 0.046$) and composition (non-statistical test)	Environmental	Costa et al. [61]
Restoration (mining)	Investigate which ants recolonized reclaimed areas in subtropical regions and evaluate the effect of different rehabilitation techniques, comparing results with Australia	Yes	Age of rehabilitation, soil penetrability, number of logs, litter and vegetation measures (three and five parameter, resp.)	Increase in species richness (non-statistical test) and change in composition (PCoA)	Ecological	Majer [62]
Restoration (mining)	Evaluate the efficacy of rehabilitation procedures in mining sites on facilitating ant recolonization and compare it with other tropical regions and climatic zones	Yes	Age of restoration, soil penetrability, litter depth, percentage of litter, grass, and herb cover, and vegetation (several parameters measured)	Species richness increased in early ages but slowed in late ages and was smaller than control site (non-statistical test). Distinct species composition in sites at early ages, intermediate ages, and control sites (ordination analyses)	Ecological	Majer [63]
Restoration (mining)	Investigate the community structure changes of different rehabilitation techniques	Yes	Rehabilitation technique	Change in species richness (non-statistical test) and composition (cluster analysis)	Ecological	Pereira et al. [64]
Road	Test the hypothesis that dirt roads are favourable landing sites for *Atta laevigata* founding queens. Analyze the importance of litter cover as a proximate cue in nest-site selection	Potential	Presence of dirt roads	The number of colonization attempts in roads was 5 to 10 times greater than that in the adjacent vegetation ($P < 0.001$)	Environmental	Vasconcelos et al. [65]

Table 1: Continued.

Disturbance	Aim	Indication	Environmental parameters	Effects on ant community	Indicator type	Reference
Seasonality	Investigate ant diversity and species composition on an island	Yes	Seasonality	Change in species richness and composition with seasonality (non-statistical test)	Environmental	Schmidt et al. [66]
Succession	Examine whether secondary forests of the Brazilian Atlantic Forest act as refugia for forest-adapted species	Yes (implicit)	Age of succession and soil type	Richness ($P < 0.001$) and composition ($P < 0.004$) of ant assemblages in secondary forests have recovered slowly and have not approached conditions typical to old-growth forests	Environmental	Bihn et al. [67]
Succession	Examine bait preferences of litter ants along a successional gradient of forest	Potential	Age of succession	Preference of ants for the type of bait changed along the successional gradient ($F = 5.52$, $P = 0.02$). In young successional stages, N baits attracted more ants than CHO baits, whereas in late successional stages, CHO baits attracted more ants	Environmental	Bihn et al. [68]
Succession	Investigate how functional diversity profile changed in a successional gradient	Potential	Age of succession	Increased diversity and change in functional groups (non-statistical test)	Environmental	Bihn et al. [69]
Succession	Verify patterns in the structure of ant communities along a successional gradient	Potential	Age of succession	Increased diversity and equitability (non-statistical test)	Environmental	Castro et al. [70]
Succession	Compare ant diversity among sites in different successional stages	Potential	Age of succession	Higher diversity in intermediary stage and change in composition (non-statistical test)	Environmental	Leal et al. [71]
Succession	Compare the diversity and composition of tree-dwelling ants in different successional stages of a seasonal deciduous forest	Potential	Age of succession	Increase in species abundance ($F = 9.26$, $P = 0.003$) and change in species composition (PCA analysis)	Environmental	Neves et al. [72]
Succession	Compare the ant species diversity related to successional stage and seasonality	Yes	Age of succession, tree richness and density	Change in species composition (DCA deterrent correspondence analysis, $P < 0.001$)	Ecological	Neves et al. [73]
Succession	Evaluate the long-term effect of fire on ant species richness	Potential	Presence of fire 15 years before	Change in species composition (cluster analyses-Euclidean distance)	Environmental	Santos et al. [74]
Succession	Assess the changes in species richness and composition between relatively pristine habitat and along a forest regeneration gradient	Yes	Age of succession	Increase in species richness (sample-based accumulation curves) and distinct species composition between pristine area and areas at regeneration (ANOSIM, $R = 0.79$, $P < 0.001$)	Environmental	Silva et al. [75]
Succession	Compare the structure of the ground ant communities in areas at different levels of restoration	Yes	Age of succession	Increase in species richness ($F = 5.1$, $P = 0.01$) and decrease in abundance ($F = 8.1$, $P < 0.001$), change in species composition (ordination analysis)	Environmental	Vasconcelos [76]

Table 1: Continued.

Disturbance	Aim	Indication	Environmental parameters	Effects on ant community	Indicator type	Reference
Succession	Determine experimentally the effects of selective logging on ground-living ants	Yes	Logging age, canopy cover, litter depth, and understory density	Species richness, evenness, and abundance per plot did not vary among treatments ($P > 0.05$). Most of the species found in the control plots were also present in the logged plots	Ecological	Vasconcelos et al. [77]
Urbanization	Compare the thermal tolerances of leaf-cutter ants (*Atta sexdens*) from colonies inside and outside an urban area	Potential	Temperature	Urban ants support higher temperatures better than rural ones, which present higher rates of mortality ($\beta = 20.54.237$, $P = 0.02$)	Environmental	Angilletta et al. [78]
Vegetation type	Inventory ants	Yes	Habitat type	Change in species richness (non-statistical test)	Environmental	Diehl et al. [79]
Vegetation type	Test how the diversity of one taxa can be a good surrogate of all diversity	Yes	Habitat type	Correlation with other taxa (Pearson correlation coefficients)	Biodiversity	Leal et al. [80]
Vegetation type	Compare ant diversity in three different forest stages (primary, reforestation, and secondary)	Potential	Habitat type	Change in diversity and exclusive species (non-statistical test)	Environmental	Lopes et al. [81]
Vegetation type	Compare the ant fauna from forests and nearby patches of savanna (Cerrado) in the Brazilian Amazon. Assess whether there is a difference in the fauna between the ground and lower vegetation strata in both habitats	Potential	Habitat type	Forests host twice as many species as savanna (sample-based rarefaction curves). In both habitats, the ground hosted more species than vegetation ($P < 0.005$). Distinct species composition between forest and savanna and between ground and vegetation within the same habitat; ant species fidelity and specificity is given by IndVal (see Table 2)	Environmental	Vasconcelos and Vilhena [82]

papers with sample-based accumulation curves.

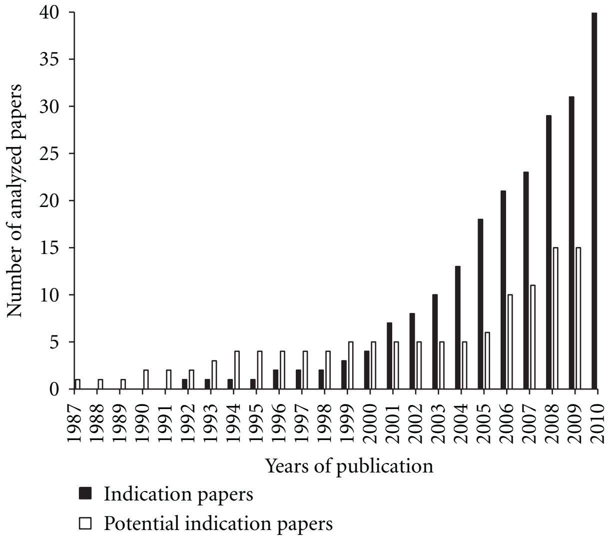


FIGURE 1: Trend of the number of analyzed papers regarding ants as indicators in Brazil. Indication papers—paper specifies (explicitly or implicitly) the intention of analyzing ants as indicators in the aim or introduction. Potential indication paper—the above criteria was not met, but the paper presents results that could potentially enable the use of ants as indicators.

hand collecting, pitfall traps, sweeping, Tretzel traps and Winkler's extractors. Among these methodologies, the most commonly used were baits (used in 26 studies), followed by hand collecting, pitfall traps and Winkler's extractors (used in 20 studies each), and Berlese extraction (used in five studies).

The majority of studies sampled ants at the soil surface (44), but some studies also considered the soil surface together with other habitats, including litter (10), vegetation (7), combination of the above (6). Some other studies did not sample ants at the soil surface, but only in the litter (11), vegetation (two), or in twigs (one), respectively.

The main impacts studied were succession (12), human land-use (11), restoration (6), and agriculture (5). Just a few papers (13) analyzed other environmental parameters besides disturbance (Table 1).

The parameters of the ant faunas that were most commonly related to the disturbance type were ant species richness or diversity indexes (42) and species composition (35) (Table 1). In these papers, if we considered only those that analyzed ant species diversity and composition rigorously (i.e., with statistical tests), the actual number of papers that analyzed ant species diversity decreased to 28, and those that analyzed ant species composition dropped to 22.

Regarding species composition, in 33 papers this parameter was sensitive to disturbance, although if we considered only those papers with statistical analyses, the number decreases to 21. Summarizing the papers that analyze species richness or diversity, the responses found were species richness or diversity increased with disturbance (1), decreased with disturbance (18), changed with disturbance (when there is any clear trend in the response of ants to disturbance) (11), and not affected by disturbance (12). If we considered only papers that tested ant species richness or diversity statistically, the numbers changed to increase with disturbance (1), decrease with disturbance (11), change with disturbance (5), and not affected by disturbance (11).

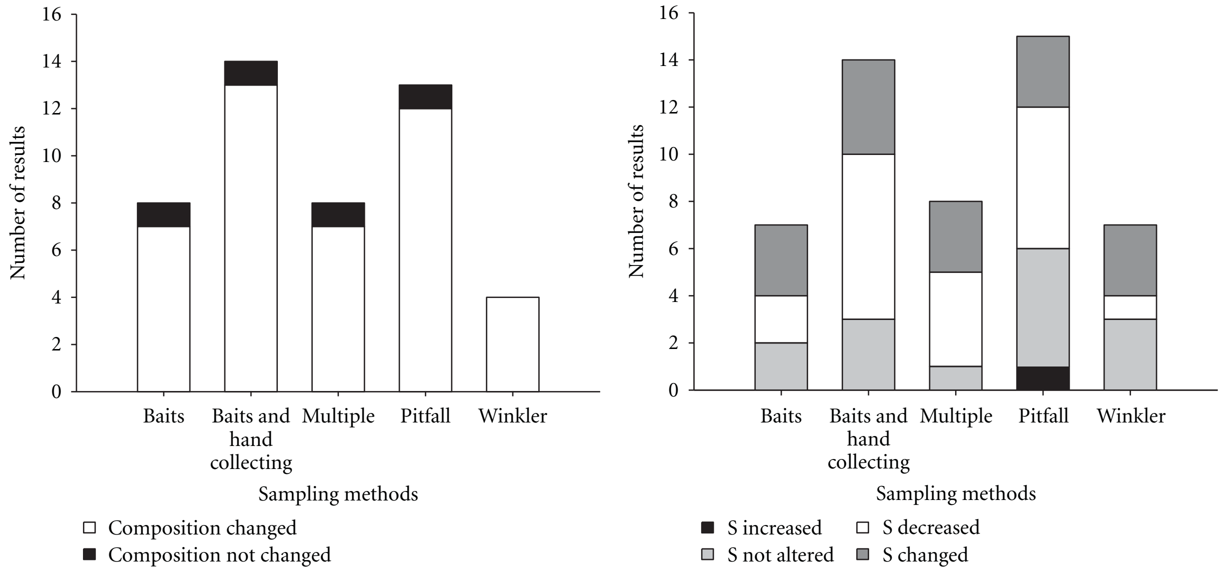
By connecting the main responses found in the papers (ant species richness, diversity, or ant species composition) to the main methodologies used to sample ants, we can verify some trends (Figure 2). First, species composition was sensitive to disturbance in the majority of papers in which this parameter was tested, irrespective of the sampling methodology, namely, baits plus hand collecting, multiple sampling methods, or pitfall traps. Second, most papers that analyzed species richness or diversity showed that these metrics were also responsive to disturbance, although the sole use of baits or the Winkler did not show any trend, while only using pitfall traps revealed a positive response of ant species richness or diversity to disturbance. Nevertheless, when we considered only those papers with statistical tests (Figure 3) or without statistical tests (Figure 4), the trend for species composition remained the same, but for species richness the use of multiple methods to sample ants showed a higher number of responses to disturbance.

The ants were used as environmental indicators in the majority of studies (42 out of 55) but were also used as ecological indicators (10 papers) and as biodiversity indicators in only one paper. In 20 papers there was a species list, and; therefore, we could determine some of the ant species that served as indicators of certain habitats. The parameters used in the papers to define a species as an indicator were frequency of ant occurrence (11 papers), presence or absence of ant species (8 papers), and the indicator value (IndVal) (1 paper). Irrespective of the parameter used by the authors, 187 ant species were defined as indicators and linked to specific habitats (Table 2). The genera with higher numbers of indicator species were *Camponotus* (18), *Pseudomyrmex* (12), *Pachycondyla* (11), *Ectatomma* (9), *Gnamptogenys* (9), *Acromyrmex* (8), and *Cephalotes* (8). The sites with the most indicator species were forest (39 species), *Eucalyptus* (37), savanna (34), control or undisturbed sites (nonburnt) (29), primary forest (25), early succession sites (19), disturbed sites (15), secondary forest (14), intermediate succession sites (13), burnt sites, low human land-use-impacted sites and pasture (9), late succession (8), and strong human land-use-impacted sites (5).

4. Discussion

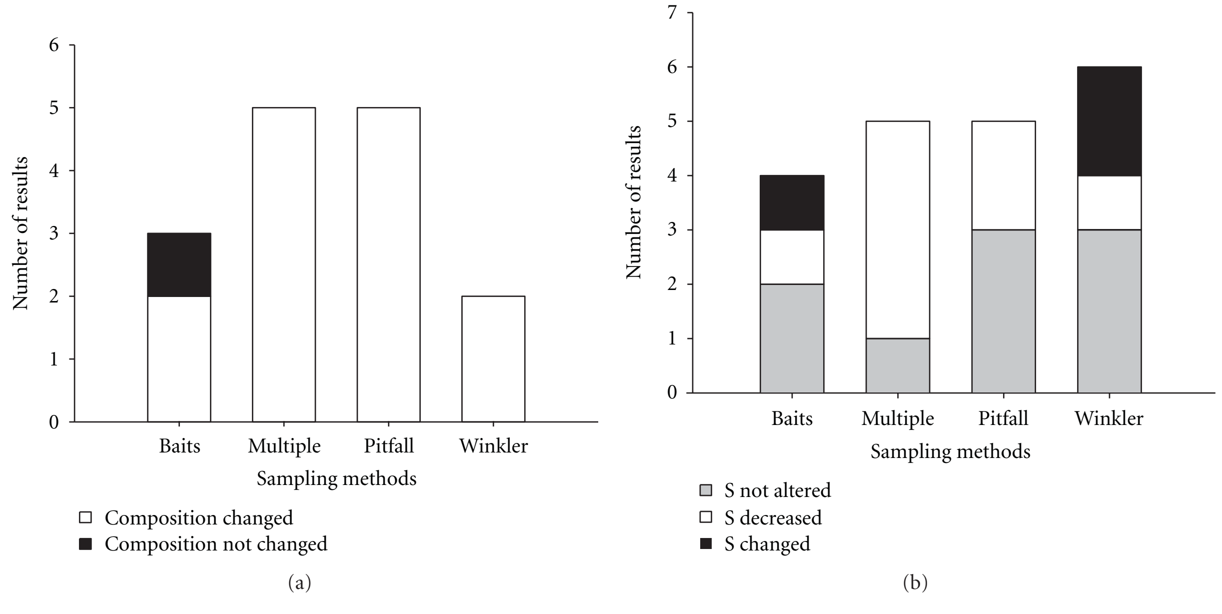
It has been possible to determine the history of research carried out in Brazil by searching for the use of ants as indicators over the last 25 years (Figure 1). From 1987 to 1991, there were only "Potential indication papers." In 1992 the first "Indication papers" were published, which increased in the following years and exceeded the "Potential indication papers" in 2001.

Regarding the idiom of the papers, it is interesting to observe that half of the papers are still published in Portuguese. In spite of the growing internationalization of Brazilian



(a) (b)

Figure 2: Papers that analyzed (a) ant species composition and/or (b) ant species richness/diversity with and without statistical tests and their responses to habitat disturbance through the use of different ant sampling methodologies. Composition changed—species composition altered by disturbance. Composition not changed—species composition not altered by disturbance. S increased—species richness or diversity increased with disturbance. S not altered—species richness or diversity not affected by disturbance. S decreased—species richness or diversity decreased with disturbance. S changed—species richness or diversity changed with disturbance when there is any clear trend in the response of ants to disturbance.



(a) (b)

Figure 3: Papers that analyzed (a) ant species composition and/or (b) ant species richness/diversity with statistical tests and their responses to habitat disturbance through the use of different ant sampling methodologies. Composition changed—species composition altered by disturbance. Composition not changed—species composition not altered by disturbance. S increased—species richness or diversity increased with disturbance. S not altered—species richness or diversity not affected by disturbance. S decreased—species richness or diversity decreased with disturbance. S changed—species richness or diversity changed with disturbance when there is any clear trend in the response of ants to disturbance.

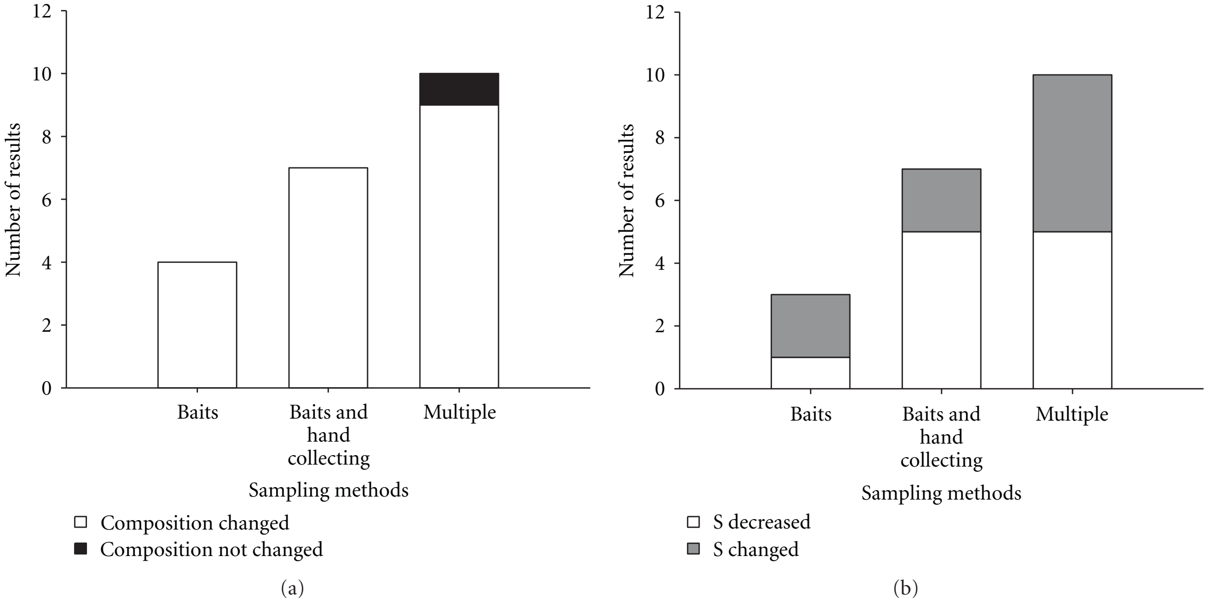


FIGURE 4: Papers that analyzed (a) ant species composition and/or (b) ant species richness/diversity without statistical tests and their responses to habitat disturbance through the use of different ant sampling methodologies. Composition changed—species composition altered by disturbance. Composition not changed—species composition not altered by disturbance. S increased—species richness or diversity increased with disturbance. S not altered—species richness or diversity not affected by disturbance. S decreased—species richness or diversity decreased with disturbance. S changed—species richness or diversity changed with disturbance when there is any clear trend in the response of ants to disturbance.

research [86, 87], many Brazilian studies that use ants as bioindicators cannot have an international impact since they are in Portuguese. We determined at least two main reasons for this. The first is the "*publish or perish*" policy in Brazilian (and worldwide) science, which demands the publication of as many papers as possible in the shortest feasible time span, in which case publishing in Portuguese can be a way to speed up publication time. The second explanation may be that, due to problems with the style of writing of the papers, many international journals reject Brazilian papers. Despite these two issues, in this historical scenario, there is an improving and maturing of bioindication studies using ants, which is shown by the explicit use of the term "indication" in these papers. Furthermore, the increasing knowledge exchange with researchers from other countries reinforces the maturation of this area of research. Examples include Brazilian scientists that complete their Ph.D. studies abroad the possibility for doctorate students to undertake international exchange programs, and the internationalization of the Brazilian Symposium of Myrmecology.

However, it is important to clarify that although some authors explicitly used the term indicator in the introduction or in the aim of their papers (our criteria defined these papers as "Indication papers"), the authors did not always in reality use ants as indicators, either because they did not sample properly (i.e., sampling in just one habitat, without different levels of the disturbance/restoration and control sites) or because they did not analyze their results rigorously (i.e., did not include a satisfactory statistical analysis). Conversely, some authors did not use the term indicator in their papers, but they did test the Potential use of ants as indicators, and were cautious in the above points.

The majority of articles that used ants as environmental indicators (sensu [7]) may be due to the fact that this is the simplest way to detect a change in the environmental state of the habitat but not necessarily the best one. The use of ecological indicators has the advantage of encompassing a broad response as they demonstrate the disturbance effect on the biota, not only for ants [6].

Moreover, the sampling of different environmental parameters and their correlation with the biota is essential, because their inclusion increases the predictive power of the study. If we recognize the environmental parameters that are most sensitive to disturbance and their effect on the biota, we may be able to more accurately monitor the effects of disturbance. Consequently, we may be able to choose the restoration effort according to the most appropriate or effective environmental parameters in order to promote the recovery of the biota [6, 7].

Regarding the number of ant sampling techniques used, although the majority of the papers used only one method, several studies (e.g., [52, 77, 88]) have highlighted the fact that ant communities show a pronounced vertical stratification, and ant faunas specific to each microhabitat may present specific ecological traits and distinct sensitivity to the same environmental impact [67, 89–91]; therefore, more than one sampling method must be considered [13]. On the other hand, the use of several sampling methods increases the financial costs and the time needed to collect, sort, and process the data [13]. Thus, since environmental monitoring programs usually have short-term goals, it is desirable to balance the benefits and costs of using several types of sampling methods compared to using only one sampling method which could achieve similar reliable results (Figures 2(a) and 2(b)), compare multiple sampling and pitfall outcomes) about the patterns and aims under investigation.

The most used sampling method in the studies was attractive baits, which are more suitable for behavioural questions [92] and are useful for verifying the presence and population trends of invasive and keystone ant species [13]. However, this sampling method results in biased information about ant diversity (e.g., species richness and composition) because many ants have selective diets, and some ants can dominate the baits to the exclusion of a broad range of other ant species [92]. This notion concerning the use of baits in bioindication papers is confirmed in Figures 3(a) and 3(b), which shows that the sole use of baits revealed apparently unchanging species composition and no trend in species richness. Thus, Underwood and Fisher [13] recommend the use of pitfall traps and litter sampling (The Winkler and/or Berlese extractors) as effective ant sampling methods for monitoring goals related to the effect of habitat disturbance and transformation on ant diversity, which is corroborated in Figures 3(a), 3(b), 4(a), and 4(b).

Species richness and diversity and species composition are the parameters of ant communities most commonly analyzed in the papers. However, species richness and diversity should be used as an evaluative method with caution, since several studies have shown that these parameters were not affected by disturbance (Table 1), and only a narrow number of papers showed a trend in the response of ant species richness to disturbance (see Figures 3 and 4). This coarse relationship of species richness to disturbance is probably because ants are generalists, so the loss of some sensitive species to disturbance is compensated by the invasion of other opportunist species or more generalists. Moreover, in dynamic sites under frequent habitat transformation and disturbance, there is no change in species richness among sites at different restoration times, because perturbation events “reset” the ant community to the same stage [93].

In this way, as Hoffmann [94] has highlighted, the disturbance induced changes in species composition, but not necessarily in species richness. Moreover, the recovery of species composition takes longer than species richness [95] and has a strong relation to the vegetation structure [19, 64, 96–99], which changes with disturbance events. Thus, species composition should be a better parameter to evaluate the effect of disturbance on ant communities, even in areas with frequent perturbations, as described by Gollan et al. [93].

Using the same argument, the quantification of the relationship between each ant species and different disturbances (or level of disturbance) or habitats should be very useful, as it is important to decrease the time spent in indication studies. The general public and stakeholders need to know rapidly if the habitat is impacted or recovering, so recognizing which species can be associated positively or negatively with disturbance or restoration is a very desirable tool.

Several of the papers we analyzed described species occurring exclusively or more frequently in specific habitats (Table 2), but we are concerned with the lack of rigour with which this has been carried out in most studies (exception in [82]), as there is no control about the specificity and fidelity of these ant species and few statistical analyses to validate the results. This lack of rigour may explain why there are some ant species with contradictory patterns of occurrence, such as species being present in disturbed *versus* undisturbed sites, such as *Acromyrmex balzani*, *Camponotus trapezoideus*, *Dorymyrmex pyramicus*, *Ectatomma tuberculatum*, *Odontomachus haematodus,* and *Pseudomyrmex tenuis* (see Table 2). Moreover, these ant species might also be generalists, and the choice of better criteria should enable us to distinguish between inappropriate sampling design and truly generalist ant species. The use of the IndVal index [8], mentioned below, is one option to overcome this drawback.

The Indicator Value (IndVal) suggested by Dufrêne and Legendre [8] combines a measure of the habitat specificity of a species to a level of disturbance, or to a disturbance state, with its fidelity within that state. The random reallocation procedure of samples within sample groups can be used to test the significance of the IndVal measure for each species. The use of this method has increased (e.g., [100–105]) and has a number of advantages over other methods [6].

Some species seem to have more consistent responses to disturbance or specificity to some habitats, but this consistency is very difficult to assert due to the lack of rigour with which the ants were related to disturbance or habitats (presence or frequency of occurrence) and the lack of standardization regarding the level of disturbance in the papers. The habitats sampled in one paper may be defined as undisturbed, which may be different from the habitats studied in another paper that are defined as more degraded (or less) and should also be defined as an undisturbed habitat. In our paper (including Table 2), we used the definition of disturbed or undisturbed given by the original authors.

Thus, following the disturbance definition used by the authors, some species are present in disturbed habitats in more than one paper, and, therefore, could be indicators of disturbed habitats, such as *Atta sexdens rubropilosa*, *Camponotus crassus*, *Camponotus melanoticus*, *Camponotus novogranadensis*, *Odontomachus meinerti*, *Pachycondyla villosa*, *Pseudomyrmex termitarius,* and *Solenopsis saevissima*. In the same way, some species could be indicators of undisturbed habitats, such as *Labidus coecus*, *Pachycondyla arhuaca*, *Pachycondyla stigma,* and *Sericomymex bondari*. There are also some species that are indicators of specific habitats, such as indicators of forests (*Discothyrea sexarticulata*, *Ectatomma lugens*, *Labidus coecus,* and *Typhlomyrmex major*) and indicators of savannas (*Camponotus latangulus*, *Pheidole fimbriata,* and *Strumigenys perparva*).

One of the major mistakes related to the use of a taxon as an indicator is the personal motivation of the researchers. There are two ways of avoiding this mistake; several taxa should be rigorously tested *a priori* to select the best one [4] or studied *a posteriori* to validate the response of the indicator [7]. Very few studies have compared how different taxa, including ants, perform under different disturbances (see [89, 101, 106–109]).

[t!]

Table 2: Species of ants defined as indicators, indicating the parameter used by the authors (Parameter) when linking each ant species to each habitat type (Habitat) and the paper (Reference).

Ant species	Parameter	Habitat	Reference
Acanthognathus brevicornis	Frequency of occurrence	Secondary forest and area at early succession	Silva et al. [75]
Acanthognathus ocellatus	Frequency of occurrence	Primary forest	Silva et al. [75]
Acanthognathus rudis	Frequency of occurrence	Primary forest	Silva et al. [75]
Acanthoponera mucronata	Frequency of occurrence	Native forest remnant	Ilha et al. [48]
Acromyrmex balzani	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
	Presence/absence	Low human land-use-impacted sites	Delabie et al. [35]
	Presence/absence	Undisturbed sites—control site	Diehl et al. [58]
Acromyrmex coronatus	Frequency of occurrence	Forest fragments	Lapola and Fowler [49]
	Frequency of occurrence	Preserved savanna	Ramos et al. [37]
Acromyrmex lobicornis	Presence/absence	Undisturbed sites—control site	Diehl et al. [58]
Acromyrmex lundi	Frequency of occurrence	Secondary forest	Schmidt and Diehl [52]
Acromyrmex niger	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
Acromyrmex rugosus	Frequency of occurrence	*Turnera ulmifolia* field	Santana-Reis and Santos [51]
Acromyrmex striatus	Presence/absence	Undisturbed sites—control site	Diehl et al. [58]
Acromyrmex subterraneus	Frequency of occurrence	Forest fragments	Lapola and Fowler [49]
Acromyrmex subterraneus brunneus	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
Acromyrmex subterraneus subterraneus	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
Acropyga decedens	Frequency of occurrence	Pasture	Dias et al. [45]
Amblyopone armigera	Frequency of occurrence	Preserved savanna	Ramos et al. [37]
	Presence/absence	Savanna—cerrado sensu stricto	Marinho et al. [50]
	Frequency of occurrence	Secondary forest and area at early succession	Silva et al. [75]
Amblyopone elongata	Frequency of occurrence	Primary forest	Silva et al. [75]
Anochetus diegensis	Frequency of occurrence	Preserved savanna	Ramos et al. [37]
Anochetus mayri	Frequency of occurrence	Control site (nonburnt)	Teixeira et al. [39]
Anochetus neglectus	Frequency of occurrence	Pasture	Dias et al. [45]
Anochetus targionii	Frequency of occurrence	Pasture	Dias et al. [45]
Apterostigma acre	Frequency of occurrence	Forest fragment	Dias et al. [45]
Apterostigma bolivianum	Frequency of occurrence	Forest fragment	Dias et al. [45]
Atta robusta	Frequency of occurrence	Control site (nonburnt)	Teixeira et al. [39]
Atta sexdens rubropilosa	Presence/absence	Area at early succession	Coelho et al. [60]
	Frequency of occurrence	Disturbed savanna	Ramos et al. [37]
	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
Azteca alfari	Presence/absence	Area at late succession stage—dry season	Neves et al. [73]
Azteca muelleri	Frequency of occurrence	Control site (nonburnt)	Teixeira et al. [39]
Basiceros disciger	Frequency of occurrence	Forest fragments	Lapola and Fowler [49]
Blepharidatta brasiliensis	Frequency of occurrence	Area at late succession stage	Vasconcelos [76]
Brachymyrmex coactus	Frequency of occurrence	Secondary forest and area at early succession	Silva et al. [75]
Camponotus arboreus	Frequency of occurrence	Control site (nonburnt)	Teixeira et al. [39]
Camponotus atriceps	Presence/absence	Reforestated area at intermediate succession stage	Coelho et al. [60]
Camponotus bidens	Presence/absence	Low human land-use-impacted sites	Delabie et al. [67
Camponotus burtoni	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
Camponotus claviscapus	Presence/absence	Undisturbed sites	Delabie et al. [35]
Camponotus crassus	Presence/absence	Burned restinga	Endringer et al. [38]
	Frequency of occurrence	Burnt site	Teixeira et al. [39]
	Frequency of occurrence	Disturbed sites	Diehl et al. [58]
	Frequency of occurrence	Secondary forest and forest edge	Leal et al. [71]

Table 2: Continued.

Ant species	Parameter	Habitat	Reference
	IndVal	Savanna—vegetation and ground stratum	Vasconcelos and Vilhena [82]
Camponotus fastigatus	Frequency of occurrence	Preserved savanna	Ramos et al. [37]
Camponotus latangulus	Frequency of occurrence	Preserved savanna	Ramos et al. [37]
	Presence/absence	Savanna—cerrado sensu stricto	Marinho et al. [50]
Camponotus leydigi	Frequency of occurrence	Area at early succession	Vasconcelos [76]
Camponotus melanoticus	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
	Frequency of occurrence	Pasture	Dias et al. [45]
	Presence/absence	Area at early succession	Coelho et al. [60]
Camponotus novogranadensis	Frequency of occurrence	Area at early succession	Vasconcelos [76]
	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
	IndVal	Forest—vegetation and ground stratum	Vasconcelos and Vilhena [82]
	Frequency of occurrence	Disturbed savanna	Ramos et al. [37]
Camponotus punctatus minutior	Frequency of occurrence	Preserved savanna	Ramos et al. [37]
Camponotus renggeri	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
Camponotus rufipes	Frequency of occurrence	Disturbed savanna	Ramos et al. [37]
	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
	Frequency of occurrence	Forest fragments	Lapola and Fowler [49]
Camponotus sericeiventris	Frequency of occurrence	Native forest remnant	Ilha et al. [48]
Camponotus trapezoideus	Frequency of occurrence	Burnt site	Teixeira et al. [39]
	Frequency of occurrence	Forest fragment	Dias et al. [45]
	Frequency of occurrence	Preserved savanna	Ramos et al. [37]
Camponotus vitatus	Presence/absence	Low human land-use-impacted sites	Delabie et al. [35]
Camponotus westermanni	Presence/absence	Strong human land-used-impacted sites	Delabie et al. [35]
Cardiocondyla obscurior	Presence/absence	Area at intermediate succession	Coelho et al. [60]
Carebara urichi	Frequency of occurrence	Preserved savanna	Ramos et al. [37]
Cephalotes atratus	Frequency of occurrence	Control site (nonburnt)	Teixeira et al. [39]
	IndVal	Forest—vegetation stratum	Vasconcelos and Vilhena [82]
Cephalotes grandinosus	Presence/absence	Forest	Lopes et al. [81]
Cephalotes minutus	Presence/absence	Area at early succession—dry season	Neves et al. [73]
	Presence/absence	Low human land-use-impacted sites	Delabie et al. [35]
Cephalotes pallidicephalus	Presence/absence	Low human land-use-impacted sites	Delabie et al. [35]
Cephalotes pavonii	Frequency of occurrence	Burnt site	Teixeira et al. [39]
Cephalotes pellans	Presence/absence	Area at intermediate succession—wet season	Neves et al. [73]
Cephalotes pusillus	IndVal	Savanna—vegetation and ground stratum	Vasconcelos and Vilhena [82]
Cephalotes simillimus	IndVal	Savanna—vegetation stratum	Vasconcelos and Vilhena [82]
Crematogaster brasiliensis	IndVal	Forest—vegetation and ground stratum	Vasconcelos and Vilhena [82]
Crematogaster erecta	Presence/absence	Area at intermediate succession	Coelho et al. [60]
	IndVal	Savanna—vegetation and ground stratum	Vasconcelos and Vilhena [82]
Crematogaster limata	IndVal	Forest—vegetation and ground stratum	Vasconcelos and Vilhena [82]
Crematogaster minutissima	IndVal	Forest—ground stratum	Vasconcelos and Vilhena [82]
Crematogaster nigropilosa	Frequency of occurrence	Native forest remnant	Ilha et al. [48]

Table 2: Continued.

Ant species	Parameter	Habitat	Reference
Crematogaster quadriformis	IndVal	Savanna—ground stratum	Vasconcelos and Vilhena [82]
Cyphomyrmex laevigatus	Frequency of occurrence	Forest fragments	Lapola and Fowler [49]
Cyphomyrmex major	Frequency of occurrence	Forest fragments	Lapola and Fowler [49]
Cyphomyrmex olitor	Frequency of occurrence	Primary forest	Silva et al. [75]
Cyphomyrmex peltatus	Frequency of occurrence	Disturbed savanna	Ramos et al. [37]
	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
	Frequency of occurrence	Forest fragments	Dias et al. [45]
Cyphomyrmex plaumanni	Frequency of occurrence	Primary forest	Silva et al. [75]
Cyphomyrmex salvini	Frequency of occurrence	Area at early succession	Vasconcelos [76]
	Frequency of occurrence	Control site (nonburnt)	Teixeira et al. [39]
Cyphomyrmex transversus	Frequency of occurrence	Preserved savanna	Ramos et al. [37]
Discothyrea sexarticulata	Frequency of occurrence	Forest fragment	Dias et al. [45]
	Frequency of occurrence	Primary forest	Silva et al. [75]
Dolichoderus attelaboides	IndVal	Forest—vegetation stratum	Vasconcelos and Vilhena [82]
Dolichoderus bispinosus	IndVal	Forest—vegetation stratum	Vasconcelos and Vilhena [82]
Dolichoderus schulzi	Presence/absence	Undisturbed sites	Delabie et al. [35]
Dolichoderus voraginosus	Presence/absence	Area at early succession—dry season	Neves et al. [73]
Dorymyrmex guianensis	IndVal	Savanna—ground stratum	Vasconcelos and Vilhena [82]
Dorymyrmex pyramicus	Frequency of occurrence	Burnt site	Teixeira et al. [39]
	Presence/absence	Undisturbed sites	Delabie et al. [35]
Dorymyrmex thoracicus	IndVal	Savanna—ground stratum	Vasconcelos and Vilhena [82]
Eciton quadriglume	Frequency of occurrence	Forest fragments	Lapola and Fowler [49]
Ectatomma brunneum	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
	Frequency of occurrence	Area at early succession	Braga et al. [54]
	Presence/absence	Low human land-use-impacted sites	Delabie et al. [35]
Ectatomma edentatum	Frequency of occurrence	Preserved savanna	Ramos et al. [37]
Ectatomma lugens	Frequency of occurrence	Area at late succession stage	Vasconcelos [76]
	IndVal	Forest—ground stratum	Vasconcelos and Vilhena [82]
Ectatomma muticum	Frequency of occurrence	Control site (nonburnt)	Teixeira et al. [39]
Ectatomma opaciventre	IndVal	Savanna—ground stratum	Vasconcelos and Vilhena [82]
Ectatomma permagnum	Frequency of occurrence	Control site (nonburnt)	Teixeira et al. [39]
	Frequency of occurrence	*Eucalyptus* forestry	Braga et al. [54]
	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
Ectatomma planidens	Frequency of occurrence	Disturbed savanna	Ramos et al. [37]
	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
Ectatomma quadridens	Frequency of occurrence	Area at early succession	Vasconcelos [76]
Ectatomma tuberculatum	Frequency of occurrence	Area at early succession	Silva et al. [75]
	Presence/absence	Burned restinga	Endringer et al. [38]
	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
	Frequency of occurrence	Area at late succession stage	Braga et al. [54]
	Frequency of occurrence	Secondary forest and forest edge	Leal et al. [71]
Forelius maranhoensis	IndVal	Savanna—ground stratum	Vasconcelos and Vilhena [82]
Gnamptogenys acuminata	Frequency of occurrence	Forest fragments	Lapola and Fowler [49]

Table 2: Continued.

Ant species	Parameter	Habitat	Reference
Gnamptogenys continua	Frequency of occurrence	Primary forest	Silva et al. [75]
Gnamptogenys horni	Frequency of occurrence	Area at late succession stage	Vasconcelos [76]
Gnamptogenys mediatrix	Frequency of occurrence	Forest fragment	Dias et al. [45]
Gnamptogenys moelleri	Frequency of occurrence	Pasture	Dias et al. [45]
	Frequency of occurrence	Secondary forest and area at early succession	Schmidt and Diehl [52]
Gnamptogenys reichenspergeri	Frequency of occurrence	Primary forest	Silva et al. [75]
Gnamptogenys striatula	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
	IndVal	Forest—ground stratum	Vasconcelos and Vilhena [82]
Gnamptogenys sulcata	Presence/absence	Area at early succession—wet season	Neves et al. [73]
Gnamptogenys tortuolosa	Frequency of occurrence	Intermediate disturbed area	Vasconcelos [76]
Heteroponera flava	Frequency of occurrence	Forest fragment	Dias et al. [45]
Heteroponera microps	Frequency of occurrence	Disturbed habitat (*Eucalyptus*)	Ilha et al. [48]
Hylomyrma balzani	Frequency of occurrence	Forest fragments	Lapola and Fowler [49]
Hylomyrma reitteri	Frequency of occurrence	Forest fragments	Lapola and Fowler [49]
Hypoponera foeda	Frequency of occurrence	Native forest remnant	Ilha et al. [48]
Hypoponera foreli	Frequency of occurrence	Preserved savanna	Ramos et al. [37]
Hypoponera opacior	Frequency of occurrence	Disturbed habitat (*Eucalyptus*)	Ilha et al. [48]
Labidus coecus	Frequency of occurrence	Forest fragments	Lapola and Fowler [49]
	Presence/absence	Undisturbed sites	Delabie et al. [35]
Labidus praedator	Frequency of occurrence	Disturbed savanna	Ramos et al. [37]
	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
	Frequency of occurrence	Secondary forest	Schmidt and Diehl [52]
Leptogenys pusilla	Frequency of occurrence	Control site (nonburnt)	Teixeira et al. [39]
Leptothorax asper	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
Leptothorax spininodis	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
Linepithema humile	Frequency of occurrence	Burnt site	Teixeira et al. [39]
	Frequency of occurrence	Disturbed savanna	Ramos et al. [37]
	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
	Frequency of occurrence	Forest fragments	Lapola and Fowler [49]
Megalomyrmex goeldii	Frequency of occurrence	Area at early succession	Silva et al. [75]
Mycetagroicus cerradensis	Frequency of occurrence	Disturbed savanna	Ramos et al. [37]
Mycetarotes paralelus	Presence/absence	Area revegetated with native species	Pereira et al. [64]
Mycetophylax conformis	Presence/absence	Strong human land-used-impacted sites	Delabie et al. [35]
Myrmicocrypta foreli	Frequency of occurrence	Preserved savanna	Ramos et al. [37]
Neivamyrmex orthonotus	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
Nesomyrmex spininodis	Presence/absence	Strong human land-used-impacted sites	Delabie et al. [35]
Octostruma balzani	Frequency of occurrence	Area at intermediate succession	Braga et al. [54]
Octostruma jheringhi	Frequency of occurrence	Forest fragment	Dias et al. [45]
	Frequency of occurrence	Preserved savanna	Ramos et al. [37]
Odontomachus affinis	Frequency of occurrence	Secondary forest	Silva et al. [75]
Odontomachus bauri	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
Odontomachus brunneus	Frequency of occurrence	Preserved savanna	Ramos et al. [37]
Odontomachus caelatus	Frequency of occurrence	Area at late succession stage	Vasconcelos [76]
Odontomachus chelifer	Frequency of occurrence	Pasture	Braga et al. [54]
	Frequency of occurrence	Preserved savanna	Ramos et al. [37]
	Frequency of occurrence	Secondary forest and area at early succession	Schmidt and Diehl [52]
	Frequency of occurrence	Secondary forest and area at early succession	Silva et al. [75]

Table 2: Continued.

Ant species	Parameter	Habitat	Reference
Odontomachus haematodus	Frequency of occurrence	Area at intermediate succession	Braga et al. [54]
	Presence/absence	Burned restinga	Endringer et al. [38]
	Frequency of occurrence	Control site (nonburnt)	Teixeira et al. [39]
	IndVal	Forest—ground stratum	Vasconcelos and Vilhena [82]
Odontomachus meinerti	Frequency of occurrence	Disturbed savanna	Ramos et al. [37]
	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
Oxyepoecus plaumanni	Frequency of occurrence	Primary forest	Silva et al. [75]
Oxyepoecus rastratus	Frequency of occurrence	Primary forest	Silva et al. [75]
Pachycondyla apicalis	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
Pachycondyla arhuaca	Frequency of occurrence	Area at late succession stage	Braga et al. [54]
	Presence/absence	Primary restinga	Endringer et al. [38]
Pachycondyla bucki	Frequency of occurrence	Primary forest	Silva et al. [75]
Pachycondyla crassinoda	IndVal	Forest—ground stratum	Vasconcelos and Vilhena [82]
Pachycondyla ferruginea	Frequency of occurrence	Secondary forest and area at early succession	Silva et al. [75]
Pachycondyla gilberti	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
Pachycondyla harpax	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
	IndVal	Forest—ground stratum	Vasconcelos and Vilhena [82]
	Presence/absence	Low human land-use-impacted sites	Delabie et al. [35]
Pachycondyla obscuricornis	Frequency of occurrence	*Eucalyptus* (reforestation)	Lapola and Fowler [49]
Pachycondyla stigma	Frequency of occurrence	Control site (nonburnt)	Teixeira et al. [39]
	Frequency of occurrence	Primary forest	Braga et al. [54]
Pachycondyla striata	Frequency of occurrence	Preserved savanna	Ramos et al. [37]
	Presence/absence	Savanna—cerrado sensu stricto	Marinho et al. [50]
	Frequency of occurrence	Secondary forest and area at early succession	Schmidt and Diehl [52]
	Frequency of occurrence	Secondary forest and area at early succession	Silva et al. [75]
Pachycondyla villosa	Presence/absence	Burned restinga	Endringer et al. [38]
	Frequency of occurrence	Disturbed savanna	Ramos et al. [37]
Paratrechina longicornis	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
	Presence/absence	Undisturbed sites	Delabie et al. [35]
Pheidole diligens	Presence/absence	Area at intermediate succession	Coelho et al. [60]
Pheidole embolopyx	Frequency of occurrence	Area at late succession stage	Vasconcelos [76]
Pheidole exigua	IndVal	Forest—ground stratum	Vasconcelos and Vilhena [82]
Pheidole fimbriata	Frequency of occurrence	Preserved savanna	Ramos et al. [37]
	Presence/absence	Savanna—cerrado sensu stricto	Marinho et al. [50]
Pheidole fracticeps	IndVal	Forest—ground stratum	Vasconcelos and Vilhena [82]
Pheidole radoszkowskii	Presence/absence	Low human land-use-impacted sites	Delabie et al. [35]
Pheidole scalaris	Presence/absence	Area at early succession—wet season	Neves et al. [73]
Pogonomyrmex abdominalis	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
Pogonomyrmex naegelii	Presence/absence	Area at intermediate succession	Coelho et al. [60]
Prionopelta punctulata	Frequency of occurrence	Secondary forest and area at early succession	Silva et al. [75]
Pseudomyrmex elongatus	Frequency of occurrence	Control site (nonburnt)	Teixeira et al. [39]
Pseudomyrmex filiformis	Frequency of occurrence	Control site (nonburnt)	Teixeira et al. [39]
Pseudomyrmex flavidulus	IndVal	Savanna—vegetation stratum	Vasconcelos and Vilhena [82]

Table 2: Continued.

Ant species	Parameter	Habitat	Reference
Pseudomyrmex gracilis	Presence/absence	Area at intermediate succession	Coelho et al. [60]
	IndVal	Savanna—vegetation stratum	Vasconcelos and Vilhena [82]
	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
Pseudomyrmex kuenckeli	Presence/absence	Undisturbed sites	Delabie et al. [35]
Pseudomyrmex oculatus	Presence/absence	Area at intermediate succession	Coelho et al. [60]
	Frequency of occurrence	Control site (nonburnt)	Teixeira et al. [39]
	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
	IndVal	Forest—vegetation stratum	Vasconcelos and Vilhena [82]
Pseudomyrmex schuppi	Presence/absence	Area at intermediate succession	Coelho et al. [60]
Pseudomyrmex sericeus	Presence/absence	Undisturbed sites	Delabie et al. [35]
Pseudomyrmex simplex	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
Pseudomyrmex spiculus	Presence/absence	Undisturbed sites	Delabie et al. [35]
Pseudomyrmex tenuis	Frequency of occurrence	Area at early succession	Vasconcelos [76]
	IndVal	Forest—vegetation and ground stratum	Vasconcelos and Vilhena [82]
	Presence/absence	Strong human land-use-impacted sites	Delabie et al. [35]
	Frequency of occurrence	Area at intermediate succession	Braga et al. [54]
	Frequency of occurrence	Control site (nonburnt)	Teixeira et al. [39]
Pseudomyrmex termitarius	Presence/absence	Area at early succession—dry season	Neves et al. [73]
	Frequency of occurrence	Pasture	Braga et al. [54]
	IndVal	Savanna—vegetation stratum	Vasconcelos and Vilhena [82]
	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
Pyramica appretiata	Frequency of occurrence	Primary forest	Silva et al. [75]
Pyramica denticulata	Frequency of occurrence	Area at early succession	Silva et al. [75]
Pyramica lygatrix	Frequency of occurrence	Primary forest	Silva et al. [75]
Pyramica rugithorax	Frequency of occurrence	Primary forest	Silva et al. [75]
Pyramica schulzi	Presence/absence	Strong human land-use-impacted sites	Delabie et al. [35]
Pyramica subdentata	Frequency of occurrence	Preserved savanna	Ramos et al. [37]
	Frequency of occurrence	Secondary forest and area at early succession	Silva et al. [75]
Pyramica zeteki	Frequency of occurrence	Preserved savanna	Ramos et al. [37]
Sericomymex bondari	Frequency of occurrence	Control site (nonburnt)	Teixeira et al. [39]
	Presence/absence	Low human land-use-impacted sites	Delabie et al. [35]
Simopelta curvata	Frequency of occurrence	Pasture (edge)	Dias et al. [45]
Solenopsis geminata	Frequency of occurrence	Area at early succession	Vasconcelos [76]
	Frequency of occurrence	*Caesalpinia echinata* forest	Santana-Reis and Santos [51]
Solenopsis saevissima	Frequency of occurrence	Disturbed sites	Ilha et al. [48]
	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
Solenopsis substituta	Frequency of occurrence	Burnt site	Teixeira et al. [39]
	Presence/absence	*Eucalyptus* forestry	Marinho et al. [50]
	IndVal	Savanna—ground stratum	Vasconcelos and Vilhena [82]
Sphinctomyrmex stali	Frequency of occurrence	Primary forest	Silva et al. [75]
Stegomyrmex vizzotoi	Frequency of occurrence	Primary forest	Silva et al. [75]
Strumigenys denticulata	Frequency of occurrence	Intermediate disturbed area	Vasconcelos [76]
Strumigenys elongata	Frequency of occurrence	Area at early succession	Silva et al. [75]
	Frequency of occurrence	Preserved savanna	Ramos et al. [37]

Table 2: Continued.

Ant species	Parameter	Habitat	Reference
Strumigenys perparva	Presence/absence	Savanna—cerrado sensu stricto	Marinho et al. [50]
	Frequency of occurrence	Preserved savanna	Ramos et al. [37]
Tapinoma melanocephalum	Frequency of occurrence	Disturbed habitat (*Eucalyptus*)	Ilha et al. [48]
	Frequency of occurrence	Forest fragments	Lapola and Fowler [49]
Trachymyrmex cornetzi	Frequency of occurrence	Control site (nonburnt)	Teixeira et al. [39]
Trachymyrmex fuscus	Frequency of occurrence	Pasture (edge)	Dias et al. [45]
Trachymyrmex zeteki	Frequency of occurrence	Primary forest	Silva et al. [75]
Typhlomyrmex major	Frequency of occurrence	Forest fragments	Lapola and Fowler [49]
	Frequency of occurrence	Primary forest	Silva et al. [75]
Typhlomyrmex pusillus	Frequency of occurrence	Primary forest	Silva et al. [75]
Wasmannia auropunctata	Presence/absence	Area at intermediate succession	Coelho et al. [60]
	Frequency of occurrence	Control site (nonburnt)	Teixeira et al. [39]
Wasmannia rochai	Presence/absence	Area at early succession	Coelho et al. [60]

The majority of studies end at the seventh step of the "Procedural steps in bioindicator studies" according to McGeoch [7], which is "Based on the nature of the relationship, either accept or reject the species, higher level taxon or assemblage as an indicator," and just investigate the nature of the relationship between the disturbance and the indicator. To validate the organism as a suitable indicator, we must move to step eight (Establish the robustness of the indicator by developing and testing appropriate hypotheses under different conditions)—establish the robustness of the indicator by testing the same relationship in other areas or at different times (to validate the indicator) [6, 14, 103].

We would like to flag some issues to improve and validate the use of ants as indicators in environmental monitoring programs, including consideration of robust criteria for the validation of ants as indicators, sampling in different seasons and under different disturbances with comparable methodologies, collecting ants with different sampling methodologies in order to recognize that the responses of different ant life styles could be different for the same disturbance, and evaluation of different environmental parameters (biotic and abiotic) to correlate with the ants' response along the disturbance/restoration gradients. The search for indicator ant species should be with analyses that consider their fidelity and specificity to the habitats (e.g., "IndVal" index), in order to more quickly achieve monitoring goals. Finally, evaluating the functional loss of ant species in disturbed habitats will improve predictions about the functional implication of the disturbance.

Moreover, incorporating new approaches that efficiently simplify the study may help to decrease the problems related to time spent identifying ant species, as suggested by Groc et al. [85]. In this study, the authors introduced a new method based on mixed-level taxonomic sufficiency, highly focused on higher-taxon surrogacy. Under this method, only ant species pre established as "indicator taxa" must be taxonomically identified to species level, while other species may be identified to higher (and easier to identify) levels, such as genera. By using this mixed-level approach, the authors argue that a considerable improvement in cost effectiveness can be achieved, mainly by reducing the necessity for well-trained taxonomists to be involved in the study. This is highly desirable in monitoring programs, where time and budget are key limiting factors.

Also, species which have been identified as possible indicators because they occur in specific habitats or conditions still require validation for reliable use as bioindicators, and their presence or frequency in specific conditions can generate testable hypothesis about their relationship with these habitats and conditions, which in turn can validate the use of these species as bioindicators.

In conclusion, we point out that the use of ants as indicators in Brazil has been improving each year. Ants are a useful tool not only because they are sensitive to environmental changes, as related in the papers we reviewed but also because they are keystone species in several ecological processes and, therefore, provide reliable inferences about the ecological and functional implications of disturbances.

We should continue to study ants in Brazil, with proper *a priori* hypothesis tests and sampling designs, statistical analysis and standardized methods, in order to reach the same widespread acceptance of ants as indicators that is common in Australia, as well as to improve our understanding of ant dynamics for predictive frameworks. Moreover, we need to build an effective bridge between our accumulated knowledge (almost 25 years of research) of ants as bioindicators and monitoring programs developed to examine natural resources and areas.

Acknowledgments

This study resulted from the research project: CRA 270/07 "Utilização de formigas como bioindicadoras de impacto ambiental e de sua recuperação em Cerrado e em Mata Atlântica." The authors are grateful to Jacques H. C. Delabie for encouraging the elaboration of this paper, to Jonathan D. Majer for his kind attention in providing several papers and to

Patty Ramirez for her valuable suggestions in the English expression. The authors received grants and funding from the FAPEMIG, CAPES, and CNPq.

References

[1] E. O. Wilson, "On the future of conservation biology: editorial," *Conservation Biology*, vol. 14, no. 1, pp. 1–3, 2000.

[2] K. S. Bawa, W. J. Kress, N. M. Nadkarni et al., "Tropical ecosystems into the 21st century," *Science*, vol. 306, no. 5694, pp. 227–228, 2004.

[3] J. K. A. Benhin, "Agriculture and deforestation in the tropics: a critical theoretical and empirical review," *Ambio*, vol. 35, no. 1, pp. 9–16, 2006.

[4] G. J. Niemi and M. E. McDonald, "Application of ecological indicators," *Annual Review of Ecology, Evolution, and Systematics*, vol. 35, pp. 89–111, 2004.

[5] P. J. Goodsell, A. J. Underwood, and M. G. Chapman, "Evidence necessary for taxa to be reliable indicators of environmental conditions or impacts," *Marine Pollution Bulletin*, vol. 58, no. 3, pp. 323–331, 2009.

[6] T. A. Gardner, *Monitoring Forest Biodiversity: Improving Conservation through Ecologically-Responsible Management*, Earthscan, London, UK, 2010.

[7] M. A. McGeoch, "The selection, testing and application of terrestrial insects as bioindicators," *Biological Reviews of the Cambridge Philosophical Society*, vol. 73, no. 2, pp. 181–201, 1998.

[8] M. Dufrêne and P. Legendre, "Species assemblages and indicator species: the need for a flexible asymmetrical approach," *Ecological Monographs*, vol. 67, no. 3, pp. 345–366, 1997.

[9] J. Hilty and A. Merenlender, "Faunal indicator taxa selection for monitoring ecosystem health," *Biological Conservation*, vol. 92, no. 2, pp. 185–197, 2000.

[10] P. J. Folgarait, "Ant biodiversity and its relationship to ecosystem functioning: a review," *Biodiversity and Conservation*, vol. 7, no. 9, pp. 1221–1244, 1998.

[11] L. Lach, C. L. Parr, and K. L. Abbott, *Ant Ecology*, Oxford University Press, Oxford, UK, 2010.

[12] D. Agosti, J. D. Majer, L. E. Alonso, and R. Schultz, *Ants: Standard Methods for Measuring and Monitoring Biodiversity*, Smithsonian Institution Press, Washington, DC, USA, 2000.

[13] E. C. Underwood and B. L. Fisher, "The role of ants in conservation monitoring: if, when, and how," *Biological Conservation*, vol. 132, no. 2, pp. 166–182, 2006.

[14] S. M. Philpott, I. Perfecto, I. Armbrecht, and C. L. Parr, "Ant diversity and function in disturbed and changing habitats," in *Ant Ecology*, L. Lach, C. L. Parr, and K. L. Abbott, Eds., pp. 137–156, Oxford University Press, Oxford, UK, 2010.

[15] J. D. Majer, "Ants: bio-indicators of minesite rehabilitation, land-use, and land conservation," *Environmental Management*, vol. 7, no. 4, pp. 375–383, 1983.

[16] B. D. Hoffmann and A. N. Andersen, "Responses of ants to disturbance in Australia, with particular reference to functional groups," *Austral Ecology*, vol. 28, no. 4, pp. 444–464, 2003.

[17] A. N. Andersen and J. D. Majer, "Ants show the way Down Under: invertebrate as bioindicators in land management," *Frontiers in Ecology and the Environment*, vol. 2, pp. 291–298, 2004.

[18] A. N. Andersen, A. Fisher, B. D. Hoffmann, J. L. Read, and R. Richards, "Use of terrestrial invertebrates for biodiversity monitoring in Australian rangelands, with particular reference to ants," *Austral Ecology*, vol. 29, no. 1, pp. 87–92, 2004.

[19] J. D. Majer, K. E. C. Brennan, and M. L. Moir, "Invertebrates and the restoration of a forest ecosystem: 30 years of research following bauxite mining in Western Australia," *Restoration Ecology*, vol. 15, no. 4, pp. S104–S115, 2007.

[20] C. Gómez, D. Casellas, J. Oliveras, and J. M. Bas, "Structure of ground-foraging ant assemblages in relation to land-use change in the northwestern Mediterranean region," *Biodiversity and Conservation*, vol. 12, no. 10, pp. 2135–2146, 2003.

[21] H. van Hamburg, A. N. Andersen, W. J. Meyer, and H. G. Robertson, "Ant community development on rehabilitated ash dams in the South African highveld," *Restoration Ecology*, vol. 12, no. 4, pp. 552–558, 2004.

[22] L. Ottonetti, L. Tucci, and G. Santini, "Recolonization patterns of ants in a rehabilitated lignite mine in Central Italy: potential for the use of Mediterranean ants as indicators of restoration processes," *Restoration Ecology*, vol. 14, no. 1, pp. 60–66, 2006.

[23] K. C. Fagan, R. F. Pywell, J. M. Bullock, and R. H. Marrs, "Are ants useful indicators of restoration success in temperate grasslands?" *Restoration Ecology*, vol. 18, no. 3, pp. 373–379, 2010.

[24] C. Castracani, D. A. Grasso, A. Fanfani, and A. Mori, "The ant fauna of Castelporziano Presidential Reserve (Rome, Italy) as a model for the analysis of ant community structure in relation to environmental variation in Mediterranean ecosystems," *Journal of Insect Conservation*, vol. 14, no. 6, pp. 585–594, 2010.

[25] J. R. Verdú, C. Numa, and O. Hernández-Cuba, "The influence of landscape structure on ants and dung beetles diversity in a Mediterranean savanna-Forest ecosystem," *Ecological Indicators*, vol. 11, no. 3, pp. 831–839, 2011.

[26] R. R. Silva and C. R. F. Brandão, "Formigas (Hymenoptera: Formicidae) como indicadores da qualidade ambiental e da biodiversidade de outros invertebrados terrestres," *Biotemas*, vol. 12, pp. 55–73, 1999.

[27] J. M. Queiroz, F. S. Almeida, and M. P. S. Pereira, "Conservação da biodiversidade e o papel das formigas (Hymenoptera: Formicidae) em agroecossistemas," *Floresta e Ambiente*, vol. 13, pp. 37–45, 2006.

[28] D. Baretta, Á. L. Mafra, J. C. P. Santos, C. V. T. Do Amarante, and I. Bertol, "Multivariate analysis of soil fauna under different soil tillage and crop management systems," *Pesquisa Agropecuaria Brasileira*, vol. 41, no. 11, pp. 1675–1679, 2006.

[29] A. O. Merlim, J. G. M. Guerra, R. M. Junqueira, and A. M. Aquino, "Soil macrofauna in cover crops of figs grown under organic management," *Scientia Agricola*, vol. 62, pp. 57–61, 2005.

[30] L. R. S. Lacau, R. Zanetti, J. H. C. Delabie et al., "Respostas das guildas de formigas (Hymenoptera: Formicidae) a práticas silviculturais em plantio de eucaliptos," *Agrotropica*, vol. 20, pp. 61–72, 2008.

[31] L. A. P. L. Nunes, J. A. Araújo Filho, and R. I. Q. Meneses, "Recolonização da fauna edáfica em áreas de caatinga submetidas a queimadas," *Caatinga*, vol. 21, pp. 214–220, 2008.

[32] L. S. Ramos, C. G. S. Marinho, R. Zanetti, J. H. C. Delabie, and M. N. Schlindwein, "Impact of formicid granulated baits on non-target ants in eucalyptus plantations according to two forms of application," *Neotropical Entomology*, vol. 32, no. 2, pp. 231–237, 2003.

[33] A. F. Silva, B. Meireles, J. Da Silva Rosa, M. W. De Oliveira, M. S. De Castro Morini, and A. F. De Oliveira, "Evaluation of the level of metals in Camponotus rufipes (Hymenoptera:

Formicidae) collected in different environments," *Sociobiology*, vol. 47, no. 2, pp. 293–304, 2006.

[34] K. S. Carvalho, A. L. B. de Souza, M. S. Pereira, C. P. Sampaio, and J. H. C. Delabie, "Comunidade de formigas epígeas no Ecótono Mata de Cipó, domínio da Mata Atlântica, BA, Brasil," *Acta Biológica Leopoldensia*, vol. 26, pp. 249–257, 2004.

[35] J. H. C. Delabie, V. R. L. D. M. Paim, I. C. Do Nascimento, S. Campiolo, and C. D. S. F. Mariano, "Ants as biological indicators of human impact in mangroves of the southeastern coast of Bahia, Brazil," *Neotropical Entomology*, vol. 35, no. 5, pp. 602–615, 2006.

[36] N. L. Hites, M. A. N. Mourão, F. O. Araújo, M. V. C. Melo, J. C. De Biseau, and Y. Quinet, "Diversity of the ground-dwelling ant fauna (Hymenoptera: Formicidae) of a moist, montane forest of the semi-arid Brazilian "Nordeste"," *Revista de Biologia Tropical*, vol. 53, no. 1-2, pp. 165–173, 2005.

[37] L. D. Ramos, R. Z. B. Filho, J. H. C. Delabie et al., "Ant communities (Hymenoptera: Formicidae) of the leaf-litter in cerrado "stricto sensu" areas in Minas Gerais, Brazil," *Lundiana*, vol. 4, no. 2, pp. 95–102, 2003.

[38] F. B. Endringer, I. A. Santos, M. Da Cunha Teixeira, and J. H. Schoereder, "Ant species richness in sand dune environments following burning (Hymenoptera: Formicidae)," *Sociobiology*, vol. 51, no. 2, pp. 415–423, 2008.

[39] M. C. Teixeira, J. H. Schoereder, J. T. Nascimento, and J. N. C. Louzada, "Response of ant communities to sand dune vegetation burning in Brazil (Hymenoptera: Formicidae)," *Sociobiology*, vol. 45, no. 3, pp. 631–641, 2005.

[40] K. S. Carvalho and H. L. Vasconcelos, "Forest fragmentation in central Amazonia and its effects on litter-dwelling ants," *Biological Conservation*, vol. 91, no. 2-3, pp. 151–157, 1999.

[41] J. P. Gomes, L. Iannuzzi, and I. R. Leal, "Resposta da comunidade de formigas aos atributos dos fragmentos e da vegetação em uma paisagem da floresta Atlântica nordestina," *Neotropical Entomology*, vol. 39, no. 6, pp. 898–905, 2010.

[42] M. S. Santos, J. N. C. Louzada, N. Dias, R. Zanetti, J. H. C. Delabie, and I. C. Nascimento, "Litter ants richness (Hymenoptera, Formicidae) in remnants of a semi-deciduous forest in the Atlantic rain forest, Alto do Rio Grande region, Minas Gerais, Brazil," *Iheringia - Serie Zoologia*, vol. 96, no. 1, pp. 95–101, 2006.

[43] R. C. Fonseca and E. Diehl, "Riqueza de formigas (Hymenoptera, Formicidae) epigéicas em povoamentos de Eucaliptus spp. (Myrtaceae) de diferentes idades no Rio Grande do Sul," *Revista Brasileira de Entomologia*, vol. 48, pp. 95–100, 2004.

[44] A. G. Castro and M. V. B. Queiroz, "Estrutura e organização de uma comunidade de formigas em agro-ecossistemas neotropical," *Anais da Sociedade Entomológica do Brasil*, vol. 16, pp. 363–375, 1987.

[45] N. S. Dias, R. Zanetti, M. S. Santos, J. Louzada, and J. Delabie, "Interaction between forest fragments and adjacent coffee and pasture agroecosystems: responses of the ant communities (Hymenoptera, Formicidae)," *Iheringia - Serie Zoologia*, vol. 98, no. 1, pp. 136–142, 2008.

[46] E. Diehl, D. F. Florencio, F. A. Schmidt, and L. V. A. Menzel, "Riqueza e composição das comunidades de formigas e de térmitas na floresta nacional de São Francisco de Paula (FLONA-SFP), RS," *Acta Biologica Leopondensia*, vol. 27, pp. 99–106, 2005.

[47] J. B. V. Gomes, A. C. Barreto, M. M. Michereff Filho et al., "Relationship among soil attributes and ant activity in restinga soils," *Revista Brasileira de Ciencia do Solo*, vol. 34, no. 1, pp. 67–78, 2010.

[48] C. Ilha, J. A. Lutinski, D. V. M. Pereira, and F. R. M. Garcia, "Riqueza de formigas (Hymenoptera: Formicidae) da Bacia da Sanga Caramuru, município de Chapecó-SC," *Biotemas*, vol. 22, pp. 95–105, 2009.

[49] D. M. Lapola and H. G. Fowler, "Questioning the implementation of habitat corridors: a case study in interior São Paulo using ants as bioindicators," *Brazilian Journal of Biology*, vol. 68, no. 1, pp. 11–20, 2008.

[50] C. G. S. Marinho, R. Zanetti, J. H. C. Delabie, M. N. Schlindwein, and L. D. S. Ramos, "Ant (hymenoptera: formicidae) diversity in eucalyptus (myrtaceae) plantations and cerrado litter in Minas Gerais, Brazil," *Neotropical Entomology*, vol. 31, no. 2, pp. 187–195, 2002.

[51] V. P. G. Santana-Reis and G. M. M. Santos, "Influência da estrutura do habitat em comunidades de formigas (Hymenoptera - Formicidae) em Feira de Santana, Bahia, Brasil," *Sientibus*, vol. 1, pp. 66–70, 2001.

[52] F. A. Schmidt and E. Diehl, "What is the effect of soil use on ant communities?" *Neotropical Entomology*, vol. 37, no. 4, pp. 381–388, 2008.

[53] A. A. Tavares, P. C. Bispo, and A. C. Zanzini, "Effect of collect time on communities of epigaeic ants (Hymenoptera: Formicidae) in areas of Eucalyptus cloeziana and cerrado," *Neotropical Entomology*, vol. 37, no. 2, pp. 126–130, 2008.

[54] D. L. Braga, J. N. C. Louzada, R. Zanetti, and J. Delabie, "Rapid evaluation of ant diversity in land use systems in Southern Bahia, Brazil," *Neotropical Entomology*, vol. 39, no. 4, pp. 464–469, 2010.

[55] J. D. Majer and J. H. C. Delabie, "Comparison of the ant communities of annually inundated and terra firme forests at Trombetas in the Brazilian Amazon," *Insectes Sociaux*, vol. 41, no. 4, pp. 343–359, 1994.

[56] K. A. B. Kalif, C. Azevedo-Ramos, P. Moutinho, and S. A. O. Malcher, "The effect of logging on the ground-foraging ant community in eastern Amazonia," *Studies on Neotropical Fauna and Environment*, vol. 36, no. 3, pp. 215–219, 2001.

[57] Y. J. Barros, V. de Freitas Melo, K. D. Sautter et al., "Soil quality indicators in lead mining and metalurgy area. II - mesofauna and plants," *Revista Brasileira de Ciencia do Solo*, vol. 34, no. 4, pp. 1413–1426, 2010.

[58] E. Diehl, C. E. Sanhudo, and E. Diehl-Fleig, "Ground-dwelling ant fauna of sites with high levels of copper," *Brazilian Journal of Biology*, vol. 64, no. 1, pp. 33–39, 2004.

[59] M. P. Pais and E. M. Varanda, "Arthropod recolonization in the restoration of a semideciduous forest in southeastern Brazil," *Neotropical Entomology*, vol. 39, no. 2, pp. 198–206, 2010.

[60] M. S. Coelho, G. W. Fernandes, J. C. Santos, and J. H. C. Delabie, "Ants (Hymenoptera: Formicidae) as bioindicators of land restoration in a brazilian atlantic forest fragment," *Sociobiology*, vol. 54, no. 1, pp. 51–63, 2009.

[61] C. B. Costa, S. P. Ribeiro, and P. T. A. Castro, "Ants as bioindicators of natural succession in savanna and riparian vegetation impacted by dredging in the Jequitinhonha River Basin, Brazil," *Restoration Ecology*, vol. 18, no. 1, pp. 148–157, 2010.

[62] J. D. Majer, "Ant recolonisation of rehabilitated bauxite mines of Pocos de Caldas, Brazil," *Journal of Tropical Ecology*, vol. 8, no. 1, pp. 97–108, 1992.

[63] J. D. Majer, "Ant recolonization of rehabilitated bauxite mines at Trombetas, Pará, Brazil," *Journal of Tropical Ecology*, vol. 12, no. 2, pp. 257–273, 1996.

[64] M. P. D. S. Pereira, J. M. Queiroz, R. Valcarcel, and A. J. Mayhé-Nunes, "Ant fauna as a tool for the monitoring of

a rehabilited sand mine at Ilha da Madeira, Itaguaí, RJ," *Ciencia Florestal*, vol. 17, no. 3, pp. 197–204, 2007.

[65] H. L. Vasconcelos, E. H. M. Vieira-Neto, F. M. Mundim, and E. M. Bruna, "Roads alter the colonization dynamics of a keystone herbivore in neotropical savannas," *Biotropica*, vol. 38, no. 5, pp. 661–665, 2006.

[66] K. Schmidt, R. Corbetta, and A. J. A. Camargo, "Formigas (Hymenoptera: Formicidae) da Ilha João da Cunha, SC: composição e diversidade," *Biotemas*, vol. 18, pp. 57–71, 2005.

[67] J. H. Bihn, M. Verhaagh, M. Brändle, and R. Brandl, "Do secondary forests act as refuges for old growth forest animals? Recovery of ant diversity in the Atlantic forest of Brazil," *Biological Conservation*, vol. 141, no. 3, pp. 733–743, 2008.

[68] J. H. Bihn, M. Verhaagh, and R. Brandl, "Ecological stoichiometry along a gradient of forest succession: bait preferences of litter ants," *Biotropica*, vol. 40, no. 5, pp. 597–599, 2008.

[69] J. H. Bihn, G. Gebauer, and R. Brandl, "Loss of functional diversity of ant assemblages in secondary tropical forests," *Ecology*, vol. 91, no. 3, pp. 782–792, 2010.

[70] A. G. Castro, M. V. B. Queiroz, and L. M. Araújo, "O papel do distúrbio na estrutura de comunidades de formigas (Hymenoptera, Formicidae)," *Revista Brasileira de Entomologia*, vol. 34, pp. 201–213, 1990.

[71] I. R. Leal, S. O. Ferreira, and A. V. L. Freitas, "Diversidade de formigas de solo em um gradiente sucessional de Mata Atlântica, ES, Brasil," *Biotemas*, vol. 6, pp. 42–53, 1993.

[72] F. S. Neves, R. F. Braga, and B. G. Madeira, "Diversidade de formigas arborícolas em três estágios sucessionais de uma floresta estacional decidual no norte de Minas Gerais," *Unimontes Científica*, vol. 8, pp. 59–68, 2006.

[73] F. S. Neves, R. F. Braga, M. M. Do EspíritoSanto, J. H. C. Delabie, G. W. Fernandes, and G. A. Sánchez-Azofeifa, "Diversity of arboreal ants in a brazilian tropical dry forest: effects of seasonality and successional stage," *Sociobiology*, vol. 56, no. 1, pp. 177–194, 2010.

[74] J. C. Santos, J. H. C. Delabie, and G. W. Fernandes, "A 15-year post evaluation of the fire effects on ant community in an area of Amazonian forest," *Revista Brasileira de Entomologia*, vol. 52, no. 1, pp. 82–87, 2008.

[75] R. R. Silva, R. S. Machado Feitosa, and F. Eberhardt, "Reduced ant diversity along a habitat regeneration gradient in the southern Brazilian Atlantic Forest," *Forest Ecology and Management*, vol. 240, no. 1–3, pp. 61–69, 2007.

[76] H. L. Vasconcelos, "Effects of forest disturbance on the structure of ground-foraging ant communities in central Amazonia," *Biodiversity and Conservation*, vol. 8, no. 3, pp. 409–420, 1999.

[77] H. L. Vasconcelos, J. M. S. Vilhena, and G. J. A. Caliri, "Responses of ants to selective logging of a central Amazonian forest," *Journal of Applied Ecology*, vol. 37, no. 3, pp. 508–514, 2000.

[78] M. J. Angilletta, R. S. Wilson, A. C. Niehaus, M. W. Sears, C. A. Navas, and P. L. Ribeiro, "Urban physiology: city ants possess high heat tolerance," *PLoS One*, vol. 2, no. 2, article no. e258, 2007.

[79] E. Diehl, F. Sacchett, and E. Z. Albuquerque, "Riqueza de formigas de solo na praia da Pedreira, Parque Estadual de Itapuã, Viamão, RS, Brasil," *Revista Brasileira de Entomologia*, vol. 49, pp. 552–556, 2005.

[80] I. R. Leal, A. G. D. Bieber, M. Tabarelli, and A. N. Andersen, "Biodiversity surrogacy: indicator taxa as predictors of total species richness in Brazilian Atlantic forest and Caatinga," *Biodiversity and Conservation*, vol. 19, no. 12, pp. 3347–3360, 2010.

[81] D. T. Lopes, J. Lopes, I. C. do Nascimento, and J. H. Delabie, "Epigeic ants diversity (Hymenoptera, Formicidae) in three environments in Mata dos Godoy State Park, Londrina, State of Paraná, Brazil," *Iheringia - Serie Zoologia*, vol. 100, no. 1, pp. 84–90, 2010.

[82] H. L. Vasconcelos and J. M. S. Vilhena, "Species turnover and vertical partitioning of ant assemblages in the Brazilian Amazon: a comparison of forests and savannas," *Biotropica*, vol. 38, no. 1, pp. 100–106, 2006.

[83] R. R. Silva and R. Silvestre, "Riqueza da fauna de formigas (Hymenoptera: Formicidae) que habita as camadas superficiais do solo em Seara, Santa Catarina," *Papéis Avulsos de Zoologia*, vol. 44, pp. 1–11, 2004.

[84] R. Silvestre and R. R. Silva, "Guildas de formigas da estação ecológica Jataí, Luiz Antônio – SP – sugestões para a aplicação do modelo de guildas como bio-indicadores ambientais," *Biotemas*, vol. 14, pp. 37–69, 2001.

[85] S. Groc, J. H. C. Delabie, J. T. Longino et al., "A new method based on taxonomic sufficiency to simplify studies on Neotropical ant assemblages," *Biological Conservation*, vol. 143, no. 11, pp. 2832–2839, 2010.

[86] C. A. Joly, R. R. Rodrigues, J. P. Metzger et al., "Biodiversity conservation research, training, and policy in são paulo," *Science*, vol. 328, no. 5984, pp. 1358–1359, 2010.

[87] A. Petherick, "High hopes for Brazilian science," *Nature*, vol. 465, no. 7299, pp. 674–675, 2010.

[88] K. T. R. Wilkie, A. L. Mertl, and J. F. A. Traniello, "Biodiversity below ground: probing the subterranean ant fauna of Amazonia," *Naturwissenschaften*, vol. 94, no. 9, pp. 725–731, 2007.

[89] J. H. Lawton, D. E. Bignell, B. Bolton et al., "Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest," *Nature*, vol. 391, no. 6662, pp. 72–76, 1998.

[90] C. R. Ribas, R. R. C. Solar, R. B. F. Campos, F. A. Schmidt, C. L. Valentim, and J. H. Schoereder, "Can ants be used as indicators of environmental impacts caused by arsenic?" *Journal of Insect Conservation*. In press.

[91] C. R. Ribas, F. A. Schmidt, R. R. C. Solar, R. B. F. Campos, C. L. Valentim, and J. H. Schoereder, "Ants as indicators of the success of rehabilitation efforts in deposits of gold mining tailings," *Restoration Ecology*. In press.

[92] B. T. Bestelmeyer, D. Agosti, L. E. Alonso et al., "Field techniques for the study of ground dwelling ants. An overview, description, and evaluation," in *Ants: Standard Methods for Measuring and Monitoring Biodiversity*, D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz, Eds., pp. 122–144, Smithsonian Institution Press, London, UK, 2000.

[93] J. R. Gollan, L. L. D. Bruyn, N. Reid, D. Smith, and L. Wilkie, "Can ants be used as ecological indicators of restoration progress in dynamic environments? A case study in a revegetated riparian zone," *Ecological Indicators*, vol. 11, no. 6, pp. 1517–1525, 2011.

[94] B. D. Hoffmann, "Using ants for rangeland monitoring: global patterns in the responses of ant communities to grazing," *Ecological Indicators*, vol. 10, no. 2, pp. 105–111, 2010.

[95] R. R. Dunn, "Recovery of faunal communities during tropical forest regeneration," *Conservation Biology*, vol. 18, no. 2, pp. 302–309, 2004.

[96] J. D. Majer, J. E. Day, E. D. Kabay, and W. S. Perriman, "Recolonization by ants in bauxite mines rehabilitated by a number of different methods," *Journal of Applied Ecology*, vol. 21, no. 1, pp. 255–257, 1984.

[97] J. D. Majer and O. G. Nichols, "Long-term recolonization patterns of ants in Western Australian rehabilitated bauxite mines with reference to their use as indicators of restoration success," *Journal of Applied Ecology*, vol. 35, no. 1, pp. 161–182, 1998.

[98] O. G. Nichols and F. M. Nichols, "Long-term trends in faunal recolonization after bauxite mining in the Jarrah forest of Southwestern Australia," *Restoration Ecology*, vol. 11, no. 3, pp. 261–272, 2003.

[99] D. C. Cardoso, T. G. Sobrinho, and J. H. Schoereder, "Ant community composition and its relationship with phytophysiognomies in a Brazilian Restinga," *Insectes Sociaux*, vol. 57, no. 3, pp. 293–301, 2010.

[100] M. A. McGeoch, B. J. Van Rensburg, and A. Botes, "The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem," *Journal of Applied Ecology*, vol. 39, no. 4, pp. 661–672, 2002.

[101] A. Nakamura, C. P. Catterall, A. P. N. House, R. L. Kitching, and C. J. Burwell, "The use of ants and other soil and litter arthropods as bio-indicators of the impacts of rainforest clearing and subsequent land use," *Journal of Insect Conservation*, vol. 11, no. 2, pp. 177–186, 2007.

[102] G. R. Pohl, D. W. Langor, and J. R. Spence, "Rove beetles and ground beetles (Coleoptera: Staphylinidae, Carabidae) as indicators of harvest and regeneration practices in western Canadian foothills forests," *Biological Conservation*, vol. 137, no. 2, pp. 294–307, 2007.

[103] R. A. da Mata, M. McGeoch, and R. Tidon, "Drosophilid assemblages as a bioindicator system of human disturbance in the Brazilian Savanna," *Biodiversity and Conservation*, vol. 17, no. 12, pp. 2899–2916, 2008.

[104] T. A. Gardner, J. Barlow, I. S. Araujo et al., "The cost-effectiveness of biodiversity surveys in tropical forests," *Ecology Letters*, vol. 11, no. 2, pp. 139–150, 2008.

[105] G. F. Smith, T. Gittings, M. Wilson et al., "Identifying practical indicators of biodiversity for stand-level management of plantation forests," *Biodiversity and Conservation*, vol. 17, no. 5, pp. 991–1015, 2008.

[106] Y. Basset, J. F. Mavoungou, J. B. Mikissa et al., "Discriminatory power of different arthropod data sets for the biological monitoring of anthropogenic disturbance in tropical forests," *Biodiversity and Conservation*, vol. 13, no. 4, pp. 709–732, 2004.

[107] Y. Basset, O. Missa, A. Alonso et al., "Changes in arthropod assemblages along a wide gradient of disturbance in gabon," *Conservation Biology*, vol. 22, no. 6, pp. 1552–1563, 2008.

[108] S. M. Philpott, W. J. Arendt, I. Armbrecht et al., "Biodiversity loss in Latin American coffee landscapes: review of the evidence on ants, birds, and trees," *Conservation Biology*, vol. 22, no. 5, pp. 1093–1105, 2008.

[109] M. Kessler, S. Abrahamczyk, M. Bos et al., "Alpha and beta diversity of plants and animals along a tropical land-use gradient," *Ecological Applications*, vol. 19, no. 8, pp. 2142–2156, 2009.

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 959715, 12 pages
doi:10.1155/2012/959715

Research Article

Annual and Seasonal Changes in the Structure of Litter-Dwelling Ant Assemblages (Hymenoptera: Formicidae) in Atlantic Semideciduous Forests

Flávio Siqueira de Castro,[1, 2] Alexandre Bahia Gontijo,[1, 2] Paulo de Tarso Amorim Castro,[3] and Sérvio Pontes Ribeiro[1, 2]

[1] *Laboratory of Evolutionary Ecology of Canopy Insects and Natural Succession, Department of Biodiversity, Evolution and Environment, Federal University of Ouro Preto, 35400-000 Ouro Preto, MG, Brazil*
[2] *Post-Graduate Program in Ecology of Tropical Biomes, Department of Biodiversity, Evolution and Environment, Federal University of Ouro Preto, 35400-000 Ouro Preto, MG, Brazil*
[3] *Departament of Geology, Federal University of Ouro Preto, EM/ Universidade Federal de Ouro Preto, 35400-000 Ouro Preto, MG, Brazil*

Correspondence should be addressed to Flávio Siqueira de Castro, fsiqueiradecastro@gmail.com and Sérvio Pontes Ribeiro, spribeiro@iceb.ufop.br

Received 1 June 2011; Revised 12 August 2011; Accepted 13 August 2011

Academic Editor: Jacques H. C. Delabie

We surveyed ant fauna in the leaf litter in an Atlantic Semideciduous forest in the State Park of Rio Doce (PERD). The work aimed to produce basic information about habitat effects on diversity, as well as about how the ant fauna in a such buffered forest habitat, as the litter layer, could respond the climate variation in a short and long term. We sampled two years in two distinct forest physiognomies, which respond to different geomorphologic backgrounds, in dry and rainy seasons. Species composition, richness and abundance of these forests were distinct. However, both forests hosted similar numbers of rare and specialized, habitat demanding species, thus suggesting both are similarly well preserved, despite distinct physiognomies. However, the lower and more open forest was, more susceptible to dry season effects, showing a steeper decline in species numbers in such season, but similar numbers in the wet seasons. The pattern varied between years, which corroborates the hypothesis of a strongly variable community in response to subtle climatic variation among years. The present results are baselines for future long term monitoring projects, and could support protocols for early warnings of global climatic changes effects on biodiversity.

1. Introduction

Species richness and composition respond to different habitat variables and abiotic factors that influence climate, seasonality, humidity, topography, and lithology [1–4]. The construction of the concept of "habitat components" is based on the interactions between abiotic and biotic variables, which result in the parameters on which the niches of species evolve [5]. One habitat component which is hardly studied is its temporal variance, due to the fact that it is highly unpredictable [6].

Forest litter is a crucial habitat compartment for mineral cycling, humidity retention, and, greatly, to biodiversity maintenance [7, 8]. Conversely, the insect fauna that dominates the litter is a fundamental factor for its transformation. In a whole tropical forest, ants and termites are the most important animals in relation to biomass and relative abundance. Ants are found in virtually all strata of forests, playing a key role in structuring ecological communities in tropical ecosystems [9]. They are responsible for processes of soil mineralization due to its extensive bioturbation activity [10], promoting changes in physical environments [7], and, consequently, a vast movement of nutrients [8, 11]. Furthermore, an ant assemblage responds positively to natural succession [12–14], causing feedback responses, such as plant species dispersal and seed collecting [15–17]. They are also responsible for important predation rates on tropical forests (e.g., army ants) [11].

For ant assemblages, the negative effects of low temperature [18], intense rainfalls (daily and cumulative), plus the positive effects of high relative humidity of the understorey and forest ground, influence directly the foraging and nesting [19]. The effect of intense rainfall may occur due to interference in the communication process between individuals, by literally washing down the worker's chemical trails, or by flooding areas with soils less susceptible to drainage [20]. Thus, these factors affect many phenological activities in the colonies [20, 21] and are crucial parameters in structuring ground-dwelling ant assemblages in tropical forests [18–20]. Additionally, it may have confounding positive effects with the rainfall, such as increasing humidity or increasing the litter volume [22], thus resulting in a difficulty to evaluate the real effects on the ants assemblages.

Therefore, the way how seasons and years (namely general weather conditions) should affect ant species parameters along time must be highly variable and unpredictable. Campos et al. [23] have shown that arboreal ant assemblage in an Atlantic semideciduous forest, in the State Park of Rio Doce, responded as strongly to host trees as to time passing, and more significantly than to seasonality. Further, the authors observed that changes in ant fauna was not affected by the host plant habitat specificities, such as being in a forest artificial border, within the forest, or in a natural lake ashore. In other words, ant species composition and relative density may respond to more subtle components of the environment.

In the present study, we aimed to evaluate the effects of habitats and temporal variation on the litter-dwelling ant species richness, abundance, and composition in this same semideciduous Atlantic forest. In order to investigate the hypothesis that temporal variation may have stronger effect than habitat specificities, we sampled in two contrasting forest physiognomies, in two different geomorphologic backgrounds.

2. Materials and Methods

2.1. Study Sites. Samples were taken in the State Park of Rio Doce (PERD-IEF), Marliéria, Minas Gerais. This is approximately 36,000 ha of protected forests and lakes, comprising part of the municipalities of Timóteo, Marliéria, and Dionísio—between the parallels 19 48 18 –19 29 24 S and meridians 42 38 30 –42 28 18 W. The park is bound in the East by the Doce River and Piracicaba River to the North [24]. The vegetation is characterized as lower montane Atlantic semideciduous forest, with a percentage of deciduous trees between 20 and 50% [25, 26]. The forest varies greatly in physiognomy and soil conditions from north to south. Also, the park preserves the largest natural lake system in the Atlantic rainforest domain (10% of its area) that resulted from geological movements around the old Doce river and affluents during the Pleistocene [27].

The climate is tropical humid mesothermal [28]. The wet season occurs from October to March and the dry season from April to September [29]. Samples were taken in August (dry season) and November (rainy season) in the years of 2005 and 2006, in two different areas: the Lagoa do Gambazinho's IMA (Integrated Monitoring Array) (hereafter LG) (southern PERD) and the Trilha Macuco ou Juquita's IMA (hereafter TM) (northern PERD) (Figure 1).

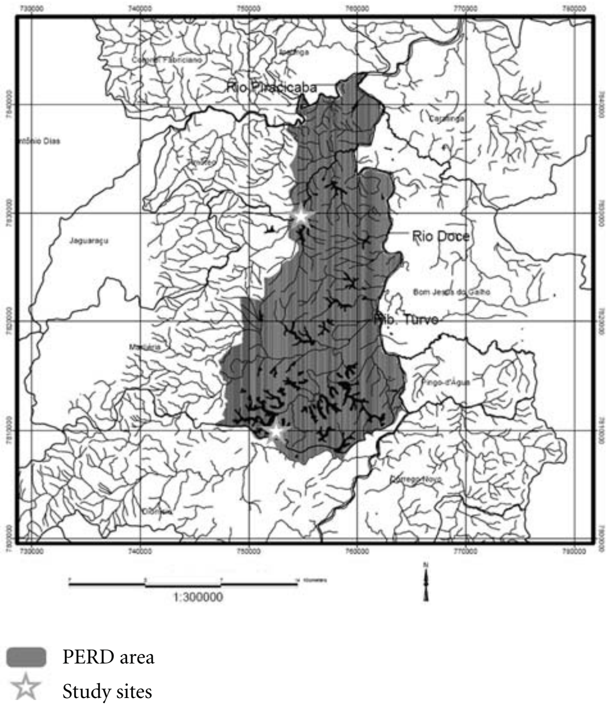


Figure 1: Map showing the location of the PERD and the study sites in relation to the surrounding region. Star at the north showing the location of Macuco's IMA (TM) and at the south showing the Gambazinho's IMA (LG) (Source: [22].)

The LG is composed by a secondary, edaphically constrained low forest vegetation (10–15 m high) [30] in an area with irregular topography, varying from hills to lowlands, with permanent and temporary swamps [31]. In the TM, there is a predominance of high and medium forest in the lowlands and medium forests in the slopes and crests, with little topographic variation, but the presence of alternating hills and lowlands. The whole area of the TM is in an old alluvial terrace, the paleochannel of the Belem River (tributary of Doce River), while LG has a distinct geological unit, and this entire area lies on a unit called litostatigragphic Mantiqueira Complex [31].

2.2. Sampling Design. The study areas are two permanent plots of 100 ha (IMA) produced during the Rio Doce TEAM Project, a long-term project coordinated by the Conservation International through the TEAM (Tropical Ecology, Assessment, and Monitoring) Initiative network [32]. The samples used in this work are part of Rio Doce TEAM Project—Ant Protocol [33]. The chosen areas are permanent plots set to attend several projects, and transects were easily set in a full random design due to the existence of open narrow research paths. Eight transects were sampled per season in both areas,

Table 1: Number of hits (records) and overall frequency (%) of ant species per IMA, LG, and TM.

Species	2005				2006				Frequency (%)
	LG		TM		LG		TM		
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	
Solenopsis (*Diplorhoptrum*) sp1	27	26	23	27	34	36	3	26	63.13
Pyramica denticulata (Mayr, 1887)	21	16	1	15	27	22	19	19	43.75
Brachymyrmex australis Forel, 1901	12	22	12	28	4	22	13	18	40.94
Strumigenys elongata Roger,1863	13	9	6	12	21	13	16	18	33.75
Hypoponera trigona (Mayr, 1887)	16	1	8	9	13	15	24	19	32.81
Pheidole diligens Smith F., 1858	1	7	11	15	11	21	15	24	32.81
Odontomachus meinerti Forel, 1905	12	11	8	19	19	7	15	12	32.19
*Solenopsis (Diplorhoptrum)*sp5	29	7	24	6	13	3	11	4	30.31
Hypoponera distinguenda Emery, 1890	13	12	1	11	18	19	12	7	29.06
Pheidole cf. *flavens* Roger, 1863	5	14	3	1	18	16	16	9	25.63
Crematogaster longispina Emery,1890	1	4	13	5	17	5	17	8	21.88
Wasmannia auropunctata (Roger,1863)	9	6	6	4	26	1	11	1	20.00
Strumigenys cf. *silvestrii* Emery, 1906		13	11	11	2		9	16	19.38
Pheidole cf. *dimidiata* (Emery, 1894)	1	6	2	1	6	17	5	18	17.50
Pheidole midas Wilson, 2003	7	11	2	5	1	9	9	11	17.19
Carebarella sp1	5	2	2	8	11	4	14	8	16.88
Sericomyrmex cf. *bondari* Borgmeier, 1937	14	5	1	9	5	12	6	1	16.56
Apterostigma gp. *pilosum* Mayr, 1865	6	8		1	11	4	13	3	14.38
Solenopsis (Diplorhoptrum) sp2	4	7	5	13	3		6	8	14.38
Brachymyrmex longicornis Forel, 1907		1	13	9			9	12	13.75
Pachycondyla gp. *harpax* (Fabricius,1804)	9	4	6		2	5	3	3	10.00
Solenopsis sp4	1		1	11			7	11	9.69
Pheidole cf. *minutula* Mayr, 1878	1		5	8	4		1	11	9.38
Brachymyrmex sp3	15	1			8	5			9.06
Pyramica crassicornis (Mayr,1887)	6	5	1	3		4	1	9	9.06
Cyphomyrmex tranversus Emery, 1894	1	1	1		4	5	7	8	8.44
Octostruma iheringi (Emery,1888)	2	1	1	1	2	7	5	7	8.13
Crematogaster (Orthocrema) sp6	3		7	4	5	2	1	3	7.81
Hylomyrma reitteri (Mayr,1887)	3	5		2	3	9		3	7.81
Solenopsis cf. *terricola* Menozzi, 1931	4	5		3	2	3	3	5	7.81
Octostruma rugifera (Mayr, 1887)		4		5		5		8	6.88
Hypoponera sp6	3	5	1	1	1	9		1	6.56
Pyramica eggersi (Emery,1890)		1			1	11	5	2	6.25
Crematogaster nigropilosa Mayr, 1887	6	7		5		1		1	6.25
Mycocepurus smithii Forel, 1893	1	3	1	3	3	2	2	4	5.94
Carebara panamensis (Wheeler, 1925)	2	2			1	4	4	5	5.63
Rogeria besucheti Kluger, 1994	2	1			4	2	4	5	5.63
Discothyrea sexarticulata Borgmeier,1954	1	2		5			4	5	5.31
Megalomyrmex modestus Emery, 1896	2	3	1	3			2	6	5.31
Crematogaster limata Smithi F., 1858	3	4		6		1	1	1	5.00
Paratrechina sp4	1			1	7	2	4		4.69
Ectatomma permagnum Forel, 1908	3	1	1	3	2		3	1	4.38
Brachymyrmex heeri Forel, 1874	6	5	1	1					4.06
Octostruma cf. *balzani* (Emery, 1894)		2		4		6	1		4.06
Carebara urichi (Wheeler, 1922)	1	1		2	1	1	1	5	3.75

Table 1: Continued.

Species	2005				2006				Frequency (%)
	LG		TM		LG		TM		
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	
Dolichoderus imitator Emery, 1894	4		4		3		1		3.75
Acromyrmex subterraneus brunneus Forel, 1912	2	2	2	1	1		3		3.44
Camponotus (Tanaemyrmex) punctulatus andigenus Emery, 1903		1	3		3	1	2	1	3.44
Hylomyrma sp2		2		1	1	3		4	3.44
Pyramica sp5	1	5				5			3.44
Strumigenys perparva (Brown, 1958)	1		1		1	1	5	1	3.13
Megalomyrmex drifti Kempf, 1961	3	4	1	1			1		3.13
Pheidole sp9						4		6	3.13
Brachymyrmex sp5	3	6							2.81
Ectatomma tuberculatum (Olivier,1792)	2		1	1	3		2		2.81
Pachycondyla venusta Forel, 1912	1		2	1	1	1		3	2.81
Pyramica alberti (Forel, 1893)				3			6		2.81
Pyramica brevicornis (Mann, 1922)		1	1	2	3	1	1		2.81
Brachymyrmex cf. *pictus* Mayr, 1887	2		1		1		4		2.50
Ectatomma suzanae Almeida, 1986	3			1			3	1	2.50
Hypoponera foreli (Mayr, 1887)	3	1	1		1		2		2.50
Hypoponera cf. *punctatissima* (Roger 1859)				2			6		2.50
Prionopelta antillana Forel, 1909	1			1	2		2	2	2.50
Pyramica subedentata (Mayr, 1887)	2			1	1		2	2	2.50
Trachymyrmex cornetzi Forel, 1912	1		1		1	3	1	1	2.50
Hypoponera sp8		3	2		2				2.19
Odontomachus haematodus (Linnaeus,1758)	1		3		1		1	1	2.19
Wasmannia cf. *sigmoidae* (Mayr, 1884)							7		2.19
Acanthognathus ocellatus Mayr, 1887		1	1	1				3	1.88
Brachymyrmex sp7	5				1				1.88
Myrmicocrypta squamosa Smith F., 1860		1		2	2	1			1.88
Pachycondyla gilberti Kempf, 1960		1			1	1	1	2	1.88
Pheidole sp13		3		2		1			1.88
Pyramica maynei (Forel, 1916)		3				2		1	1.88
Solenopsis sp16			1	3	2				1.88
Strumigenys precava (Brown, 1954)	1	2					2	1	1.88
Acropyga goeldii Forel, 1893		1						4	1.56
Apterostigma sp5					3		2		1.56
Brachymyrmex sp4	4					1			1.56
Camponotus (Tanaemyrmex) melanoticus Emery, 1894	1	1			1	2			1.56
Megalomyrmex goeldii Forel, 1912		5							1.56
Pheidole sp12	5								1.56
Solenopsis sp6	2	3							1.56
Linepithema pulex Wild, 2007	1		1	1	1			1	1.56
Wasmannia sp3	1	1	2						1.25
Cryptomyrmex longinodus Férnandez & Brandão, 2003		2				2			1.25
Amblyopone lurilabes Lattke, 1991				1		2		1	1.25
Crematogaster acuta (Fabricius,1804)		4							1.25

Table 1: Continued.

Species	2005				2006				Frequency (%)
	LG		TM		LG		TM		
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	
Gnamptogenys porcata (Emery,1896)		1					1	2	1.25
Paratrechina steinheili (Forel, 1893)		1	3						1.25
Pheidole sp14	1			1				2	1.25
Pheidole sp16			1					3	1.25
Wasmannia rochai Forel, 1912			1	1		1		1	1.25
Amblyopone cf. *armigera* Mayr, 1897	1						1	1	0.94
Brachymyrmex sp8					1	2			0.94
Camponotus (Mymocladoecus) latangulus Roger, 1863		2		1					0.94
Camponotus (Myrmophaenus) novogranadensis Mayr, 1870	1	1		1					0.94
Crematogaster sp3	2					1			0.94
Cyphomyrmex peltatus (Kempf, 1966)		1					2		0.94
Eurhopalothrix prox. *bruchi* Santischi, 1922		1		1			1		0.94
Gnamptogenys gracilis (Santischi, 1929)	1							2	0.94
Octostruma sp4				1		1		1	0.94
Paratrechina sp6					1		2		0.94
Solenopsis sp14				2				1	0.94
Trachymyrmex prox. *relictus* Borgmeier, 1934			1		1		1		0.94
Azteca cf. *alfari* Emery, 1893	1	1							0.63
Camponotus femoratus (Fabricius,1804)		1						1	0.63
Cephalotes pusillus (Klug,1824)	1		1						0.63
Crematogaster curvispinosa Mayr, 1862	2								0.63
Hylomyrma sp3	1						1		0.63
Hypoponera sp12	1	1							0.63
Megalomyrmex silvestrii Wheeler W.M., 1909				1		1			0.63
Mycocepurus goeldii Forel, 1893	2								0.63
Myrmelachista (Hincksidris) sp2			1		1				0.63
Pachycondyla verenae (Forel, 1922)	1					1			0.63
Pheidole sp4					1			1	0.63
Pseudomyrmex tenius (Fabricius, 1804)			2						0.63
Rogeria microma Kempf, 1961	2								0.63
Solenopsis sp3						2			0.63
Stegomyrmex olindae Feitosa, Brandão & Diniz, 2008							2		0.63
Wasmannia cf. *lutzi* Forel, 1908	2								0.63
Acanthognathus prox. *rudis* Brown & Kempf, 1969		1							0.31
Acropyga smithii Forel, 1893						1			0.31
Anochetus diegensis Forel, 1912				1					0.31
Brachymyrmex sp9					1				0.31
Camponotus (Tanaemyrmex) balzani Emery, 1894		1							0.31
Camponotus (Myrmoclaedocus) bidens Mayr, 1870			1						0.31
Camponotus (Mymocladoecus) crassus (Mayr, 1862)			1						0.31
Camponotus (Mymocladoecus) rectangularis Emery, 1890	1								0.31

Table 1: Continued.

Species	2005				2006				Frequency (%)
	LG		TM		LG		TM		
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	
Camponotus (Myrmobrachys) trapezoideus Mayr, 1870		1							0.31
Carebara pilosa Férnandez, 2004								1	0.31
Cephalotes maculatus (Smith F.,1876)	1								0.31
Cerapachys splendens Borgmeier, 1957		1							0.31
Crematogaster sp8								1	0.31
Dolichoderus lutosus Smith F., 1858				1					0.31
Eciton burchelli (Westwood, 1842)		1							0.31
Gnamptogenys sp3					1				0.31
Heteroponera angulata Borgmeier, 1959		1							0.31
Hypoponera sp10					1				0.31
Hypoponera sp13		1							0.31
Hypoponera sp17							1		0.31
Labidus coecus (Latreille, 1802)		1							0.31
Linepithema iniquum (Mayr, 1870)			1						0.31
Myrmelachista sp1	1								0.31
Myrmelachista sp3							1		0.31
Neivamyrmex sp1						1			0.31
Nesomyrmex spininoidis Mayr, 1887	1								0.31
Nesomyrmex wilda Smith M.R., 1943			1						0.31
Pachycondyla ferruginea Smithi F., 1858		1							0.31
Pachycondyla villosa inversa Smith F., 1858							1		0.31
Pheidole fallax Mayr, 1870							1		0.31
Pheidole sp17					1				0.31
Pseudomyrmex gp. *pallidus* Smith F., 1855			1						0.31
Pyramica appretiata (Borgmeier, 1954)		1							0.31
Rogeria scobinata (Kluger, 1994)		1							0.31
Solenopsis (Euophthalma) globularia Smith F., 1858				1					0.31
Solenopsis sp15								1	0.31
Strumigenys sublonga Brown, 1958							1		0.31
Strumigenys schmalzi Emery, 1905		1							0.31
Wasmannia villosa Emery, 1894					1				0.31

thus 16 per year, with 10 samples of 1 m^2 litter per transect, using the apparatus of Mini-Winkler [34], equidistant 10 m one from another, summing up 320 samples on two years. Each transect had its exact position previously sorted using random numbers and a plotted map of the transect, thus assuring a fully random sampling design.

Ants were taken to the lab, sorted, and identified to genera. Species confirmations were achieved in collaboration with the Myrmecological laboratory of CEPLAC, Bahia. The collection is saved in both CEPLAC and in the collection of the Laboratory of Evolutionary Ecology of Canopy Insects, in DEBIO/ICEB/UFOP.

2.3. Data Analysis. In order to evaluate the effect of accumulation of species in each sampling unit and for all observed data, we made species accumulation curves (Coleman method), which devise the expected richness for random subsamples of the data set grouped [35, 36]. Calculations were made using the computer program EstimateS version 8 [35]. The Coleman curve is essentially the same to a rarefaction curve and more efficient computationally [37, 38]. The Abundance-based Coverage Estimator (ACE) was used as estimator of species richness [35, 39], because the coefficient of variation (CV) was larger (CV = 0.519) than abundance distribution. When the CV was larger than CV > 0.5, Chao [39] and Colwell [35] recommend Chao 1 and ACE as the best estimates for abundance-based richness.

A nonsmetric multidimensional scale analysis (NMDS) was used to demonstrate overall differences in species composition between the two areas. The ordination was carried out for the data on species presence and absence in each plot, using the Jaccard index. We used analysis of similarities (ANOSIM) [40] to test for differences in species composition between areas. In order to investigate patterns of similarity between the ant communities in both areas, we used the relative differences between R-value of the ANOSIM test [41]. These analyses were performed using the software PAST [42].

Factorial analysis of variance (ANOVA) models [43], with Poisson distribution of data (which is automatically log-transformed in the model in order to best fit the distribution) [44], were used to analyse the results. The statistical package GLZ-Generalized Linear/Nonlinear Models (Statsoft Statistica 7.0 software) was used when generating analyses of the frequency of occurrence of ants (number of records) and the total number of species for each sample (transect) in different areas, seasons, and between years. Wald's test was used to verify the true parameter value based on the sample estimate, assuming that the value of $P < 0.05$ is significant. The measures of relative abundance (frequency of species per transect) were based on the number of occurrences of species per point (each 1 m^2 of the transect), summing up 10 possible occurrences of each species per transect, or 40 per season/IMA.

3. Results

In total 2851 individuals, 48 genera and 160 morphospecies were identified and recorded, belonging to 11 subfamilies: Amblyoponinae, Cerapachyinae, Dolichoderinae, Ecitoninae, Ectatomminae, Formicinae, Heteroponerinae, Myrmicinae, Ponerinae, Proceratiinae, and Pseudomyrmicinae. Most of species and genera found belong to the subfamily Myrmicinae, followed by Formicinae and Ponerinae. Only four of the 11 subfamilies of ants were not common to the two areas: Cerapachyinae, Ecitoninae, and Heteroponerinae were found only in the TM, while Pseudomyrmicinae was found only in LG.

The number of genera occurrences was very similar between the two sites. LG showed 40 genera, being four habitat-specific genera: *Cephalotes*, *Myrmelachista, Pseudomyrmex,* and *Stegomyrmex*. TM had 44 genera, eight habitat-specific genera: *Acropyga, Anochetus, Cerapachys*, *Cryptomyrmex, Eciton*, *Heteroponera*, *Labidus,* and *Neivamyrmex* (Table 1). In both areas, we found typical litter-forest genera (*Stegomyrmex* in LG, *Cerapachys* and *Cryptomyrmex* in TM), typical forest species or species only recently described, for example, *Wasmannia villosa* and *Stegomyrmex olindae* in LG, and the typical soil ant *Cerapachys splendens* and *Cryptomyrmex longinodus* in TM. New species for science, being in process of description, were also found, as *Hylomyrma* sp2 (MZUSP).

Species richness did not reach stabilized at the end of the sampling, even after combining all samples ($n = 32$; Figure 2). The total species richness of the ant community per transect (1 ha) was estimated to be around 200 species, and rare-faction curve was reached to be around 160 species (Coleman's method) (Figure 2). For both IMA, species richness was similar (rarefied species richness for 122 occurrences Coleman method = 4.22 ± 1.63 for LG and 4.27 ± 1.53 for TM, Figure 2). However, differences in species composition were detected among areas, as revealed by NMDS (ANOSIM, $R = 0.23$, $P < 0.001$; Figure 3).

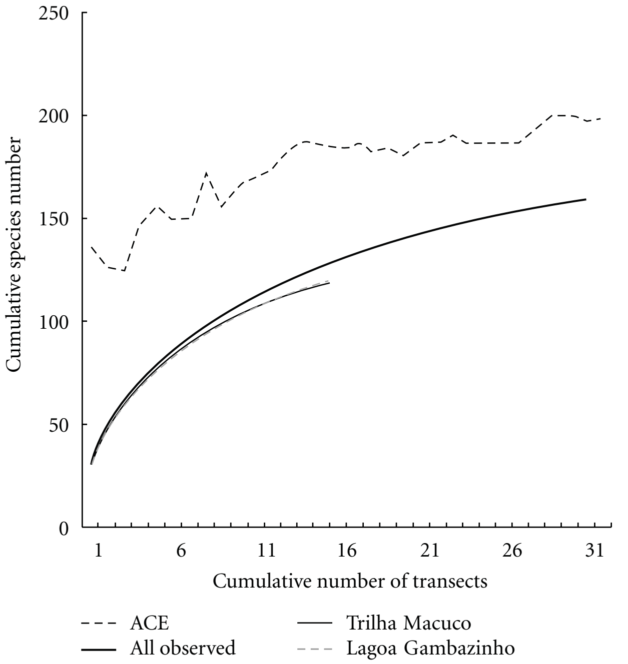


Figure 2: Accumulation curve of species richness (obtained by Coleman's method) for all sampling (solid black line), for Lagoa Gambazinho (dashed grey line), and for Trilha Macuco (thin black line). The overall species richness for both IMAs was estimated with Chao 2.

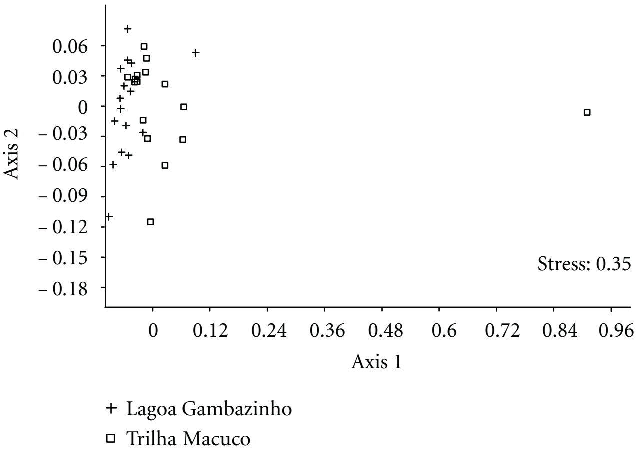


Figure 3: NonMetric Dimensional Scale (NMDS) ordination of species composition of the ant community in both IMA as sampled by Mini-Winkler.

Regardless seasonal and yearly variations, species richness was very similar between both areas (Factorial ANOVA, Wald $X^2(1) = 1.06$, $P = 0.30$). The LG had 126 species, 36 of these habitat-specific species, and the TM showed 124 species and 35 habitat-specific species (Figure 4 and

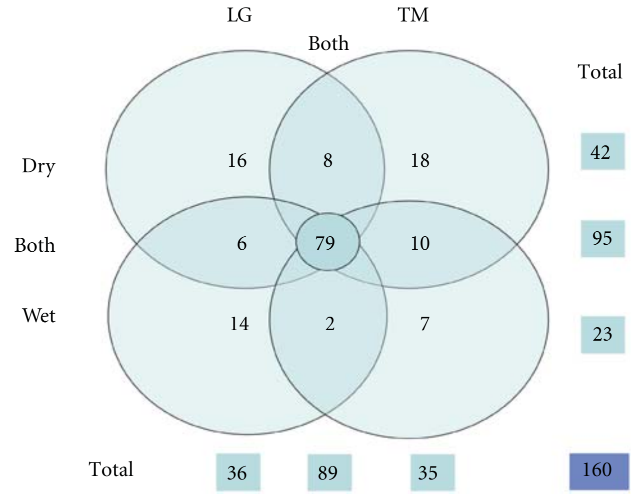


Figure 4: Diagram representing the number and distribution of ant species in both IMA (Lagoa Gambazinho and Trilha Macuco) and in two seasons (dry and wet). Separation criteria were unique to each of the IMA and weather stations (large circles), collected in both IMA (intersections of top and bottom), collected in two seasons (intersections of left and right), and collected in two IMA and in two seasons or in at least one weather station (central circle).

Table 1). However, the species richness found were quite different between the dry period (42 species) and the rainy season (24 species), and this difference was due to a strong reduction of species in LG, the low and more open forest, during the dry periods (Figure 5(a)). It is worth to notice that there were more species in common between the areas during the dry season than in rainy season. Species such *Azteca* cf. *alfari*, *Brachymyrmex* cf *pictus*, *B.* sp5, *Camponotus* (*Tanaemyrmex*) *balzani*, *Paratrechina steinheili*, *Hypoponera* sp12, *Solenopsis* sp5, and *Wasmannia* sp3 were found only in the dry season, while *Brachymyrmex* sp8 and *Pheidole* sp4 were found only in wet season (Figure 4 and Table 1). Species richness declined in the LG in the dry season, when compared to TM or to itself in the rainy season, but only for 2006 (Factorial ANOVA, Climatic Season Year, Wald $X^2(1) = 6.81$, $P = 0.009$; Figure 5(a)). The inconsistency of this decline in 2005 resulted in a lack of significant differences in species richness between areas (Factorial ANOVA, Wald $X^2(1) = 0.46$,$P = 0.50$; Factorial ANOVA, IMA Climatic Season Year, Wald $X^2(1) = 0.50$, $P = 0.48$) (Figure 5(a)).

A similar interaction effect between area and year effects (Factorial ANOVA, IMA Year, Wald $X^2(1) = 7.34$, $P = 0.006$) and the effects of season and year (Factorial ANOVA, Climatic Season Year, Wald $X^2(1) = 17.70$, $P = 0.00003$) defined the variance in ant abundance between the areas. Likewise species richness, the ant abundance declined strongly in the dry season of 2006 and only. In the present case, the strength of this interaction was perceptible in the three levels, thus reflecting in the mean numbers of ants between areas, greater in the TM, the tallest forest (Factorial ANOVA, IMA Climatic Season Year Wald, $X^2(1) = 5.02$, $P = 0.02$; Figure 5(b)).

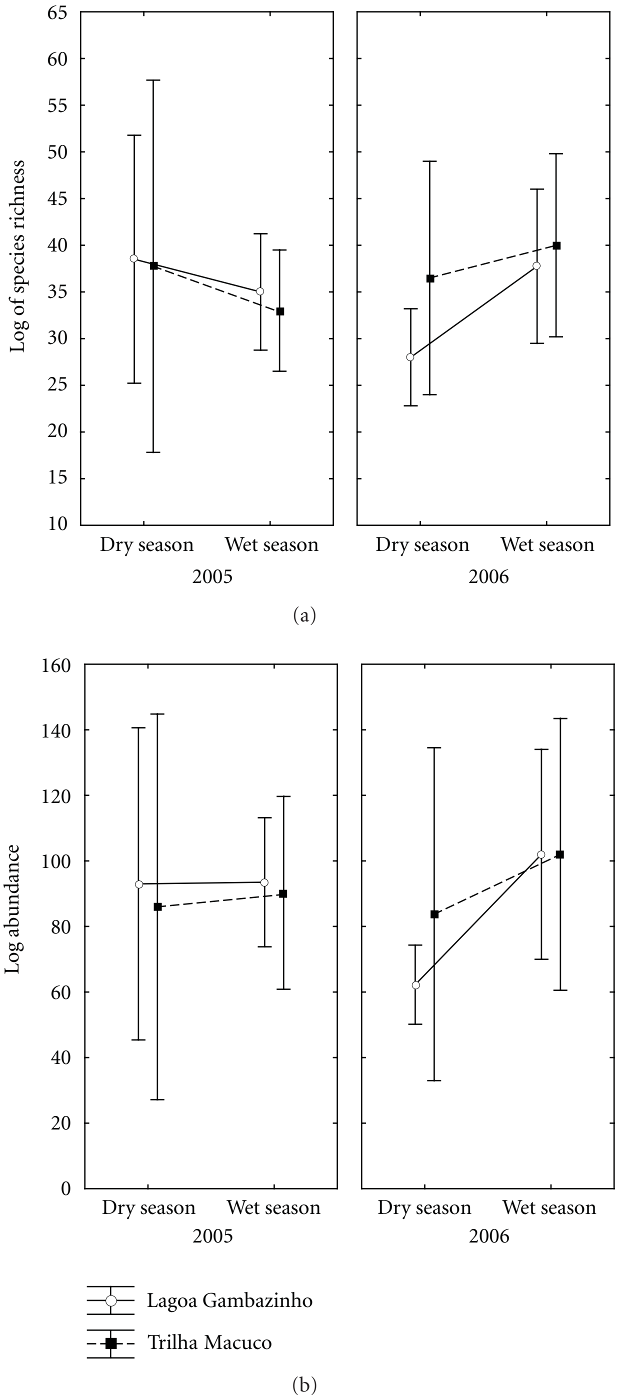


Figure 5: Species richness (a) and relative abundance (b) (number of occurrences on transects) of ant species in both IMA, in two seasons (dry and wet), and in two years (2005 and 2006).

The overall mean abundance was also very similar between areas (Factorial ANOVA, Wald $X^2(1) = 1.46$, $P = 0.23$). The 10 most abundant species throughout the sampling were *Solenopsis* sp1, followed by *Pyramica denticulata*, *Brachymyrmex australis*, *Hypoponera trigona*, *Strumigenys* *elongata*, *Pheidole diligens*, *Odontomachus meinerti*, *H. distinguenda*, *S.* sp5, and *P.* cf. *flavens*. However, at LG, the species *B. australis* and *P. diligens*, were not among the most abundant species. In this area, besides the other eight previously mentioned, we found *Crematogaster longispina* and *Wasmannia auropunctata* amongst the most abundant. In the TM, *Solenopsis* sp5 was not as abundant as the others, while *P.* cf. *dimidiata* was found among the most abundant. Regarding rare species, the LG presented 36 species, 20 of these were habitat-specific species, while in TM were 33 rare species, and also 20 habitat-specific species (Table 1).

As observed for relative abundance, there was an increase in species richness in the wet season in both areas. However, despite low species richness in the dry season, species composition varied smoothly between years in both areas. The data of the rainy season in LG, for example, showed that the total number of species increased from 67 to 72 in a year to another, and the number of rare species (singletons) decreased from 26 to 21 species (38.8% to 29.2% of species). Values of relative abundance (number of occurrences per sampling event, or 4 transects and 40 points for either season/IMA) of intermediate species (species that were neither among the 10 most abundant or among singletons) varied greatly between years (Table 1), which was related to the variation in numbers of predatory ants species richness and abundance.

4. Discussion

The global ground-dwelling ant diversity in Rio Doce was remarkably high, as well as composed of rare and habitat-demanding species and genera (see below). The ant species richness in the forest litter was substantially higher than ants or general arthropods species in the canopy of these same forests [23, 45, 46]. In addition, it was comparably as high as in other tropical forests and sometimes comparable to the species richness found and wetter and closer equatorial forests [13, 19, 36, 38].

In spite of differences in physiognomy and geomorphology found in both areas, the overall mean values of species richness and abundance were not statistically different between these forest types, although there were substantial differences in relation to species composition. However, one could expect to sample more species, especially rare predators and cryptic specialists species in TM than in the LG, due to the tree heights, a better structured understorey, apparent constancy of conditions in the former compared to the latter. These conditions should allow high availability of resources and quality of sites for feeding and nesting areas [47, 48]. The TM pristine semideciduous forest was denser in trees, which also had larger basal area than the open, apparently secondary LG [31]. Among many other ecological implications, these traits imply in greater litter biomass in TM compared to LG.

In a close wet and tall forest, there might have less variation in abiotic conditions, such as local atmospheric humidity and temperature [19], and, sometimes, as is the case of PERD, this may be further buffered by a smooth and continuous topography [31]. On the other hand, ecological variables such as increased litter production in association with the high heterogeneity of the vegetation may also happen in association to close and tall forests [49], which results in high spatial complexity, allowing diversification of conditions, thus sheltering a large number of species of ants and other invertebrates in the litter and soil [31, 45, 48, 50–52]. Other studies in tropical forests have corroborated that differences of litter ants species diversity and distribution respond to habitats with low and high structural heterogeneity [53–55].

Hence, TM should have the best conditions for more habitat-demanding ant species than LG, unless the habitat conditions in the latter are rather natural too. The region around LG has indeed a more open canopy and lower tree heights than TM, but the cause for its physiognomic pattern is subject of debate. Although the area was impacted by a fire in 1967, there would have been time enough for full recover. Soares [31] and Ribeiro et al. [46] have discussed that a great deal of the observed differences in vegetation are natural rather than result of human past disturbance. Data suggest that physiognomic differences between the two studied areas are evolutionary rather than ecological, and both may sustain equivalent levels of heterogeneity. Indeed, the geomorphologic origins of both forests ought to have stronger effect on their productivity and then on their canopy traits that relate to understorey microclimate and heterogeneity. Hence, despite apparent vulnerability of LGs and its low resistance to the dry season extreme desiccation, both forests are equivalently rich and populated with ecologically demanding species. Such pattern only could happen if both places had long enough favourable conditions for species evolution.

The occurrence of rare species of ants in the LG, for example, *Stegomyrmex olindae*, so far found only in humid and mature forests [56], *Cryptomyrmex longinodus* (first occurrence in the southeastern Brazil; Fernández, personal communication), *Strumigenys sublonga* (cryptic species collected by first time in tropical semideciduous forest in Minas Gerais, Castro unpublished data), *Eurhopalothrix* prox. *bruchi,* and *Octostruma* species, support that this forest, whatever the human impacts suffered in the past, has several ant species typical of environments with greater habitat structural complexity and a well-preserved long evolutionary history. It is quite likely that edaphic-evolving condition found in the LG forest is the best explanation for the fact. This also may explain the fact that there is not any widely distributed tall and closed forest in southern PERD as a whole.

Seasonal effects are important regulators of ecological communities in tropical forests, especially plants and invertebrates [5]. Seasonal effects were more perceptible in 2006 than in 2005, concerning both species richness and abundance. According to PERD climatic station data and our microclimatic records, the 2005 had a dry season with little rainfall, mild air temperatures, and high mean relative humidity, rising up to 80% in the winter driest days. The year of 2006 was characterized by a dry season hotter than 2005, regarding air temperature in the understorey, with abrupt changes in rainfall regimen, unlike 2005, even though we sampled exactly in the same time of the year. For instance, it rained practically every day in August 2006 (a usually very dry month), while in 2005 rainfall was recorded in only four days during the same month. In the rainy season, in relation to data of temperature and humidity, there was no significant dispatch from the expected and the understorey reached values at or near 100% relative humidity in both years. However, in November 2005, the accumulated rainfall index ranged from 312.5 to 330.61 mm (daily rain 89 ± 4 mm), while in 2006, it ranged from 48.43 to 29.99 mm (daily rain 17 ± 5 mm) [57].

These data suggest that in 2006, the rainy season started abnormally earlier (in August). In tropical forests, the cycle of ants colonies is synchronized with the seasonal rainfall and temperature [21], and, although the mechanism is not well known, in the more humid and hot (above 30 C and 50% of relative humidity), the faster is the development of ant colonies [20]. Nevertheless, the unpredictable start of rains may have a very negative effect in some habitats, by taking the colony not prepared for the change. On the other hand, a badly defined dry season in 2006, with subsequent early onset of the rainy season, may have provided a better partition of resources available for ant assemblage in both areas, especially preys, which could reflect the fast recovery and increasing abundance of predators in the wet season. Indeed, in 2005, some specialist predatory ants were rare or absent, as some species of the genus *Strumigenys* and *Pyramica*, known as specialist predators of Collembola, *Discothyrea sexarticulata*, a predator of spider eggs, and the generalist large predators as *Ectatomma* and *Pachycondyla* species, predators of insects and invertebrates with similar body size or also larger [58].

In conclusion, our results showed that contrasting forest types may have similar total ant species richness, as well as a similar amount of rare and ecologically specialized species. These similarities between these forests suggest that litter-dwelling species may have high resilience, related to the litter habitat conditions, to changes and disturbances in both ecological and evolutionary times.

Acknowledgments

The authors thank the staff of Project TEAM Rio Doce/CI TEAM Initiative, the financial and logistical support, the IEF-MG field structure in PERD, and their respective staff for their assistance in the field to carry out the assessments. By the comments and suggestions, Prof. Dr. Ricardo I. Campos, UFV. By identifying the material: Laboratory of Myrmecology CEPEC/CEPLAC, Professor Dr. Jacques Delabie and Wesley Duarte da Rocha, and MZUSP, Professor Dr. Carlos Roberto Brandão, Rodrigo Feitosa and Flávia Esteves. By the aid of collection and sorting of material to trainees of the Laboratory of Ecology and Biological Sciences course of UFOP, scholars and volunteers, and our lab technician Jaci. They are also grateful to FAPEMIG for scholarships for master's granted. S. P. Riberiross is granted by CNPq.

References

[1] R. J. Huggett, *Geoecology—An Evolutionary approach*, Routledge, London, UK, 1995.

[2] J. L. S. Ross, *Geomorfologia—Ambiente e Planejamento*, Editora Contexto, 5th edition, 2000.

[3] P. D. Raven, R. F. Evert, and S. E. Eichhorn, *Biologia Vegetal*, Editora Guanabara Koogan, Rio de Janeiro, Brazil, 6th edition, 2001.

[4] H. J. Schenk, C. Holzapfel, J. G. Hamilton, and B. E. Mahall, "Spatial ecology of a small desert shrub on adjacent geological substrates," *Journal of Ecology*, vol. 91, no. 3, pp. 383–395, 2003.

[5] M. Begon, C. R. Townsend, and J. L. Harper, *Ecologia: De Indivíduos a Ecossistemas*, Editora Artmed, São Paulo, Brazil, 4th edition, 2007.

[6] T. J. Valone, J. H. Brown, and E. J. Heske, "Interactions between rodents and ants in the Chihuahuan Desert: an update," *Ecology*, vol. 75, no. 1, pp. 252–255, 1994.

[7] P. J. Folgarait, "Ant biodiversity and its relationship to ecosystem functioning: a review," *Biodiversity and Conservation*, vol. 7, no. 9, pp. 1221–1244, 1998.

[8] P. Lavelle and A. V. Spain, *Soil Ecology*, Kluwer Academic, Dodrecht, The Netherlands, 2001.

[9] C. A. Brühl, G. Gunsalam, and K. E. Linsenmair, "Stratification of ants (Hymenoptera, Formicidae) in a primary rain forest in Sabah, Borneo," *Journal of Tropical Ecology*, vol. 14, no. 3, pp. 285–297, 1998.

[10] B. Gunadi and H. A. Verhoef, "The flow of nutrients in a Pinus merkusii forest plantation in central Java; the contribution of soil animals," *European Journal of Soil Biology*, vol. 29, no. 3-4, pp. 133–139, 1993.

[11] B. Hölldobler and E. O. Wilson, *The Ants*, Belknap Press of Harvard University Press, Cambridge, Mass, USA, 1990.

[12] H. G. Fowler, "Provas de melhoria ambiental," *Ciência Hoje*, vol. 24, pp. 69–71, 1998.

[13] H. L. Vasconcelos, M. F. Leite, J. M. S. Vilhena, A. P. Lima, and W. E. Magnusson, "Ant diversity in an Amazonian savanna: relationship with vegetation structure, disturbance by fire, and dominant ants," *Austral Ecology*, vol. 33, no. 2, pp. 221–231, 2008.

[14] C. B. Costa, S. P. Ribeiro, and P. T. A. Castro, "Ants as bioindicators of natural succession in Savanna and Riparian Vegetation impacted by dredging in the Jequitinhonha River Basin, Brazil," *Restoration Ecology*, vol. 18, no. 1, pp. 148–157, 2010.

[15] M. A. Pizo and P. S. Oliveira, "The use of fruits and seeds by ants in the Atlantic forest of Southeast Brazil," *Biotropica*, vol. 32, no. 4 B, pp. 851–861, 2001.

[16] P. R. Guimarães Jr., R. Cogni, M. Galetti, and M. A. Pizo, "Parceria surpreendente," *Ciência Hoje*, vol. 187, no. 32, pp. 68–70, 2002.

[17] K. A. B. Kalif, P. R. S. Moutinho, C. Azevedo-Ramos, and S. A. O. Malcher, "Formigas em florestas alteradas," *Ciência Hoje*, vol. 187, no. 32, pp. 70–72, 2002.

[18] A. N. Andersen, "Global ecology of rainforest ants. Functional groups in relation to environment stress and disturbance," in *Ants Standard Methods for Measuring and Monitoring Biodiversity*, D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz, Eds., pp. 25–34, Smithsonian Institute Press, London, UK, 2000.

[19] M. Kaspari and M. D. Weiser, "Ant activity along moisture gradients in a Neotropical forest," *Biotropica*, vol. 32, no. 4, pp. 703–711, 2000.

[20] M. Kaspari, "Primer on ant ecology," in *Ants Standard Methods for Measuring and Monitoring Biodiversity*, D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz, Eds., pp. 9–24, Smithsonian Institute Press, London, UK, 2000.

[21] M. Kaspari, J. Pickering, J. T. Longino, and D. Windsor, "The phenology of a Neotropical ant assemblage: evidence for continuous and overlapping reproduction," *Behavioral Ecology and Sociobiology*, vol. 50, no. 4, pp. 382–390, 2001.

[22] H. Höfer, C. Martius, and L. Beck, "Decomposition in an Amazonian rain forest after experimental litter addition in small plots," *Pedobiologia*, vol. 40, no. 6, pp. 570–576, 1996.

[23] R. I. Campos, J. P. Scares, R. P. Martins, and S. P. Ribeiro, "Effect of habitat structure on ant assemblages associated to two pioneer tree species (Hymenoptera: Formicidae)," *Sociobiology*, vol. 47, pp. 722–723, 2006.

[24] "IEF—Instituto Estadual de Florestas," 2009, http://www.ief.mg.gov.br/component/content/306?task=view.

[25] W. P. Lopes, *Florística e fitossociologia de um trecho de vegetação arbórea no Parque Estadual do Rio Doce, Minas Gerais, Viçosa*, M.S. thesis, Universidade Federal de Viçosa, Minas Gerais, Brazil, 1998.

[26] H. P. Veloso, A. L. R. Rangel Filho, and J. C. A. Lima, *Classificação da vegetação brasileira, adaptada a um sistema universal*, IBGE, Rio de Janeiro, Brazil, 1991.

[27] M. R. M. Meis and J. G. Tundisi, "Geomorphologycal and limnological processes as a basis for lake typology. The middle Rio Doce lake system," in *Limnological Studies on the Rio Doce Valley Lakes*, J. G. Tundisi and Y. Saijo, Eds., pp. 25–48, Brasilian Academy of Sciences, Rio de Janeiro, Brazil, 1997.

[28] F. Z. Antunes, "Caracterização climática do Estado de Minas Gerais," *Informe Agropecuário*, vol. 12, pp. 1–13, 1986.

[29] J. P. Gilhuis, *Vegetation survey of the Parque Florestal Estadual do Rio Doce, MG, Viçosa*, M.S. thesis, Universidade Federal de Viçosa, Minas Gerais, Brazil, 1986.

[30] M. F. Goulart, S. P. Ribeiro, and M. B. Lovato, "Genetic, morphological and spatial characterization of two populations of *Mabea fistulifera* mart. (Euphorbiaceae), in different successional stages," *Brazilian Archives of Biology and Technology*, vol. 48, no. 2, pp. 275–284, 2005.

[31] J. P. Soares, *Estudo da Relação entre as Características Abióticas e Bióticas na Compartimentação de Comunidades Ecológicas no Parque Estadual do Rio Doce/MG com Base na Geomorfologia e na Interação Inseto-Planta*, M.S. thesis, Universidade Federal de Ouro Preto, Ouro Preto, Brazil, 2006.

[32] "TEAM initiative—web site," 2011, http://www.teamnetwork.org/pt-br.

[33] P. Batra, "TEAM—ant protocol," 2006, http://www.teamnetwork.org/portal/server.pt/gateway/PTARGS_0_124600_95397_0_0_18/TEAMAnt-PT-EN-2.1.pdf.

[34] B. T. Bestelmeyer, D. Agosti, L. E. Alonso et al., "Field techniques for the study of ground-dwelling ant: an overview, description, and evaluation," in *Ants Standard Methods for Measuring and Monitoring Biodiversity*, D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz, Eds., pp. 122–144, Smithsonian Institute Press, London, UK, 2000.

[35] R. K. Colwell, "Estimates: Statistical estimation of species richness and shared five species from samples," version 8, 2006 http://purl.oclc.org/estimates .

[36] J. H. C. Delabie, B. Jahyny, I. C. Do Nascimento et al., "Contribution of cocoa plantations to the conservation of native ants (Insecta: Hymenoptera: Formicidae) with a special emphasis on the Atlantic Forest fauna of southern Bahia, Brazil," *Biodiversity and Conservation*, vol. 16, no. 8, pp. 2359–2384, 2007.

[37] R. K. Colwell and J. A. Coddington, "Estimating terrestrial biodiversity through extrapolation," *Philosophical transactions of the Royal Society*, vol. 345, no. 1311, pp. 101–118, 1994.

[38] H. L. Vasconcelos, A. C. C. Macedo, and J. M. S. Vilhena, "Influence of topography on the distribution of ground-dwelling ants in an Amazonian forest," *Studies on Neotropical Fauna and Environment*, vol. 38, no. 2, pp. 115–124, 2003.

[39] A. Chao, "Species richness estimation," in *Encyclopedia of Statistical Sciences*, N. Balakrishnan, C. B. Read, and B. Vidakovic, Eds., pp. 7909–7916, Wiley, New York, NY, USA, 2005.

[40] K. R. Clarke, "Non-parametric multivariate analyses of changes in community structure," *Australian Journal of Ecology*, vol. 18, no. 1, pp. 117–143, 1993.

[41] F. S. Neves, V. H. F. Oliveira, M. M. Espírito-Santo et al., "Successional and seasonal changes in a community of dung beetles (Coleoptera: Scarabaeinae) in a Brazilian Tropical Dry Forest," *Natureza & Conservação*, vol. 8, no. 2, pp. 160–164, 2010.

[42] Ø. Hammer, D. A. T. Harper, and P. D. Ryan, "Past: paleontological statistics software package for education and data analysis," *Palaeontologia Electronica*, vol. 4, no. 1, pp. XIX–XX, 2001.

[43] R. R. Sokal and F. J. Rohlf, *Biometry*, W.H. Freeman and Co., New York, NY, USA, 3rd edition, 1995.

[44] L. L. Sørensen, J. A. Coddington, and N. Scharff, "Inventorying and estimating subcanopy spider diversity using semiquantitative sampling methods in an afromontane forest," *Environmental Entomology*, vol. 31, no. 2, pp. 319–330, 2002.

[45] R. I. Campos, H. L. Vasconcelos, S. P. Ribeiro, F. S. Neves, and J. P. Soares, "Relationship between tree size and insect assemblages associated with *Anadenanthera macrocarpa*," *Ecography*, vol. 29, no. 3, pp. 442–450, 2006.

[46] S. P. Ribeiro, J. P. Soares, R. I. Campos, and R. P. Martins, "Insect herbivores species associated to pioneer tree species: contrasting within forest and ecotone canopy habitats," *Revista Brasileira de Zoociências*, vol. 10, pp. 141–152, 2008.

[47] R. R. Silva, R. S. Machado Feitosa, and F. Eberhardt, "Reduced ant diversity along a habitat regeneration gradient in the southern Brazilian Atlantic Forest," *Forest Ecology and Management*, vol. 240, no. 1–3, pp. 61–69, 2007.

[48] R. Pacheco, R. R. Silva, M. S. C. Morini, and C. R. F. Brandão, "A comparison of the leaf-litter ant fauna in a secondary atlantic forest with an adjacent pine plantation in southeastern Brazil," *Neotropical Entomology*, vol. 38, no. 1, pp. 55–65, 2009.

[49] S. I. Do Carmo Pinto, S. V. Martins, N. F. De Barros, and H. C. T. Dias, "Litter production in two successional stages of a tropical semideciduous forest in the mata do paraíso forest reserve in Viçosa, MG," *Revista Arvore*, vol. 32, no. 3, pp. 545–556, 2008.

[50] R. K. Didham, J. Ghazoul, N. E. Stork, and A. J. Davis, "Insects in fragmented forests: a functional approach," *Trends in Ecology and Evolution*, vol. 11, no. 6, pp. 255–260, 1996.

[51] R. K. Didham and N. D. Springate, "Determinants of temporal variation in community structure," in *Arthropods of Tropical Forests: Spatio-Temporal Dynamics and Resource Use in the Canopy*, Y. Basset, V. Novotny, S. Miller, and R. Kitching, Eds., vol. 1, pp. 28–39, Cambridge University Press, Cambridge, UK, 1 edition, 2003.

[52] C. R. Ribas, J. H. Schoereder, M. Pic, and S. M. Soares, "Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness," *Austral Ecology*, vol. 28, no. 3, pp. 305–314, 2003.

[53] J. H. Lawton, D. E. Bignell, B. Bolton et al., "Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest," *Nature*, vol. 391, no. 6662, pp. 72–76, 1998.

[54] S. A. Lassau and D. F. Hochuli, "Effects of habitat complexity on ant assemblages," *Ecography*, vol. 27, no. 2, pp. 157–164, 2004.

[55] S. A. Lassau, G. Cassis, P. K. J. Flemons, L. Wilkie, and D. F. Hochuli, "Using high-resolution multi-spectral imagery to estimate habitat complexity in open-canopy forests: can we predict ant community patterns?" *Ecography*, vol. 28, no. 4, pp. 495–504, 2005.

[56] R. M. Feitosa, C. R. F. Brandão, and J. L. M. Diniz, "Revisionary studies on the enigmatic neotropical ant genus *Stegomyrmex* emery, 1912 (Hymenoptera: Formicidae: Myrmicinae), with the description of two new species," *Journal of Hymenoptera Research*, vol. 17, no. 1, pp. 64–82, 2008.

[57] CPTEC-INPE, BDC—Banco de Dados Climáticos, Portal de Tecnologia da Informação para Meteorologia, 2009, http://bancodedados.cptec.inpe.br/climatologia/Controller.

[58] R. R. Silva, C. R. F. Brandão, and J. H. C. Delabie, "Formigas (Hymenoptera)," in *Bioecologia e Nutrição de Insetos: Base Para o Manejo Integrado de Pragas*, A. R. Panizzi and J. R. P. Parra, Eds., vol. 1, pp. 1–56, Embrapa Soja, Brazil, 2009.

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 973897, 9 pages
doi:10.1155/2012/973897

Research Article

Contribution of Cytogenetics to the Debate on the Paraphyly of *Pachycondyla* spp. (Hymenoptera, Formicidae, Ponerinae)

Cléa dos Santos Ferreira Mariano,[1, 2] Silvia das Graças Pompolo,[3] Janisete Gomes Silva,[1] and Jacques Hubert Charles Delabie[2, 4]

[1] *Departamento de Ciências Biológicas, Universidade Estadual de Santa Cruz, Km 16 Rodovia Ilhéus-Itabuna, 45650-000 Ilhéus, BA, Brazil*
[2] *Laboratório de Mirmecologia, Centro de Pesquisas do Cacau (CEPEC/CEPLAC), Caixa Postal 7, 45600-000 Itabuna, BA, Brazil*
[3] *Laboratório de Citogenética de Insetos, Departamento de Biologia Geral, Universidade Federal de Viçosa, 35570-000 Viçosa, MG, Brazil*
[4] *Departamento de Ciências Agrárias e Ambientais, Universidade Estadual de Santa Cruz, Km 16 rodovia Ilhéus-Itabuna, 45650-000 Ilhéus, BA, Brazil*

Correspondence should be addressed to Cléa dos Santos Ferreira Mariano, camponotu@hotmail.com

Received 16 June 2011; Accepted 29 July 2011

Academic Editor: Fernando Fernández

We present evidence of the paraphyly of the ant genus *Pachycondyla* resulting from our cytogenetic studies on 29 populations in 18 species from Brazil and French Guyana. It is likely that karyotypes with a large number of chromosomes and comprising mostly small acrocentric chromosomes in species within the *Pachycondyla stricto sensu* group resulted from a succession of centric fission events. On the other hand, karyotypes with a small chromosome number comprising mostly metacentric chromosomes are also interpreted as little derived and tend to undergo centric fission. The karyotypes of the group *Neoponera* are more heterogeneous and probably undergo successive cycles of rearrangements tending to increase the chromosome number by centric fission. The *apicalis* and *verenae* complexes form two probable sister groups that evolved independently due to centric fissions (*verenae*) and pericentric inversions (*apicalis*). Our results reveal the karyotype diversity in the genus and reinforce the hypothesis on the paraphyly of *Pachycondyla*.

1. Introduction

Among the Ponerinae, the genus *Pachycondyla* (Ponerinae, Ponerini) is one of the most ancient known genera of ants and still extant. A fossil species, *Pachycondyla rebekkae* Rust and Andersen, was found in calcareous rocks from the early Tertiary (± 55 million years) in formations in northwest Denmark [1]. The current distribution of this genus (*Pachycondyla sensu* Brown, in Bolton, [2]) is pantropical with 197 valid species [3, 4]. A recent review of the New World species of *Pachycondyla* reports 92 species alone in the Neotropics and characterizes 18 complexes of species based on morphological characters [4].

According to Kempf [5], *Pachycondyla* comprised only 10 species in the Neotropical region, whereas other Neotropical taxa currently included in this group [3, 4] were distributed within the genera *Neoponera, Mesoponera, Pachycondyla, Termitopone,* and *Trachymesopus* in his catalogue. This classification was maintained until Bolton [2] proposed a synonymization based on arguments already discussed by Brown [6]. According to Schmidt's conclusions [7], and recently commented by Ward [8] who called it the "*Pachycondyla* problem," the group of ants currently denominated "genus *Pachycondyla*" is paraphyletic. Taking into account only the Neotropical taxa, this taxon would comprise six species groups (according to Schmidt's classification) not necessarily related.

Cytogenetic studies on insects not only can significantly contribute to the understanding of morphological characteristics but also can shed some light on taxonomic and evolutionary aspects, as, for instance, on groups of species in sympatry [9] competing for the same resources or cryptic species complexes [10, 11]. In the order Hymenoptera, cytotaxonomy has been used by Baldanza et al. [12], Hoshiba and Imai [13], Gokhman [14], and Gokhman and Kuznetsova [15] as a character for taxonomic and evolutionary studies. The determination of a karyotype and the occasional observation of the occurrence of chromosome rearrangements are especially important to make inferences regarding evolutionary or speciation processes. Since gene expression is regulated at least partially by the location of neighboring genes, chromosome alterations can result in phenotype alterations [16] and drive speciation processes. Thus, the understanding of karyotype evolution is valuable for evolutionary, phylogenetic, and taxonomic studies [17, 18] and can be used as a tool to evaluate species diversity.

Regarding Formicidae, Lorite and Palomeque [19] report more than 750 morphospecies with known chromosome number, which is still a relatively small number considering the diversity of this family estimated to be about 21.000 species [20]. In the Ponerinae, cytogenetic studies have been published for 95 morphospecies in 12 genera with chromosome numbers ranging between $2n = 8$ and $2n = 120$ [19], which is a considerable variation when compared to the remaining ant families, except for Myrmeciinae. It is noteworthy that karyotype variation among populations of the same species is frequent in the genera *Myrmecia* [21] and *Pachycondyla* [22–25]. Among the Ponerinae, *Pachycondyla* has been the most studied genus (40 morphospecies) and also the one with the highest variation in chromosome number $2n = 12 - 104$ [19]. Several hypotheses have been tested to understand karyotype evolution in ants including the fusion, fission, and modal hypotheses summarized by Imai et al. ([26], see also [19, 27]). In 1988, Imai and collaborators proposed the Minimum Interaction Theory that states that the chromosome interactions in the interphasic nucleus are responsible for changes in the karyotypes [28, 29]. The same research group [21, 27] developed the karyographic method as a tool that allows to visually explain karyotype evolutionary processes based on metaphase rearrangements. Although this method has not been much used [18, 21, 30–32], it is the only way to compare a large set of karyotype data and make inferences about the studied groups, except for comparative studies using molecular cytogenetic techniques [33, 34].

According to Lorite and Palomeque [19], the chromosome groups reported in Formicidae suggest the occurrence of different patterns of karyotype evolution in different taxonomic groups. Aiming at contributing to the knowledge of Neotropical poneromorphs, our research group has been developing interdisciplinary studies on different species of the subfamily Ponerinae. In this study, we investigated a series of Neotropical taxa within the genus *Pachycondyla sensu* Brown (Table 1) whose monophyly has been questioned by some authors [7, 23]. We also discussed hypotheses regarding the evolution of lineages that comprise this taxon, which is so important for the conservation of forest biomes in the Neotropical region [4].

2. Material and Methods

Colonies of *Pachycondyla* spp. were collected in 13 localities (Table 2) in several states in Brazil and in French Guyana in areas of the Atlantic rainforest, cocoa plantations, Caatinga, and the Amazonian rainforest between 2000 and 2010. In order to make comparisons feasible, we used original and published information as shown in Table 2.

Species identification was carried out following the review by MacKay and MacKay [4] and the species complexes proposed by them. However, aiming at comparing the studied taxa, we also refer to the previous classification by Kempf [5], to the synonymization of different genera of Ponerinae under *Pachycondyla* by Brown *in* Bolton [2] and to a recent generic reclassification proposed by Schmidt [7] but still not fully formalized (Table 1).

Mitotic metaphases were obtained from cerebral ganglia and male gonads treated with 0.005% colchicine for 20–40 minutes and the chromosomes were stained with Giemsa 2% according to Imai et al. [29]. The images were captured using Image-Pro Discovery version 4.5 software under a clear field microscope. Metaphases of some the taxa studied were used to exemplify chromosome patterns.

Our analyses were based on chromosome number and morphology. Unpublished information or available in literature [19, 35–37, Mariano et al., unpublished information] on chromosome number and their structure in the Ponerinae subfamily and for *Pachycondyla sensu* Brown is used for comparison. Chromosomes were classified according to Imai's terminology [38]. The karyotypes studied were grouped and compared mainly based on Schmidt's classification [7]. Inferences on karyotype evolution in groups within *Pachycondyla sensu* Brown were carried out based on karyographs following Imai and Crozier [27] and Imai et al. [21]. Such an analysis allows for the discussion of the direction of karyotype evolution at the taxonomic group level (Figures 1 and 6).

3. Results

A graphic comparison of the karyotype diversity among Neotropical species of Ponerinae and the taxa within the genus *Pachycondyla sensu* Brown is shown in a histogram (Figure 2). Species within the genus *Pachycondyla sensu* Brown and the Neotropical species in the same genus were discriminated from the remaining genera belonging to the subfamily Ponerinae. We found an ample chromosome variation, which had already been observed in Ponerinae, showing the extreme karyotype heterogeneity within this subfamily, especially when compared with the remaining subfamilies of Formicidae, except for the Australian Myrmeciinae [19].

The Neotropical taxa within the genus *Pachycondyla sensu* Brown studied and their respective classification according to Kempf [5], Bolton [2], Schmidt [7], and MacKay and MacKay [4] are listed in Table 1. Our results comprise four groups similar to Schmidt's proposal [7], and among these groups, *Neoponera* was the largest in this study and also the group with the most variable chromosome

Table 1: List of species considered here, generic classification according to Kempf, 1972 [5]; Brown [6] *in* Bolton, 1995 [2]; Schmidt's (2009) proposition for genera names; *Pachycondyla* species complex according to MacKay and MacKay's [4] and taxonomic unit names used in this study and based on ecological, cytogenetic, and morphological evidences.

Pachycondyla species	Genera according to Kempf, 1972 [5]	Genus according to Brown *in* Bolton, 1995 [2]	Schmidt's (2009) genera name proposition	MacKay and MacKay's [4] *Pachycondyla* species complex	Name of the taxonomic unit used in this study
Pachycondyla apicalis (Latreille, 1802)	*Neoponera*	*Pachycondyla*	*Neoponera*	*apicalis*	*Neoponera-apicalis*
Pachycondyla arhuaca (Forel, 1901)	*Mesoponera*	*Pachycondyla*	*Pachycondyla (Incertae Sedis)*	*arhuaca*	—
Pachycondyla carinulata (Roger, 1861)	*Neoponera*	*Pachycondyla*	*Neoponera*	*crenata*	*Neoponera-crenata*
Pachycondyla concava (Mackay and Mackay, 2010)	—	*Pachycondyla*	—	*emiliae*	*Neoponera-emiliae*
Pachycondyla constricta (Mayr, 1884)	*Mesoponera*	*Pachycondyla*	*Mayaponera*	*constricta*	—
Pachycondyla crassinoda (Latreille, 1802)	*Pachycondyla*	*Pachycondyla*	*Pachycondyla*	*crassinoda*	*Pachycondyla*
Pachycondyla crenata (F Smith, 1858)	*Neoponera*	*Pachycondyla*	*Neoponera*	*crenata*	*Neoponera-crenata*
Pachycondyla curvinodis (Forel, 1899)	*Neoponera*	*Pachycondyla*	*Neoponera*	*foetida*	*Neoponera-foetida*
Pachycondyla gilberti (Kempf, 1960)	*Trachymesopus*	*Pachycondyla*	*Pseudoponera*	*stigma*	*Pseudoponera*
Pachycondyla goeldii (Forel, 1912)	*Neoponera*	*Pachycondyla*	*Neoponera*	*crenata*	*Neoponera-crenata*
Pachycondyla harpax (Fabricius, 1804)	*Pachycondyla*	*Pachycondyla*	*Pachycondyla*	*crassinoda*	*Pachycondyla*
Pachycondyla impressa (Roger, 1861)	*Pachycondyla*	*Pachycondyla*	*Pachycondyla*	*crassinoda*	*Pachycondyla*
Pachycondyla inversa (F Smith, 1858)	*Neoponera*	*Pachycondyla*	*Neoponera*	*foetida*	*Neoponera-foetida*
Pachycondyla marginata (Roger, 1861)	*Termitopone*	*Pachycondyla*	*Neoponera*	*laevigata*	*Neoponera*
Pachycondyla metanotalis (Luederwaldt, 1918)	*Pachycondyla*	*Pachycondyla*	*Neoponera*	*emiliae*	*Pachycondyla*
Pachycondyla moesta (Mayr, 1870)	*Neoponera*	*Pachycondyla*	*Neoponera*	*crenata*	*Neoponera-crenata*
Pachycondyla stigma (Fabricius, 1804)	*Trachymesopus*	*Pachycondyla*	*Pseudoponera*	*stigma*	*Pseudoponera*
Pachycondyla striata (Smith, 1858)	*Pachycondyla*	*Pachycondyla*	*Pachycondyla*	*crassinoda*	*Pachycondyla*
Pachycondyla succedanea (Roger, 1863)	*Trachymesopus*	*Pachycondyla*	*Pseudoponera*	*stigma*	*Pseudoponera*
Pachycondyla unidentata Mayr, 1862	*Neoponera*	*Pachycondyla*	*Neoponera*	*crenata*	*Neoponera-crenata*
Pachycondyla venusta (Forel, 1912)	*Neoponera*	*Pachycondyla*	—	*emiliae*	*Neoponera-emiliae*
Pachycondyla verenae (Forel, 1922)	*Neoponera*	*Pachycondyla*	*Neoponera*	*apicalis*	*Neoponera-verenae*
Pachycondyla villosa (Fabricius, 1804)	*Neoponera*	*Pachycondyla*	*Neoponera*	*foetida*	*Neoponera-foetida*

Table 2: Chromosome number and karyotypes of 29 Neotropical *Pachycondyla* populations/species. FG: French Guyana, others: Brazil: BA: state of Bahia, MG: state of Minas Gerais, SP: state of São Paulo. Referred to as *P.* gp. *venusta* in the original publication.

Species	2*n*	Karyotype	Locality/coordinates	Reference
P. apicalis	2*n* = 36	28M + 8A	Ilhéus-BA; 14 45 S 39 13 W	[25]
P. apicalis	2*n* = 40	30M + 10A	Belmonte-BA; 16 05 S 39 12 W	[25]
P. apicalis	2*n* = 68	48M + 20A	Uruçuça-BA; 14 34 S 39 16 W	[25]
P. arhuaca	2*n* = 36	36A	FG: Chutes Voltaire 05 27 N 54 03 W	this study
P. concava	2*n* = 54	6M + 48A	Itororó-BA; 15 7 S 40 5 W	[35]
P. carinulata	2*n* = 24	4M + 20A	Ilhéus-BA; 14 45 S 39 13 W	[35]
P. constricta	2*n* = 30	30A	Ilhéus-BA; 14 45 S 39 13 W	[35]
P. crassinoda	2*n* = 62	22M + 40A	Ilhéus-BA; 14 45 S 39 13 W	[14]
P. crenata	2*n* = 26	2M + 24A	Viçosa-MG; 20 45 S 45 52 W	[23]
P. curvinodis	2*n* = 26	4M + 22A	Ilhéus-BA; 14 45 S 39 13 W	[35]
P. curvinodis	2*n* = 28	22M + 6A	Una-BA; 15 16 S 39 05 W	[35]
P. gilberti	2*n* = 12	10M + 2A	Arataca-BA; 15 15 S 39 24 W	this study
P. goeldii	2*n* = 24	24A	FG: Petit Saut; 05 20 N 53 41 W	[35]
P. harpax	2*n* = 96	12M + 84A	Ilhéus-BA; 14 45 S 39 13 W	[24]
P. impressa	2*n* = 94	8M + 86A	Ibicuí-BA; 14 53 S 40 02 W	this study
P. inversa	2*n* = 30	20M + 10A	Ilhéus-BA; 14 45 S 39 13 W	[35]
P. marginata	2*n* = 46	28M + 18A	Viçosa-MG; 20 45 S 45 52 W	[35]
P. moesta	2*n* = 26	26A	Viçosa-MG; 20 45 S 45 52 W	[23]
P. metanotalis	2*n* = 70	16M + 54A	Camacã-BA; 15 23 S 39 33 W	this study
P. stigma	2*n* = 12	12M	Porto Seguro-BA; 16 23 S 39 10 W	this study
P. striata	2*n* = 104	4M +100A	Camacã-BA; 15 23 S 39 33 W	[24]
P. succedanea	2*n* = 14	14M	FG: Chutes Voltaire 05 27 N 54 03 W	this study
P. unidentata	2*n* = 12	12M	Ilhéus-BA; 14 45 S 39 13 W	[35]
P. venusta	2*n* = 48	26M + 22A	Viçosa-MG; 20 45 S 45 52 W	[35]
P. verenae	2*n* = 42	30M + 12A	Ilhéus-BA; 14 45 S 39 13 W	[25]
P. verenae	2*n* = 62	14M + 48A	Ilhéus-BA; 14 45 S 39 13 W	[25]
P. verenae	2*n* = 58 – 60	14M + 44A	Viçosa-MG; 20 45 S 45 52 W	[25]
P. verenae	2*n* = 64	12M + 52A	Rio Claro-SP; 22 23 S 47 32 W	[25]
P. villosa	2*n* = 34	12M +22A	Ilhéus-BA; 14 45 S 39 13 W	[35]

number and karyotypes (Table 2). We present information on taxa within nine of the 18 species complexes defined by MacKay and MacKay [4] (Table 2). When comparing these classifications, there is unanimity among the authors solely on the *Pachycondyla stricto sensu* group. There is a certain consensus regarding the group *Neoponera* according to Kempf's catalogue [5] and Schmidt's proposal [7] (Table 1). Although Schmidt [7, page 197] has placed *Pachycondyla metanotalis* Luederwaldt, 1918 in his clade *Neoponera*, we followed Kempf's classification [5] for the aforementioned species since Schmidt's proposal is not backed by any new data, for the fact that *P. metanotalis* is a soil-dwelling species as most species in the clade *Pachycondyla* [5, 7], for morphological criteria not detailed herein, and because its karyotype is much closer to other species in the *Pachycondyla stricto sensu* group than to the *Neoponera* in this study.

A total of 29 populations was studied (Table 2), and several different populations were sampled for some taxa, therefore each line in this table represents one of these such populations as they can have different karyotypes with distinct characteristics. The chromosomes are classified [38] according to if they are acrocentric (A) or metacentric (M). The chromosome complements found are extremely variable showing from a few metacentric chromosomes ($2n = 12$) of large size (*Pachycondyla unidentata* Mayr, 1862) to a large number of minute acrocentric chromosomes ($2n = 104$ in *Pachycondyla striata* (Smith, 1858) (Table 2) and confirming the tendency shown in Figure 1: karyotypes with a few chromosomes have large chromosomes whereas karyotypes with a large number of chromosomes have small chromosomes (see examples in Figure 3).

The simple observation of chromosome morphology reveals great similarity among karyotypes of *Pachycondyla crassinoda* (Latreille, 1802), *Pachycondyla harpax* (Fabricius, 1804), *Pachycondyla impressa* Roger, 1861, *P. metanotalis*, and *P. striata* (group *Pachycondyla sensu stricto*) and also in the karyotypes of *Pachycondyla gilberti* (Kempf, 1960), *Pachycondyla succedanea* (Roger, 1863), and *Pachycondyla*

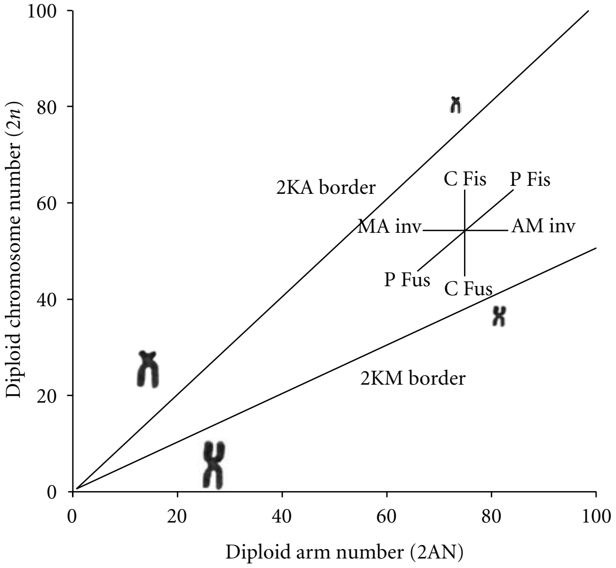


Figure 1: Karyograph adapted from Imai et al. [21] for ants. Since the genome is approximately constant for the whole Formicidae family, a proportional smaller chromosome size corresponds to the increase in the chromosome number. 2KA border: upper limit to the number of acrocentric chromosomes in diploid cells; 2KM border: lower limit to the number of metacentric chromosomes in diploid cells. C Fis: centric fission, C Fus: centric fusion, P Fis: pericentric fission, P Fus: pericentric fusion, AM inv: acrocentric-metacentric inversion, MA inv: metacentric-acrocentric inversion.

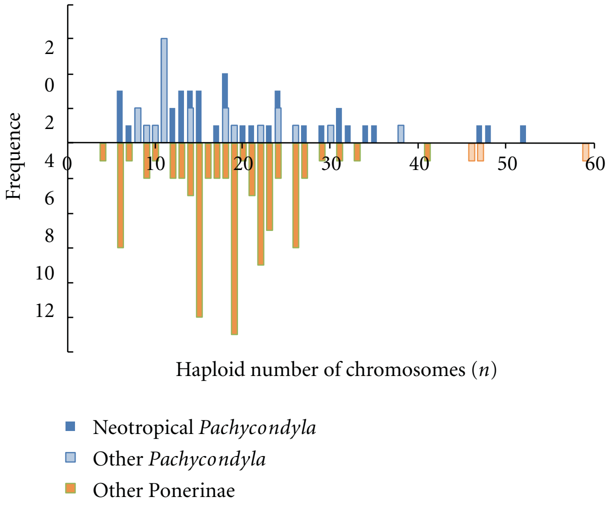


Figure 2: Distribution and frequency of haploid chromosome numbers in the Ponerinae subfamily, up to the X-axis: *Pachycondyla* spp.; down to the X-axis: other Ponerinae. The bars in lighter color in the range of "other Ponerinae" represent the known karyotypes in the *Dinoponera* genus (ref: as in Table 1 for Neotropical *Pachycondyla* spp.; for the others (genera *Anochetus*, *Centromyrmex*, *Cryptopone*, *Diacamma*, *Dinoponera*, *Hypoponera*, *Leptogenys*, *Odontomachus*, *Odontoponera*, *Platythyrea*, *Ponera*): [19, 36, 37, 39], *Hypoponera* spp.: $n = 6, 19$; *Leptogenys* spp.: $n = 15, 21$; *Platythyrea* spp.: $n = 20, 22$; *Thaumatomyrmex* spp.: $n = 10, 21, 31$ [Mariano et al., unpublished information]).

stigma (Fabricius, 1804) (group *Pseudoponera*), which coincidentally also form such groups according to Kempf [40], Schmidt [7], and MacKay and MacKay [4] (Table 2).

The study of the several clusters of *Pachycondyla sensu* Brown using the karyograph method (Figure 4) shows the clustering of species within the *Pachycondyla sensu stricto* group, all with a large number of acrocentric chromosomes, of species of *Pseudoponera*, with predominately metacentric chromosomes, and the great variation found in the karyotypes of species classified within the group *Neoponera*. The point distribution suggests that the most frequent rearrangements in these karyotypes were centric fissions and pericentric inversions (A-M type), and these rearrangements favor an increase in the number of chromosomes. Except for an isolated point on the right close to the 2KM limit in Figures 4 and 5 (which represents the population of *Pachycondyla apicalis* (Latreille, 1802) from Uruçuca), the karyotypes with larger numbers of chromosomes also tend to have mostly acrocentric chromosomes.

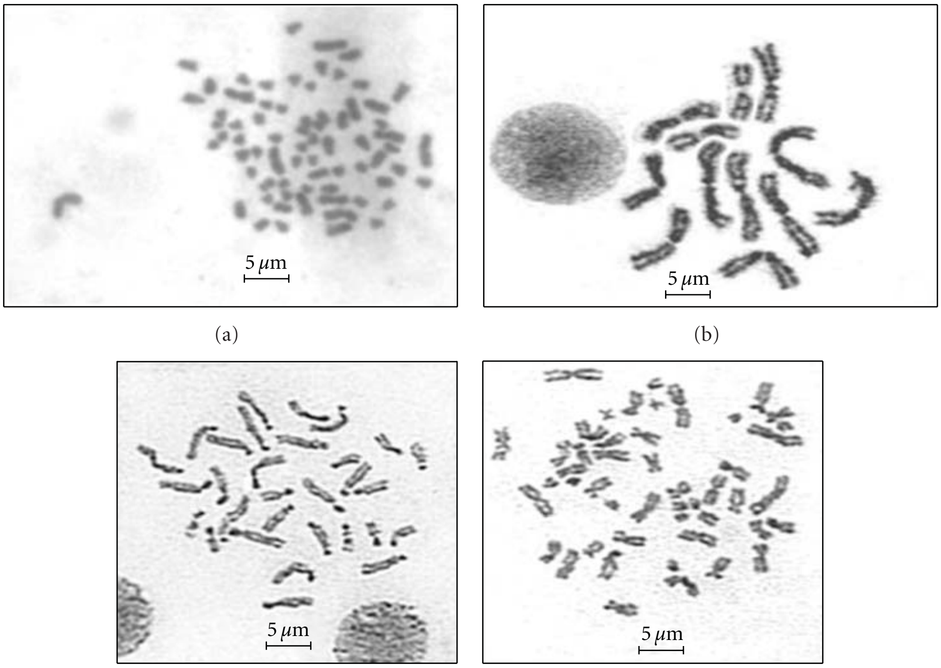
Some species have the same chromosome number but their morphology can be quite variable as a result of the aforementioned rearrangements. Six species have karyotypes that comprise only one morphological type of chromosome; in three of these species the karyotype is comprised of acrocentric chromosomes exclusively, and the other three species have karyotypes with only metacentric chromosomes (Table 2, Figures 4 and 5). In the karyograph, which shows taxa within the group *Neoponera* (11 species, 16 karyotypes, Figure 5), we highlighted the clusters of species within the *apicalis, crenata, emiliae, foetida,* and *verenae* groups.

Finally, we hypothesized the possible pathways of karyotype evolution in several groups of the Neotropical *Pachycondyla sensu* Brown for which we have enough data (nomenclature according to the last column of Table 1): *Neoponera apicalis*, *Neoponera crenata, Neoponera foetida*, *Neoponera verenae*, *Pseudoponera* and *Pachycondyla sensu stricto*. The representation (Figure 6) follows the model suggested by Imai and Crozier [27] developed for the interpretation of mammal karyotype evolution and is based on a hypothesis of karyotype variation essentially driven by fission.

4. Discussion

We can observe groups associated to the taxonomic position of species (Table 1) and some coincided with Schmidt's proposal [7], which splits *Pachycondyla* into 13 clades, with *Mayaponera* and *Neoponera* (both endemic), *Pseudoponera,* and *Pachycondyla* for the Neotropical Region.

Contrary to what has been reported for genera such as *Atta, Acromyrmex,* and *Pheidole,* in which the species already studied have a constant or not so variable karyotype [19], the karyotype groupings are extremely variable in species of *Pachycondyla* as well as in some distinct populations of the nominal species. Chromosome morphology is also variable, and it is noteworthy that, in most karyotypes with large chromosome numbers ($n > 11$, according to



(a) (b)

(c) (d)

Figure 3: Metaphasic plates representing the different chromosome patterns found in *Pachycondyla* species. (a) *Pachycondyla impressa*, $2n = 70$, karyotype with a high number of chromosomes, mostly acrocentric. (b) *Pachycondyla unidentata*, $2n = 12$, karyotype with a low number of chromosomes, comprised exclusively by type M chromosomes of large size. (c) *Pachycondyla arhuaca*, $2n = 36$, Karyotype comprised exclusively by type A chromosomes. (d) *Pachycondyla venusta*, $2n = 54$, Karyotype comprised by types A and M chromosomes, a pattern found in many species and very common in the *Neoponera* group.

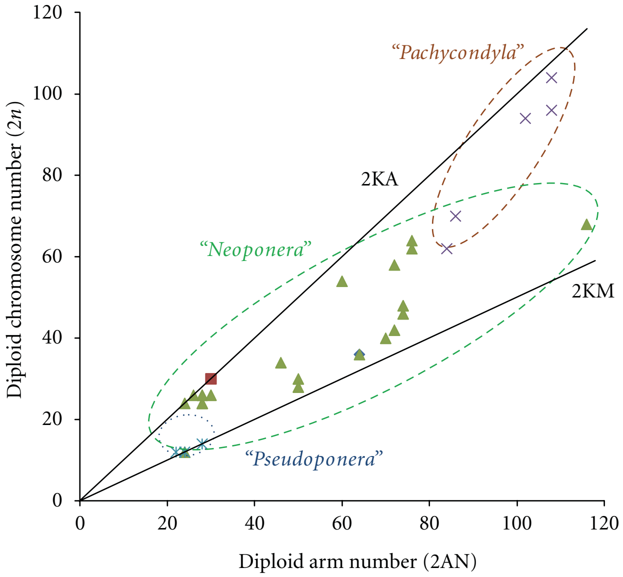


Figure 4: Karyograph of the Neotropical *Pachycondyla sensu* Brown. The ellipses circle the more representative species groups of our sampling according Schmidt [7] (see Table 1); two isolated points (square, diamond) represent single taxa not incorporated in a group (*P. arhuaca*, *P. constricta*).

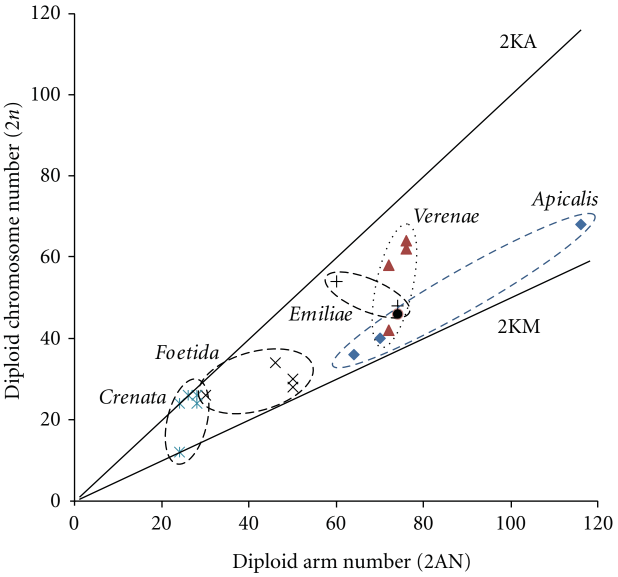


Figure 5: Karyograph of the Neotropical *Neoponera* according the Schmidt's proposal. The ellipses circle the more representative species groups (last column of Table 1); an isolated black circle represents a single species (*P. marginata*) not incorporated in a group.

the criteria of Imai et al., [41]), the chromosomes are submetacentric and acrocentric, which allows us to infer that fission and pericentric inversions (A-M ou M-A) are the most frequent chromosome rearrangements in the evolution of these karyotypes. These rearrangements can be either responsible or coadjuvant in speciation processes, especially in the complexes of cryptic species sampled in this study (*apicalis*, *verenae*, and *foetida* groups).

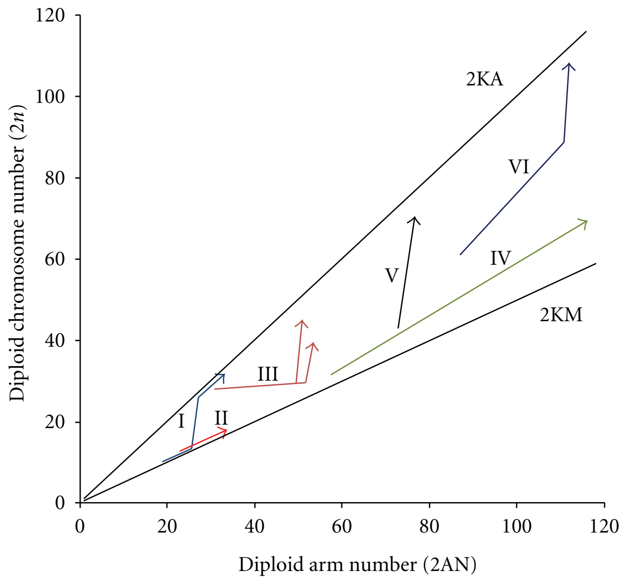


FIGURE 6: Possible pathways of karyotype evolution in several groups of Neotropical *Pachycondyla sensu* Brown. The Roman numbers correspond to the more representative species groups studied here (nomenclature according the last column of Table 1): I: *Neoponera-crenata*; II: *Pseudoponera*; III: *Neoponera-foetida*; IV: *Neoponera-apicalis*; V: *Neoponera-verenae*; VI: *Pachycondyla sensu stricto*. This schematic representation follows the suggested model of Imai and Crozier [27] for karyotypical evolution in mammals and is based on a hypothesis of a karyotype variation essentially driven by fission.

According to MacKay and MacKay [4], even though *Pachycondyla sensu* Brown is morphologically heterogeneous, the morphological characters were not consistent enough to justify splitting the group into distinct genera. However, similarly to Schmidt's [7], our results question the monophyly of *Pachycondyla* in its current acceptation. Thus, our results suggest the cooccurrence of multiple genera once there are totally independent patterns of karyotype evolution that strongly converge with Schmidt's conclusions [7]. We found groups with distinct patterns of karyotype evolution thus organized.

(a) Karyotypes with a large number of chromosomes and comprising mostly small acrocentric chromosomes in species within the *Pachycondyla stricto sensu* group (*P. crassinoda, P. harpax, P. impressa, P, metanotalis,* and *P. striata*) which most likely resulted from a succession of centric fission events (Figures 3(a), 6). These karyotypes follow the same pattern of those found in the three species of *Dinoponera* with available cytogenetic information [42], which is the sister genus of the clade *Pachycondyla* according to Schmidt [7].

(b) Karyotypes with a small chromosome number (n 11 according to criteria in Imai et al. [41]) and comprising mostly metacentric chromosomes correspond to the pattern found in species within the group *Pseudoponera* (*P. cauta, P. gilbertii*, and *P. stigma*) and can be interpreted as little derived karyotype patterns which tend to undergo centric fission (Figure 3(b)).

(c) The karyotypes of *Neoponera* exemplify the karyotype evolution according to the model proposed by Imai et al. [21]: the karyotypes undergo successive cycles of rearrangements tending to increase the chromosome number by centric fission. The species included in *Neoponera* are considered the most diverse morphologically and behaviorally among the ponerine [7] and this diversity translates into the variety of karyotypes (Figure 3(c)).

(d) The case of populations within the taxa *P. apicalis* and *P. verenae* studied herein exemplifies an interesting evolutionary model based on biogeography. The two forms coexist along their range, which comprises practically only tropical and subtropical terrestrial environments in the Neotropical Region [25, 43]. A more refined analysis of the morphological criteria suggests that each nominal taxon is a complex of cryptic species of allopatric distribution [25], which is corroborated by the cytogenetic study: the *apicalis* and *verenae* complexes form two probable sister groups that probably evolved independently due mainly to centric fissions (*verenae*) and pericentric inversions (*apicalis*) (Figures 5 and 6).

All these examples adequately illustrate the karyotype heterogeneity in *Pachycondyla* and reinforce the argument of the cooccurrence of several genera, at least in the Neotropical region. The cytogenetic studies indicate groupings that do not seem to have recent ancestry and also strongly suggest the paraphyly of the "*Pachycondyla* problem," according to Ward [8], as each group follows a distinct evolutionary pattern (Figure 4).

Some of these patterns are not exclusive of the species represented herein; they have been reported in known ant karyotypes such as in species of the Australian genus *Myrmecia* [21] and corroborate the occurrence of different evolutionary patterns in insects.

The diversity of karyotypes found in the known species of *Pachycondyla* in the Neotropics is supported by the antiquity of this group of ants and reinforces a tendency observed in karyotypes of Formicidae: the increase and diversification of chromosome number and morphology in a basal subfamily such as Ponerinae contrasting with the low variation and relative stability in some genera of more derived subfamilies such as Dolichoderinae, Formicinae, and Myrmicinae [22, 44]. A similar phenomenon was observed in the Australian Myrmeciinae [21, 26], but the idea formerly well accepted that these ants are basal and ancestral is no longer supported by recent molecular phylogenies [45]. This situation leads to the very intriguing question of what is shared by the Myrmeciinae and Ponerinae to be so variable with respect to their karyotypes whereas karyotypes seem to be rather uniform in related subfamilies?

Among the ants, it is noteworthy the occurrence of cryptic species complexes and sibling species: morphologically indistinguishable species recently diverged (sibling-species) or that maintain strongly convergent characters (cryptic species), and not separable using the traditional methods of identification [10, 11], in which characters such as behavior, chemical signature, and karyotype composition act as mechanisms of reproductive isolation (in Neotropical *Pachycondyla*, see, for instance, Lucas et al. [46]). Such a phenomenon has been reported for ants and many other organisms, and there are likely to be different speciation processes as there are multiple species concepts [47]. Thus, the use of different criteria for the description of species (alpha level taxonomy) is justified, and these criteria have been tested using the integrated taxonomy approach, which consists of using complementary areas such as molecular genetics, ecology, behavior, cytogenetics, and chemistry among others [48]. This approach strengthens the necessity of interdisciplinary studies and emphasizes the importance of multiple tools for taxonomic studies, a consensus among several authors [48, 49]. Therefore, besides confirming the validity of a species recognized by other methods, cytogenetics can contribute to the study of the origin and definition of species limits, as well as to the understanding of the evolution of organisms [49]. We hope our study will shed some light on the classification of the genus *Pachycondyla*, which still needs further disentangling.

Acknowledgments

The authors acknowledge D Denis, JRM Santos, JCS Carmo and Sr. Manoel for their help in field work and LSR Nascimento and EA Santos for their help in slide preparation. This study was funded by FAPESB and CNPq. JHCD acknowledges his research grant from CNPq. This is a contribution of the Program PRONEX FAPESB CNPq, project PNX0011/2009: "Rede Multidisciplinar de Estudos sobre Formigas Poneromorfas do Brasil." In accordance with section 8.6 of the ICZNs International Code of Zoological Nomenclature, printed copies of the edition of Psyche containing this article are deposited at the following six publicly accessible libraries: Green Library (Stanford University), Bayerische Staatsbibliothek, Library—ECORC (Agriculture & Agri-Food Canada), Library—Bibliotheek (Royal Belgium Institute of Natural Sciences), Koebenhavns Universitetsbibliotek, University of Hawaii Library.

References

[1] J. Rust and N. M. Andersen, "Giant ants from the Paleogene of Denmark with a discussion of the fossil history and early evolution of ants (Hymenoptera: Formicidae)," *Zoological Journal of the Linnean Society*, vol. 125, no. 3, pp. 331–348, 1999.

[2] B. Bolton, *A New General Catalogue of the Ants of the World*, Harvard University Press, Cambridge, Mass, USA, 1995.

[3] B. Bolton, G. Alpert, P. S. Ward, and P. Naskrecki, *Bolton's Catalogue of Ants of the World 1758-2005*, Harvard University Press, Cambridge, Mass, USA, Harvard University Press.

[4] W. P. MacKay and E. E. MacKay, *The Systematics and Biology of the New World Ants of the Genus Pachycondyla (Hymenoptera: Formicidae)*, The Edwin Mellen Press, Lewiston, NY, USA, 2010.

[5] W. W. Kempf, "Catálogo abreviado das formigas da Região Neotropical," *Studia Entomoogica*, vol. 15, pp. 3–344, 1972.

[6] W. L. Brown Jr., "A comparison of the Hylean and Congo-West African rain forest ant faunas," in *Tropical Forest Ecosystems in Africa and South America: A Comparative Review*, B. J. Meggers, E. S. Ayensu, and W. D. Duckworth, Eds., pp. 161–185, Smithsonian Institution Press, Washington, DC, USA, 1973.

[7] C. A. Schmidt, *Molecular philogenetics and taxonomic revision of ponerine ants (Hymenoptera: Formicidae: Ponerinae)*, Ph.D. thesis, University of Arizona, 2010.

[8] P. S. Ward, "Integrating molecular phylogenetic results into ant taxonomy (Hymenoptera: Formicidae)," *Myrmecological News*, vol. 15, pp. 21–29, 2011.

[9] M. S. Guerra and M. J. Souza, *Como Observar Cromossomos: Um Guia de Técnicas em Citogenética Vegetal, Animal e Humana*, Ribeirão Preto, São Paulo, Brazil, 2002.

[10] D. Bickford, D. J. Lohman, N. S. Sodhi et al., "Cryptic species as a window on diversity and conservation," *Trends in Ecology and Evolution*, vol. 22, no. 3, pp. 148–155, 2006.

[11] B. Seifert, "Cryptic species in ants (Hymenoptera: Formicidae) revisited: we need a change in the alpha-taxonomic approach," *Myrmecological News*, vol. 12, pp. 149–166, 2009.

[12] F. Baldanza, L. Gaudio, and G. Viggiani, "Cytotaxonomic studies of *Encarsia* Forster (Hymenoptera: Aphelinidae)," *Bulletin of Entomological Research*, vol. 89, no. 3, pp. 209–215, 1999.

[13] H. Hoshiba and H. T. Imai, "Chromosome evolution of bees and wasps (Hymenoptera, Apocrita) on the basis of C-banding pattern analyses," *Japanese Journal of Entomology*, vol. 61, no. 3, pp. 465–492, 1993.

[14] V. E. Gokhman, "Implication of chromosomal analysis for the taxonomy of parasitic wasps (Hymenoptera)," *Entomological Review*, vol. 86,, pp. 1–10, 2006.

[15] V. E. Gokhman and V. G. Kuznetsova, "Comparative insect karyology: current state and applications," *Entomological Review*, vol. 86, pp. 352–368, 2006.

[16] M. Ridley, *Evolução*, Artmed, Porto Alegre, Brasil, 2003.

[17] H. C. MacGregor, *An Introduction to Animal Cytogenetics*, Chapman & Hall, London, UK, 1993.

[18] C. S. F. Mariano, J. H. C. Delabie, L. A. O. Campos, and S. G. Pompolo, "Trends in karyotype evolution in the ant genus *Camponotus* (Hymenoptera: Formicidae)," *Sociobiology*, vol. 42, no. 3, pp. 831–839, 2003.

[19] P. Lorite and T. Palomeque, "Karyotype evolution in ants (Hymenoptera: Formicidae), with a review of the known ant chromosome numbers," *Myrmecological News*, vol. 13, pp. 89–102, 2010.

[20] D. Agosti and N. F. Johnson, "Antbase," version (05/2005), 2009, antbase.org .

[21] H. T. Imai, R. W. Taylor, and R. H. Crozier, "Experimental bases for the minimum interaction theory. I. Chromosome evolution in ants of the *Myrmecia pilosula* species complex (Hymenoptera: Formicidae: Myrmeciinae)," *Japanese Journal of Genetics*, vol. 69, no. 2, pp. 137–182, 1994.

[22] C. S. F. Mariano, *Evolução cariotípica em diferentes grupos de Formicidae*, Ph.D. thesis, Universidade Federal de Viçosa, Minas Gerais, Brasil, 2004.

[23] C. S. F. Mariano, S. G. Pompolo, S. Lacau, and J. H. C. Delabie, "Questions sur la monophylie du taxon *Pachycondyla* Smith,

1858: approche cytogénétique sur le sous-genre *Pachycondyla* sensu Emery, 1901 (Hymenoptera: Formicidae: Ponerinae)," *Bulletin de la Société Entomologique de France*, vol. 111, pp. 299–304, 2006.

[24] C. S. F. Mariano, S. G. Pompolo, D. S. Borges, and J. H. C. Delabie, "Are the Neotropical ants *Pachycondyla crenata* (Roger) and *Pachycondyla mesonotalis* (Santschi) (Formicidae, Ponerinae) good species? A cytogenetic approach," *Myrmecologische Nachrichten*, vol. 8, pp. 277–280, 2006.

[25] J. H. C. Delabie, C. S. F. Mariano, L. F. Mendes, S. G. Pompolo, and D. Fresneau, "Problemas apontados por estudos morfológicos, ecológicos e citogenéticos no gênero *Pachycondyla* na Região Neotropical: o caso do complexo *apicalis*," in *Insetos Sociais: da Biologia à Aplicação*, E. F. Vilela, I. A. Santos, J. H. Schoereder et al., Eds., pp. 196–222, Editora da Universidade Federal de Viçosa, Minas Gerais, Brazil, 2008.

[26] H. T. Imai, R. H. Crozier, and R. W. Taylor, "Karyotype evolution in Australian ants," *Chromosoma*, vol. 59, no. 4, pp. 341–393, 1977.

[27] H. T. Imai and R. H. Crozier, "Quantitative analysis of directionality in mammalian karyotype evolution," *The American Naturalist*, vol. 116, no. 4, pp. 537–569, 1980.

[28] H. T. Imai, T. Maruyama, T. Gojobori, Y. Inoue, and R. H. Crozier, "Theoretical bases for karyotype evolution. 1. The minimum-interaction hypothesis," *The American Naturalist*, vol. 128, pp. 900–920, 1986.

[29] H. T. Imai, R. W. Taylor, M. W. Crosland, and R. H. Crozier, "Modes of spontaneous chromosomal mutation and karyotype evolution in ants with reference to the minimum interaction hypothesis," *Japanese Journal of Genetics*, vol. 63, no. 2, pp. 159–185, 1988.

[30] H. T. Imai, Y. Satta, and N. Takahata, "Integrative study on chromosome evolution of mammals, ants and wasps based on the minimum interaction theory," *Journal of Theoretical Biology*, vol. 210, no. 4, pp. 475–497, 2001.

[31] H. T. Imai, Y. Satta, M. Wada, and N. Takahata, "Estimation of the highest chromosome number of eukaryotes based on the minimum interaction theory," *Journal of Theoretical Biology*, vol. 217, no. 1, pp. 61–74, 2002.

[32] A. E. Spotorno, L. I. Walker, S. V. Flores, M. Yevenes, J. C. Marín, and C. Zuleta, "Evolución de los filotinos (Rodentia, Muridae) en los Andes del Sur," *Revista Chilena de Historia Natural*, vol. 74, pp. 151–166, 2001.

[33] A. T. Sumner, *Chromosomes: Organization and Function*, Blackwell Publishing, Oxford, Uk, 2003.

[34] M. S. Guerra, *FISH: Conceitos e Aplicações na Citogenética*, Sociedade Brasileira de Genética, Ribeirão Preto, Brasil, 2004.

[35] C. S. F. Mariano, J. H. C. Delabie, J. R. M. Santos, and S. G. Pompolo, "Evolução cariotipica em *Pachycondyla* spp. (Ponerinae) neotropicais," *Biológico*, vol. 69, suplemento 2, pp. 409–412, 2007.

[36] C. S. F. Mariano, S. G. Pompolo, L. A. C. Barros, E. Mariano-Neto, S. Campiolo, and J. H. C. Delabie, "A biogeographical study of the threatened ant *Dinoponera lucida* Emery (Hymenoptera: Formicidae: Ponerinae) using a cytogenetic approach," *Insect Conservation and Diversity*, vol. 1, pp. 161–168, 2008.

[37] C. S. F. Mariano, I. S. Santos, S. Groc et al., "The karyotypes of *Gigantiops destructor* (Fabricius) and other ants from French Guiana (Formicidae)," *Annales de la Société Entomologique de France*, vol. 47, pp. 140–146, 2011.

[38] H. T. Imai, "Mutability of constitutive heterochromatin (C-bands) during eukaryotic chromosomal evolaution and their cytological meaning," *Japanese Journal of Genetics*, vol. 66, no. 5, pp. 635–661, 1991.

[39] I. S. Santos, M. A. Costa, C. S. F. Mariano, J. H. C. Delabie, V. Andrade-Souza, and J. G. Silva, "A cytogenetic approach to the study of Neotropical *Odontomachus* and *Anochetus* ants (Hymenoptera: Formicidae)," *Annals of the Entomological Society of America*, vol. 103, no. 3, pp. 424–429, 2010.

[40] W. W. Kempf, "As formigas do gênero *Pachycondyla* Fr. Smith no Brasil," *Revista Brasileira de Entomologia*, vol. 10, pp. 189–204, 1962.

[41] H. T. Imai, C. Baroni Urbani, M. Kubota et al., "Karyological survey of Indian ants," *Japanese Journal of Genetics*, vol. 59, pp. 1–32, 1984.

[42] C. S. F. Mariano, E. C. Sposito, A. L. Lopes, S. G. Pompolo, and J. H. C. Delabie, "Análises cariotípicas comparativas no gênero *Dinoponera* Roger (Ponerinae: ponerini)," in *Proceedings of the 17th Simpósio de Mirmecologia*, pp. 140–142, Campo Grande, MG, Brazil, 2005.

[43] A. L. Wild, "Taxonomic revision of the *Pachycondyla apicalis* species complex (Hymenoptera: Formicidae)," *Zootaxa*, no. 834, pp. 1–25, 2005.

[44] C. S. F. Mariano, "Questões atuais da biologia das formigas vistas sob um ângulo citogenético," in *Proceedings of the 20th Simpósio de Mirmecologia*, Ouro Preto, MG, Brazil, 2009.

[45] C. S. Moreau, C. D. Bell, R. Vila, S. B. Archibald, and N. E. Pierce, "Phylogeny of the ants: diversification in the age of angiosperms," *Science*, vol. 312, no. 5770, pp. 101–104, 2006.

[46] C. Lucas, D. Fresneau, K. Kolmer, J. Heinze, J. H. C. Delabie, and D. B. Pho, "A multidisciplinary approach to discriminating different taxa in the species complex *Pachycondyla villosa* (Formicidae)," *Biological Journal of the Linnean Society*, vol. 75, no. 2, pp. 249–259, 2002.

[47] E. Mayr, "Wu's genic view of speciation," *Journal of Evolutionary Biology*, vol. 14, no. 6, pp. 866–867, 2001.

[48] B. C. Schlick-Steiner, F. M. Steiner, B. Seifert, C. Stauffer, E. Christian, and R. H. Crozier, "Integrative taxonomy: a multisource approach to exploring biodiversity," *Annual Review of Entomology*, vol. 55, pp. 421–438, 2010.

[49] J. M. Padial and I. De La Riva, "A response to recent proposals for integrative taxonomy," *Biological Journal of the Linnean Society*, vol. 101, no. 3, pp. 747–756, 2010.

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 390748, 8 pages
doi:10.1155/2012/390748

Research Article

Ant Community Structure (Hymenoptera: Formicidae) in Two Neighborhoods with Different Urban Profiles in the City of São Paulo, Brazil

Alcione Piva and Ana Eugênia de Carvalho Campos

Unidade Laboratorial de Referência em Pragas Urbanas, Instituto Biológico, Avenida Conselheiro Rodrigues Alves, 1252 São Paulo, SP, Brazil

Correspondence should be addressed to Ana Eugênia de Carvalho Campos, anaefari@biologico.sp.gov.br

Received 24 May 2011; Revised 18 July 2011; Accepted 1 August 2011

Academic Editor: Fernando Fernández

Some ant species are highly abundant in cities, may form huge unicolonial populations with thousands of individuals able to displace native fauna, and impoverish ecological relationships in urban environments. In this work, we study the ant community in two neighborhoods with different urban profiles, one recently populated and another from the 1900s in the city of São Paulo, Brazil. Two hundred and ninety houses were sampled with baits for ant collections. Results show that the recent urbanized neighborhood with greater disturbance favors opportunistic and dominant species to colonize it, like *Tapinoma melanocephalum*. We also made a temporal analysis in the ancient neighborhood, collecting ants after ten years from a first survey. *T. melanocephalum* has a broader range than ten years ago, displaced other ant species, but confronts with *Pheidole megacephala* that was not found in the recent urbanized neighborhood.

1. Introduction

Some ant species promote severe problems in Brazil, especially exotic ones with invading status, which were accidentally introduced in the country and may be found with huge populations, displacing native ant fauna, other arthropod species, and even vertebrates [1]. Among the most common invading species found in Brazilian cities, *Pheidole megacephala* (Fabricius, 1783), *Tapinoma melanocephalum* (Fabricius, 1793), *Nylanderia fulva* (Mayr, 1862), and *Paratrechina longicornis* (Latreille, 1802) [2–5] are highlighted.

Around the world, recordings on *P. megacephala* point this species as one of the most dominant and aggressive tramp ant species. In 1908, the big-headed ant invaded a Caribbean island, and surveys show that this is the only ant species found in that environment [6]. The same data were found in two, from five islands surveyed in Florida [7]. In Australia, *P. megacephala* displaced dominant Dolichoderinae species, Camponotini, and other *Pheidole* species in forested areas [8]. The big-headed ant biomass in areas where it dominates is 18 times greater than the native ant species biomass where it does not occur [9]. In a study conducted in urban areas from the Brazilian Cerrado, *P. megacephala* predominated in areas with low conservation efforts [5].

Tapinoma melanocephalum originated from the Indo-Pacific region is one of the ant species with broader distribution [10]. As in other parts of the world, it was the most abundant species in a neighborhood in the city of São Paulo [3], in a hospital in the Central-Eastern Brazil [11], in residences in Ilhéus [2], Uberlândia [4], and Mogi das Cruzes [12].

But not only are these common worldwide tramp ants found in Brazilian cities. Others, native or exotic, are also household invaders. *Brachymyrmex* sp., *Solenopsis saevissima* (F. Smith, 1855), *S. invicta* Buren, 1972, *Monomorium* spp., *Crematogaster* sp., *Cyphomyrmex* sp., *Cardiocondyla* sp., *Linepithema humile* (Mayr, 1868), *Dorymyrmex* sp., *Camponotus* spp., and *Pachycondyla* sp. [2, 3, 13, 14].

Studies have focused on the biology of invading species and found out that they share some common characteristics like multiple queens, polidomic nests with a huge cooperation net among the nests, without any aggressive behavior [15], and also their clear association with disturbed environments [16]. On the other hand, one might understand which are the patterns and characteristics in the urban environment to shelter invading ant species and use this knowledge to promote satisfactory management and control. In this way, Clarke et al. [17] examined soil characteristics and type of vegetation in urban parks in San Francisco, USA, and concluded that soil moisture positively affects ant species richness, and percent of natural area that is forested was negatively related. Forys and Allen [18] established a positive correlation between exotic and native ant species in Florida. The authors stated that the same biotic and abiotic characteristics may favor both species. But they highlighted that an increase on urban sprawl leads to an increase on the number of exotic ant species, once they are known to displace native ant fauna.

In New York, a study revealed that besides introduced species that are usually favored by disturbance, this process must be much more complex than it is known [19]. In this survey, *Tetramorium caespitum* (L.), a generalist exotic species that nests in cracks on sidewalks, was the most collected ant, but in most streets, it occurred with other ant species, exotic or native to the USA. This same ant species was also collected in a survey conducted in the surroundings of Montreal close to a forested area [20].

For this purpose, two neighborhoods were surveyed, and ant presence was associated to recent or ancient urbanization and other abiotic factors furnished by man.

2. Material and Methods

2.1. Surveyed Neighborhoods. Ant collections were made in households in two neighborhoods in the city of São Paulo: Vila Mariana and Itaquera.

Itaquera is located in the Eastern side of the city of São Paulo 20 Km apart from downtown. Its 55.32 km^2 have low- and medium-density residential areas, few apartment buildings, an environmental protection area with a rainforest remaining with 867.60 hectares, and an industrial and an agriculture area. Besides the first residences date from the 1900s, the urbanization process initiated 35 years ago and is still growing.

Vila Mariana is 26.87 km^2, 5 Km from downtown, with median- and high-density residential blocks, with many apartment buildings and commercial areas. There are no industrial, agricultural, or environmental protection areas. Urbanization process started in the 1900s, and most houses are from the 1950s. Today, some houses are being substituted by modern apartment buildings, but still ancient houses are found, and most of them are well preserved.

Ant collections were performed in Vila Mariana in two periods: from December 1998 to October 1999 and ten years later, from December 2009 to January 2011. In Itaquera, collections were made from December 2009 to January 2011.

Two hundred and ninety houses were sampled: 132 in Vila Mariana in the period 1998/1999, 79 in Vila Mariana (2009–2011), and 79 in Itaquera (2009–2011).

Households were randomly chosen. We could repeat the ant collection in the same 25 houses in Vila Mariana in 2009–2011 after 10 years. The other 54 houses were surveyed for the first time in the recent years. Baits based on dehydrated liver, pineapple cake, and honey were set in 7 cm length straws which were placed in the houses, 15 baits in each house and three in each room: living room, bedroom, kitchen, bathroom, and outdoors (peridomiciliar area). In addition, manual collections were also performed using brushes and a bottle-type vacuum. The baits were left for 24 hours, and collected ants were taken to the laboratory for identification and counting. In addition to the collections, it was also filled in a form with data relating to the environment as house conservation, cleanness, number of children, and presence of pets.

2.2. Statistical Analysis. We used descriptive statistics with graphics and tables. Categorical and numerical variables for neighborhood characterization were obtained from a form filled in for each ant collection (Table 1). We computed percentage values for categorical analysis (number of floors and children, pet and garden presence) and the mean number for numerical variables (number of rooms per house, number of residents and house age).

Association analysis was calculated for the five most collected ant species in the three samples. For that purpose, the Pearson's chi-square test was used or the Fisher's exact test (for expected values less than 5).

For numerical variables, the Mann-Whitney test was used to compare two categories, and the Kruskal-Wallis Test was used to compare three or more categories due to the absence of normal distribution from the variables [21]. The level of 5% of significance was used ($P < 0.05$). The SAS system for Windows (statistical analysis system), version 8.02, was used for statistical analysis [22].

Relative frequency was calculated to analyze the most frequent ant species indoors and outdoors in each neighborhood, in each period of collection.

Shannon diversity index, equitability index, and Simpson's Index were calculated with the BioDap software [23] in order to record ant community in the neighborhoods.

3. Results

3.1. Ant Community. It was collected 7.249 ant specimens in the 132 collections in Vila Mariana in 1998/1999, 6.477 specimens in the 79 collections in Vila Mariana in 2009–2011, and 12.054 specimens in the 79 collections in Itaquera in 2009–2011 (Table 2).

In Itaquera, 33 ant species were found, most native to Brazil, but 4 were exotic ones. In Vila Mariana, we collected 23 ant species in 1998/1999, 3 were exotic, and from 2009–2011 we collected 25 ant species and 4 were exotic.

Table 1: Data from surveyed households in Vila Mariana and Itaquera neighborhoods in the city of São Paulo, Brazil.

Control number	() Itaquera		() Vila Mariana	Date: / /
Address				
Contact			() Single-story house	() Two-story house
Number of rooms ()	Number of residents ()		Children: () Yes	() No
House age:			Garden: () Yes	() No
			Pets: () Yes	() No
Conservation condition	() Very good	() Good	() Bad	() Very bad
Cleanness condition	() Very good	() Good	() Bad	() Very bad

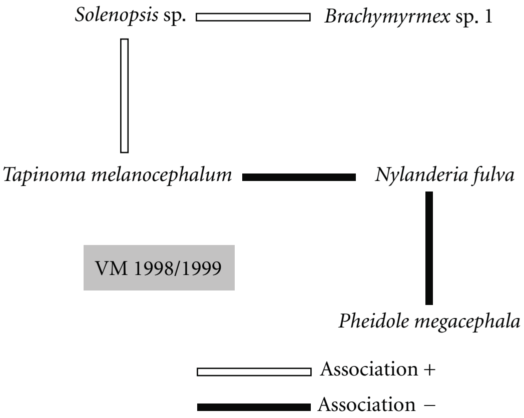


Figure 1: Community structure of house-infesting ants in Vila Mariana, São Paulo, from 1998 to 1999.

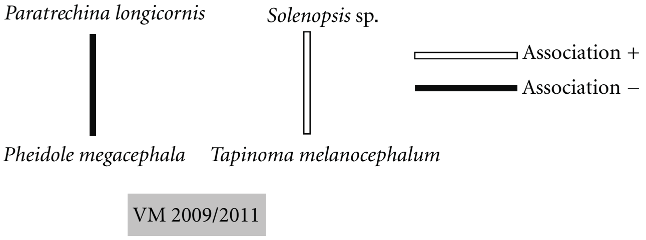


Figure 2: Community structure of house-infesting ants in Vila Mariana, São Paulo, from 2009 to 2011.

Tapinoma melanocephalum was the most abundant species in the three collections (VM 1998/1999, VM 2009–2011, and ITA 2009–2011).

In Vila Mariana, ten years later, it was found an increase on *T. melanocephalum* frequency and a decrease on the other ant species frequency as *N. fulva*, *Brachymyrmex* sp. 1, and *Solenopsis* sp., which are all native to Brazil. *L. humile*, also native to Brazil and found in 1998/1999, was not found in the surveys from 2009 to 2011. This is a species that could have had success in dominating the neighborhood. But the exotic big-headed ant, *P. megacephala,* expanded its foraging range ten years later. Besides its high frequency in Vila Mariana, *P. megacephala* was not found in Itaquera.

Ten years ago, *N. fulva* was the most frequent species, present in more than 40% of the sampled houses in Vila Mariana. Its occurrences were even indoors and outdoors. In 1998/1999, *P. longicornis* was also found outdoors with *N. fulva.* Our last survey from 2009 to 2011 showed that *P. longicornis*' frequency increased almost 3 times (Table 2), but its occurrence was limited to the peridomiciliar area. As *N. fulva, P. longicornis* is also an invasive ant species and can be displacing the native *N. fulva.* But the association analysis of *N. fulva* was negative with *T. melanocephalum* and *P. megacephala* (Figure 1) in the survey from 1998 to 1999. Thus, *N. fulva* may not succeed in colonizing Vila Mariana all these years, once it competed with three other invasive ants. As we calculated the association only among the five most frequent species, *P. longicornis* did not enter in 1998/1999 analysis.

From 2009 to 2011, few associations could be established among the ant species, but *P. longicornis* frequency increased and showed negative association with *P. megacephala* (Figure 2).

T. melanocephalum was mainly collected indoors (living rooms, bedrooms, kitchens, and bathrooms). When we compared samples from *T. melanocephalum* in 1998/1999 and ten years later, its relative frequency increased from 18% to 53% inside houses. *P. megacephala* indoor frequency was the same ten years later, but it expanded its foraging areas outdoors from 2009 to 2011. *Brachymyrmex* sp. 1 and *Solenopsis* sp. frequencies decreased in the outdoors in the last samples (Figure 3).

We analyzed the same 25 houses surveyed in 1998/1999 and 2009–2011, and data do not show significant differences from the 79 surveyed houses analyzed together (Figure 4). *T. melanocephalum* and *P. megacephala* are the most frequent species, and *N. fulva* decreased its frequency in ten years (Figure 4).

The number of ant species per house varied from 1 to 10 (Figure 5). The number of houses with only one ant species increased in the survey from 2009 to 2011 in Vila Mariana, due to *T. melanocephalum* increase.

In the opposite, Itaquera shows more houses with more ant species, compared to Vila Mariana.

The diversity indexes revealed that Vila Mariana has a more diverse and balanced ant community compared to Itaquera. The temporal analysis showed a decrease in the ant diversity in Vila Mariana (Table 3).

Table 2: Ant species richness and relative frequency in Vila Mariana (VM 1998/1999 and VM 2009–2011) and Itaquera (ITA 2009–2011), in the city of São Paulo, Brazil.

Taxon	Relative frequency (%) VM 1998/1999	Relative frequency (%) VM 2009–2011	Relative frequency (%) ITA 2009–2011
Acromyrmex sp. 1	—	—	3.80
Brachymyrmex sp. 1	36.36	17.72	8.86
Brachymyrmex sp. 2	—	6.33	—
Brachymyrmex sp. 3	—	1.27	—
Camponotus (*Tanaemyrmex*) sp. 1	6.82	1.27	1.27
Camponotus crassus (Mayr, 1862)	—	1.27	7.59
Camponotus rufipes (Fabricius, 1775)	—	—	6.33
Camponotus sp. 1	1.52	—	—
Camponotus sp. 2	—	2.53	—
Cardiocondyla sp. 1	15.15	—	1.27
Crematogaster sp.	1.52	—	1.27
Cyphomyrmex sp. 1	0.76	1.27	3.80
Dorymyrmex sp. 1	0.76	—	3.80
Ectatomma sp. 1	—	1.27	5.06
Nesomyrmex sp. 1	5.30	2.53	16.46
Linepithema humile (Mayr, 1868)	10.61	—	—
Linepithema sp. 1	—	—	3.80
Linepithema sp. 2	—	—	1,27
Monomorium floricola Jerdon, 1851	—	6.33	5.06
Monomorium pharaonis (Linnaeus, 1758)	—	—	2,53
Monomorium sp.	6.06	—	—
Nylanderia fulva (Mayr, 1862)	40.15	5.06	17.72
Octostruma sp. 1	—	—	1.27
Pachycondyla sp. 1	0.76	2.53	3.80
Pachycondyla sp. 2	—	—	1.27
Paratrechina longicornis (Latreille, 1802)	6.06	17.72	22.78
Pheidole dimidiata Emery, 1894	7.58	2.53	1.27
Pheidole fallax Mayr, 1870	3.79	—	1,27
Pheidole megacephala (Fabricius, 1783)	24.24	37.97	—
Pheidole risii Forel, 1892	0.76	1.27	1.27
Pheidole sp. 1	—	7,59	2,53
Pheidole sp. 2	—	—	1.27
Pheidole sp. 3	—	—	3.80
Pheidole sp. 4	—	7.59	2.53
Pheidole sp. 5	—	—	1.27
Pheidole sp. 6	0.76	1.27	—
Pheidole sp. 7	0.76	—	—
Pheidole nubila Emery, 1906	0.76	—	6.33
Hypoponera sp. 1	—	1.27	—
Pseudomyrmex termitarius (Smith, 1855)	—	1.27	1.27
Solenopsis sp.	23.48	7.59	25.32
Solenopsis (Diplorhoptrum) sp. 1	12.12	3.80	2.53
Tapinoma melanocephalum (Fabricius, 1793)	19.70	56.96	79.75
Wasmannia auropunctata (Roger, 1863)	—	3.80	—

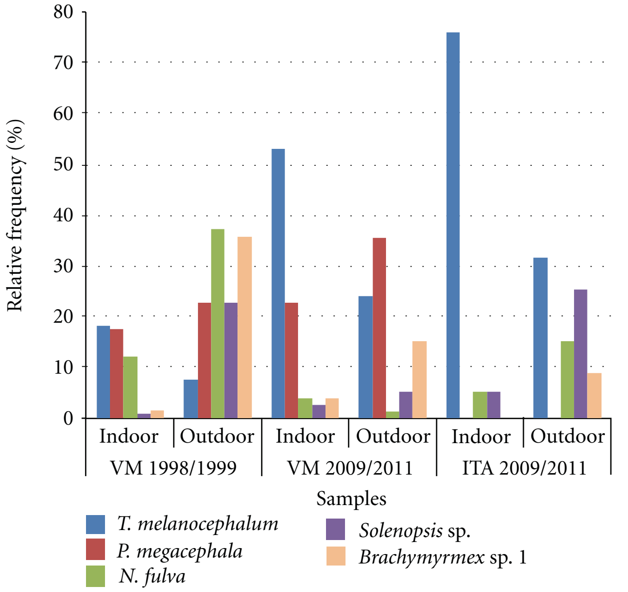


Figure 3: Relative frequencies of the most common sampled ant species in Vila Mariana from 1998 to 1999 (VM 1998/1999), 2009 to 2011 (VM 2009–2011) and Itaquera, from 2009 to 2011 (ITA 2009/2011), in the city of São Paulo.

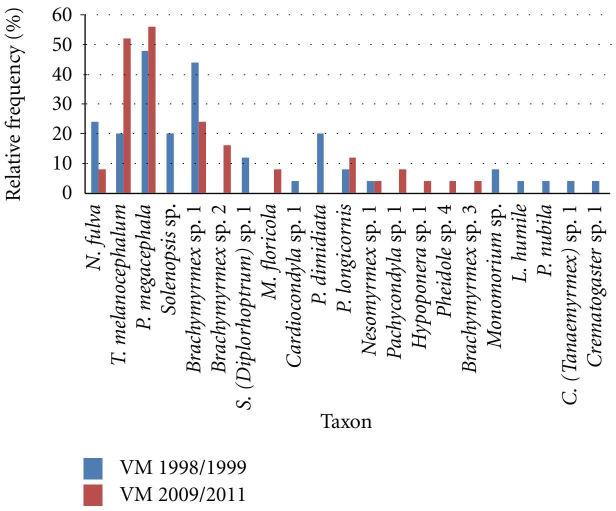


Figure 4: Relative frequency of ant species collected in the same 25 houses in 1998/1999 and 2009–2011, in Vila Mariana (VM), São Paulo, Brazil.

3.2. Neighborhood Profiles. Itaquera is a neighborhood with small- and single-story houses, recently constructed, with more children and few areas of gardens and backyards. The worst conserved and with less cleanness houses were found there. In Vila Mariana, houses are bigger, more ancient than in Itaquera, with a large number of two-story houses, and with more gardens and backyards (Table 4).

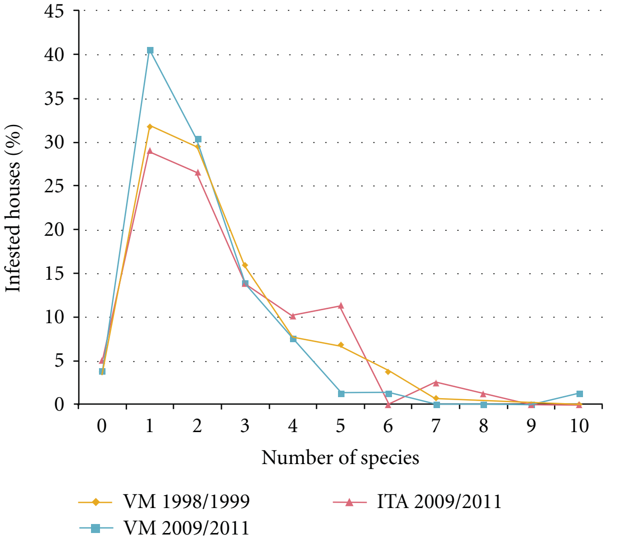


Figure 5: Number of ant species collected per house in Vila Mariana (VM), 1998/1999 and 2009–2011, and Itaquera (ITA) in the city of São Paulo, Brazil.

Table 3: Species richness, Shannon-Wiener diversity index (H′), equitability (E), and Simpson's diversity index (D) in Vila Mariana and Itaquera, in the city of São Paulo.

	Vila Mariana (1998/1999)	Vila Mariana (2009–2011)	Itaquera (2009–2011)
Species richness	24	25	33
H′	1.87	1.42	0.96
E	0.60	0.44	0.27
D	0.207	0.381	0.648

Table 4: Characteristics of houses sampled in Vila Mariana and Itaquera, in the city of São Paulo, Brazil.

Characteristic	Vila Mariana (1998/1999)	Vila Mariana (2009–2011)	Itaquera (2009–2011)
One-story houses (%)	11.4	15.2	74.7
Two-story houses (%)	88.6	84.8	25.3
Mean number of rooms per house	9.4	8.1	4.8
Mean of residents per house	3.4	3.4	3.7
Houses with children (%)	20.8	16.4	43.5
Mean house age (years)	44.8	49.9	25.1
Houses with gardens (%)	85.6	72.1	34.1
Houses with pets (%)	47.3	50.6	60.7

3.3. Comparative Analysis between Ant Samples and Environment Characteristics. The Mann-Whitney and Kruskal-Wallis tests showed that more ant species were found in single-story houses ($P = 0.007$), mainly in their outdoors, and in both neighborhoods, in both periods of collections. *T. melanocephalum* was more frequent in houses with children ($P = 0.001$). On the other hand, *P. megacephala* was more frequent in houses without children ($P = 0.007$). Yet, according to the Mann-Whitney test, the highest frequencies of ant specimens outdoors ($P < 0.001$), as the number of ant species ($P = 0.002$), are higher in external areas in houses with gardens and backyards. *P. megacephala* is mainly found in houses with gardens and backyards ($P < 0.001$). Houses without pets showed the highest species richness even indoors ($P = 0.042$), and outdoors ($P = 0.016$), the worst conserved houses showed species richness ($P = 0.042$) and pour cleanness houses showed higher ant abundance ($P = 0.047$).

4. Discussion

Tapinoma melanocephalum was the most common species in Vila Mariana in both studied periods and in Itaquera. Other surveys in urban areas also pointed to this same species [4, 14, 24] as one of the most common ants in urban environments. *T. melanocephalum* is distributed throughout the world [10] and recruits a huge number of workers when a food resource is found [13], explaining its high abundance in our samples. As in São Paulo, in a survey conducted in New York in 2010, an exotic species was the most collected [19].

After ten years, it expanded its range in Vila Mariana as did *P. megacephala* and *P. longicornis,* contributing to the displacement of *N. fulva*, *Brachymyrmex* sp. 1, and *Solenopsis* sp. populations. *P. megacephala* is an aggressive and dominant ant species known to displace native ant fauna where it is introduced [7–9]. *P. longicornis* was pointed by Forys and Allen [18] as the most common ant species in the region of Lower Florida Keys, and it was positively associated with the increase of urban development.

In a survey conducted in 1994 in a banana crop in southeastern Brazil, Fowler et al. [25] reported negative association between *T. melanocephalum* and *P. longicornis*. From 80 surveyed banana farms, 31 showed *P. longicornis* and 18 had *T. melanocephalum* presence, and in none of them both species were collected together. In our study, *P. longicornis* association was not analyzed with other ant species in Vila Mariana in 1998/1999 once its frequency and abundance were too low. But frequency data compared in both collected periods in Vila Mariana showed that this species is expanding its range. When association analysis was calculated to the most recent ant collections in Vila Mariana, *P. longicornis* only showed negative association with *P. megacephala*. This is explained by the fact that *P. longicornis* was not collected inside households, only outdoors where we also found *P. megacephala*. As *T. melanocephalum* occurrence is more frequent indoors than outdoors, they did not establish any ecological association.

In the central-eastern Brazil, surveys showed *P. megacephala* in ancient neighborhoods, with intense commercial activities and without expressive green areas [4], environments similar to Vila Mariana. Pacheco and Vasconcelos [5] also found this species in commercial areas and poorly preserved. In fact, commercial areas were also reported in a survey conducted by Menke et al. [26] with several invading ant species, as we have found in Vila Mariana. Therefore, it cannot be affirmed that this species prefers such urban environments. The establishment and dominance of invading species are related to several biotic and abiotic factors that must be better studied.

For *T. melanocephalum* to establish its nests, cleanness and resident habitats seem not to be relevant, but they can be decisive to their high frequency and abundance. In Itaquera, around 43% of the total sampled houses showed regular or very bad cleanness, and almost 25% were poorly preserved. Such conditions favor food offering and shelter [27] in order to promote suitable conditions for ant colonies development. Therefore, the best condition observed in Itaquera to be a good environment for *T. melanocephalum* was the absence of other ant species, as dominant as the ghost ant is, like *P. megacephala*.

Children presence may favor *T. melanocephalum* establishment, once data were similar in Vila Mariana after one decade and when the neighborhoods were separately analyzed. Children may offer more food on several rooms of the house favoring this opportunistic ant species.

A decrease on the ant diversity in Vila Mariana after 10 years was found when we calculated the Shannon-Wiever diversity index, but even though it is higher than in Itaquera. The low ant diversity in Itaquera must be attributed to *T. melanocephalum* abundance. Simpson's index corroborates this statement, once its value was higher in Itaquera, pointing to the dominance of one ant species.

An interesting data showed by the comparative analysis using the Mann-Whitney test between the collections from 2009 to 2011 in the two different neighborhoods is that *T. melanocephalum* was found in the peridomiciliar area in Itaquera and Vila Mariana equally. Peridomiciliar in these neighborhoods was different, with more gardens and backyards in Vila Mariana. But *T. melanocephalum* occurrence outdoors was lower than indoors, in both neighborhoods, probably due to the competition with other ant species and to abiotic factors such as temperature and moisture. In a survey conducted in 2009 by Wetterer [10], he reports that the ghost ant is restricted to indoors once the species can live wherever man is. He also emphasizes that it is found in tropical and subtropical zones in latitudes higher than 30°. MacGown and Hill [28] confirm this statement and comment that, besides, it is found in the United States and in some states in Canada; the occurrences are in greenhouses and other warm places, strengthening that temperature influences its distribution, but it can be solved when occupies human dwellings with controlled temperature. In our work, *T. melanocephalum* was found mainly in the indoors even though there were differences among houses and human habits in both neighborhoods. Menke et al. [26] also highlight the role of cities as a refuge for generalist species that show more tolerance to dryer and hotter environments.

Differences in the environment outdoors are not significant for *T. melanocephalum* once this is not the most favorable environment for its establishment.

Itaquera has a recent urbanization process; new households, streets, and avenues have been continually built as other landscape transformation caused by such processes, what may favor opportunistic ant species with flexible adjustments to such disturbances, like *T. melanocephalum*.

Many authors discuss this fact like Tschinkel [16] who suggested that *S. invicta* whose native environment is seasonally flooded and is a species that easily adapts to highly disturbed environments, even in different continents. When native ant populations were compared with invasive/exotic ant species in recent and ancient urban areas, the exotic species succeed in establishing in recent urbanized areas [29], while the native species remained in the ancient urban areas. Native and exotic species distribution in a city is still a not very well-explained question although the preference from exotic species for disturbed environments is known. Studies suggest that there is a series of relationships between biotic and abiotic factors that makes this question so complex [18, 19].

This explains the species richness found in Itaquera compared to Vila Mariana and the high dominance by *T. melanocephalum* in the former neighborhood, a still unknown ant species but intimately linked to the São Paulo citizens.

Yet, the number of houses with several ant species in Itaquera is related to the green area that surrounds the neighborhood and many species that are not common to urban areas like *Acromyrmex* sp., *C. crassus, C. rufipes, Cyphomyrmex* sp., *Linepithema* spp., *Octostruma* sp., and 9 *Pheidole* species. The bad conservation of houses in Itaquera also may contribute to the establishment of ants inside and in the peridomiciliar areas of the houses.

Acknowledgment

The authors thank those residents who permitted the ant collections in their homes. This paper was presented at the 7th International Conference on Urban Pests, in Ouro Preto, August, 2011.

References

[1] D. A. Holway, L. Lach, A. V. Suarez, N. D. Tsutsui, and T. J. Case, “The causes and consequences of ant invasions,” *Annual Review of Ecology and Systematics*, vol. 33, pp. 181–233, 2002.

[2] J. H. Delabie, I. C. Nascimento, P. Pacheco, and A. B. Casimiro, “Community structure of house-infesting ants (Hymenoptera: Formicidae) in southern Bahia, Brazil,” *Florida Entomologist*, vol. 78, no. 2, pp. 264–270, 1995.

[3] A. Piva and A. E. C. Campos-Farinha, “Estrutura de comunidade das formigas urbanas do bairro da Vila Mariana na cidade de São Paulo,” *Naturalia*, vol. 24, pp. 115–117, 1999.

[4] N. S. Soares, L. D. O. Almeida, C. A. Gonçalves, M. T. Marcolino, and E. A. M. Bonetti, “Survey of ants (Hymenoptera: Formicidae) in the urban area of Uberlândia, MG, Brazil,” *Neotropical Entomology*, vol. 35, no. 3, pp. 324–328, 2006.

[5] R. Pacheco and H. L. Vasconcelos, “Invertebrate conservation in urban areas: Ants in the Brazilian Cerrado,” *Landscape and Urban Planning*, vol. 81, no. 3, pp. 193–199, 2007.

[6] W. M. Wheeler, “The ants of Porto Rico and the Virgin Islands,” *Bulletin of the American Museum of Natural History*, vol. 24, pp. 117–158, 1908.

[7] J. K. Wetterer and B. C. O’Hara, “Ants (Hymenoptera: Formicidae) of the dry tortugas, the outermost Florida Keys,” *Florida Entomologist*, vol. 85, no. 2, pp. 303–307, 2003.

[8] C. Vanderwoude, L. A. Lobry De Bruyn, and A. P. N. House, “Response of an open-forest ant community to invasion by the introduced ant, *Pheidole megacephala*,” *Austral Ecology*, vol. 25, no. 3, pp. 253–259, 2000.

[9] B. D. Hoffmann and C. L. Parr, “An invasion revisited: the African big-headed ant (*Pheidole megacephala*) in northern Australia,” *Biological Invasions*, vol. 10, pp. 1171–1181, 2008.

[10] J. K. Wetterer, “Worldwide spread of the ghost ant, *Tapinoma melanocephalum* (hymenoptera: For-micidae),” *Myrmecological News*, vol. 12, pp. 23–33, 2009.

[11] M. F. M. Zarzuela, M. C. C. Ribeiro, and A. E. C. Campos-Farinha, “Distribuição de formigas em um hospital da região sudeste do Brasil,” *Arquivos do Instituto Biológico*, vol. 69, no. 1, pp. 85–87, 2002.

[12] C. M. Kamura, M. S. C. Morini, C. J. Figueiredo, O. C. Bueno, and A. E. C. Campos-Farinha, “Ant communities (Hymenoptera: Formicidae) in an urban ecosystem near the Atlantic Rainforest,” *Brazilian Journal of Biology*, vol. 67, no. 4, pp. 635–641, 2007.

[13] A. E. C. Campos-Farinha, J. J. Justi, E. C. Bergmann, F. J. Zorzenon, and S. M. R. Netto, “Formigas Urbanas,” *Bol. Técn. Inst. Biol.*, no. 8, pp. 5–20, 1997.

[14] J. H. Klotz, J. R. Mangold, K. M. Vail, L. R. Davis Jr., and R. S. Patterson, “A survey of the urban pest ants (Hymenoptera: Formicidae) of Peninsular Florida,” *Florida Entomologist*, vol. 78, no. 1, pp. 109–118, 1995.

[15] S. Cremer, L. V. Ugelvig, F. P. Drijfhout et al., “The evolution of invasiveness in garden ants,” *PLoS One*, vol. 3, no. 12, Article ID e3838, 2008.

[16] W. R. Tschinkel, “Distribution of the fire ants *Solenopsis invicta* and *S. geminata* (Hymenoptera: Formicidae) in northern Florida in relation to habitat and disturbance,” *Annals of the Entomological Society of America*, vol. 81, no. 1, pp. 76–81, 1988.

[17] K. M. Clarke, B. L. Fisher, and G. LeBuhn, “The influence of urban park characteristics on ant (Hymenoptera, Formicidae) communities,” *Urban Ecosystems*, vol. 11, no. 3, pp. 317–334, 2008.

[18] E. A. Forys and C. R. Allen, “The impacts of sprawl on biodiversity: the ant fauna of the lower Florida Keys,” *Ecology and Society*, vol. 10, no. 1, article no. 25, 2005.

[19] M. Pećarević, J. Danoff-Burg, and R. R. Dunn, “Biodiversity on broadway—enigmatic diversity of the societies of ants (formicidae) on the streets of New York City,” *PLoS One*, vol. 5, no. 10, Article ID e13222, 2010.

[20] J. P. Lessard and C. M. Buddle, “The effects of urbanization on ant assemblages (Hymenoptera: Formicidae) associated with the Molson Nature Reserve, Quebec,” *Canadian Entomologist*, vol. 137, no. 2, pp. 215–225, 2005.

[21] S. Siegel and N. J. Castellan Jr., *Estatística Não-Paramétrica para Ciências do Comportamento*, Artmed, Porto Alegre, Brazil, 2006.

[22] SAS Institute Inc, *The SAS System for Windows (Statistical Analysis System)*, version 8.02., Cary, NC, USA, 1999–2001.

[23] G. C. Thomas, “Biodap – Ecological, Diversity and its measurement,” 2010, http://nhsbig.inhs.uiuc.edu/populations/bio-dap.zip.

[24] P. Chacón de Ulloa, “Urban ants,” in *Introduction to the Ants in the Neotropics*, F. Fernández, Ed., pp. 351–359, Research Institute of Biological Resources Alexander von Humboldt, Bogotá, Colombia, 2003.

[25] H. G. Fowler, M. N. Schlindwein, and M. A. Medeiros, “Exotic ants and community simplification in Brazil: a review of the Impact of exotic ants on native ant assemblages,” in *Exotic Ants: Biology, Impact and Control of Introduced Species*, D. F. Williams, Ed., pp. 151–162, Westview Press, Boulder, Colo, USA, 1994.

[26] S. B. Menke, B. Guénard, J. O. Sexton, M. D. Weiser, R. R. Dunn, and J. Silverman, “Urban areas may serve as habitat and corridors for dry-adapted, heat tolerant species: an example from ants,” *Urban Ecosystems*, vol. 14, pp. 135–163, 2011.

[27] O. C. Bueno and A. E. C. Campos-Farinha, “As formigas domésticas,” in *Insetos e Outros Invasores de Residências*, F. A. M. Mariconi, Ed., pp. 135–180, FEALQ, Piracicaba, Brazil, 1999.

[28] J. MacGown and J. V. G. Hill, “Tapinoma melanocephalum (Hymenoptera: Formicidae), a new exotic ant,” *Journal of the Missisipi Academy of Sciences*, vol. 54, pp. 172–174, 2009.

[29] R. M. Plowes, J. G. Dunn, and L. E. Gilbert, “The urban fire ant paradox: native fire ants persist in an urban refuge while invasive fire ants dominate natural habitats,” *Biological Invasions*, vol. 9, no. 7, pp. 825–836, 2007.

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 516058, 24 pages
doi:10.1155/2012/516058

Research Article

The Ant Genus *Dorymyrmex* Mayr (Hymenoptera: Formicidae: Dolichoderinae) in Colombia

Fabiana Cuezzo[1] **and Roberto J. Guerrero**[2, 3]

[1] *CONICET, INSUE, Facultad de Ciencias Naturales e IML, Miguel Lillo 205, T4000JFE San Miguel de Tucumán, Argentina*
[2] *Grupo de Investigación en Insectos Neotropicales, Instituto de Investigaciones Tropicales (INTROPIC), Universidad del Magdalena, Carrera 32 No. 22-08, Santa Marta, Colombia*
[3] *Instituto de Zoología y Ecología Tropical, Facultad de Ciencias, Universidad Central de Venezuela, Caracas, Venezuela*

Correspondence should be addressed to Fabiana Cuezzo, cuezzof@yahoo.com.ar

Received 27 May 2011; Accepted 28 July 2011

Academic Editor: Jacques H. C. Delabie

The aim of this paper is to actualize the taxonomy of *Dorymyrmex*, by addressing problems at both the genus and the species levels. We also explore the taxonomy and distribution of *Dorymyrmex* in Colombia. We list, diagnose, and key nine species in the country, including three new species: *Dorymyrmex amazonicus* n. sp. Cuezzo & Guerrero, *Dorymyrmex xerophylus* n. sp. Cuezzo & Guerrero, and *Dorymyrmex tuberosus* n. sp. Cuezzo & Guerrero. We provide a detailed description of these new species based on the worker caste and, where possible, other castes. All localities where *Dorymyrmex* was collected or cited in the literature were mapped to provide a graphical view of its range.

1. Introduction

Dorymyrmex Mayr [1] is one of the most diverse and complex genera of the ant subfamily Dolichoderinae from a taxonomical and biogeographical point of view. In a recent study, Ward et al. [2] provided a detailed phylogeny of Dolichoderinae based on molecular data and proposed an internal arrangement of this subfamily in four tribes, based in one unrooted topology: (((Dolichoderini, Leptomyrmecini), Bothriomyrmecini, Tapinomini)). *Dorymyrmex* is considered by these authors as a monophyletic member of Leptomyrmecini and sister group of *Forelius* Emery, 1888 [3].

This genus has a strictly American distribution, inhabiting in the Nearctic and Neotropical regions and containing more than 90 species, several undescribed. Reasons for considering as an especially difficult group of ants include variability within species in color, pilosity, sculpture, and size. The majority of species are actually poorly defined, often distinguished only on the basis of color. No broader modern taxonomic key exists at species level. The most recent contribution to solve the taxonomic jungle of *Dorymyrmex* was Snelling [4], who built on work by Trager [5] to clarify the taxonomy of the Nearctic species.

Despite being considered by many ant collectors as “road side weeds”, several species of *Dorymyrmex* shown a high degree of endemicity, specialized habitat preferences, and varied population structure. Some species may serve as potential agents of biological control of annual crop pests [5, page 12]. Species of *Dorymyrmex* nest preferentially in dry or disturbed habitats, generally in soil without vegetation cover. Several species are known to attend aphids and other hemipterous insects. Such behavior is common in other Dolichoderinae genera and related subfamilies.

The main purposes of this paper are to provide a redefinition of *Dorymyrmex* using morphological characters from worker, queen, and male and to make a revision of the genus in Colombia. We describe three new species and provide a key to workers of all nine species found in Colombia. This is the first contribution of a series of systematic studies about this still poorly known ant genus.

2. Materials and Methods

2.1. Studied Material Belongs to the Following Institutions

CASC: California Academy of Sciences, San Francisco, California, USA.

CEUM: Insect Collection, Universidad del Magdalena, Santa Marta, Magdalena, Colombia.

IAvH: Insect Collection Instituto Alexander von Humboldt, Villa de Leyva, Boyacá, Colombia.

ICN: Insect Collection, Instituto de Ciencias Naturales, Universidad Nacional, Bogotá D.C., Colombia.

IFML: Instituto Fundación Miguel Lillo, Tucumán, Argentina.

LACM: Los Angeles County Museum of Natural History, Los Angeles, California, USA.

MCZC: Museum of Comparative Zoology, Cambridge, Massachusetts, USA.

MHNG: Muséum d'Histoire Naturelle, Geneva, Switzerland.

MZSP: Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil.

NHMB: Natural History Museum of Basel, Switzerland.

USNM: United States National Museum of Natural History/Smithsonian Institution, Washington D.C., USA.

2.2. Primary Type Material Examined

2.2.1. Dorymyrmex amazonicus **Holotype**. Amazonas, Leticia, 4 13 08 S 69 56 29 W, 06 Jun 1976, COLOMBIA (ICN). Paratypes: 2w, Amazonas, Leticia, 4 13 08 S 69 56 29 W, 06 Jun 1976, COLOMBIA: 1w (CASC), 1w (IFML).

2.2.2. Dorymyrmex bicolor **Syntypes**. 1w and 1q, Phoenix, USA (MCZC); 2w, Tucson, Arizona, USA (MHNG).

2.2.3. Dorymyrmex biconis **Syntypes**. 2w, Sierra Nevada de Santa Marta, San Antonio, Guajira Prov., COLOMBIA (MHNG).

2.2.4. Dorymyrmex brunneus **Lectotypes**. 2w, São Paulo, BRAZIL (MHNG) designed by Kempf 1975: 375 [6].

2.2.5. Dorymyrmex goeldii **Syntypes**. 2w, Pará, BRAZIL (MHNG).

2.2.6. Dorymyrmex insanus **Neotype**. 1w, Interstate 20, 12 mi E Big Spring, Howard Co., Texas, USA, 16 April 1981, coll. by W. F. Buren, (USNM) designed by Snelling 1995: 4 [4].

2.2.7. Dorymyrmex tuberosus **Holotype**. 1w, Santander: Bucaramanga, UIS, 906 m., 7 21 0.12 N 73 20 1.22 W, COLOMBIA, Jun 2003, N. Ruiz & F. Fernández coll., (ICN). Paratypes: 7w, Bolivar, San Juan Nepomuceno, 24.Oct.1990 F. Bekker leg. Ex *Manihot esculenta*, COLOMBIA: 2w, (USNM); same data and loc. than holotype, 4w, (ICN), 1w (CASC).

2.2.8. Dorymyrmex xerophylus **Holotype**. 1w, Magdalena, Santa Marta, Vereda Mosquito, 11 10 23.6 N 74 10 45 W 96 m, manual collection; 03 Jan 2008, R. Guerrero, coll., COLOMBIA (ICN). Paratypes: 1w, La Guajira, Zona El Cerrejón, 11 1 59.88 N 72 39 0 W, 240 m, COLOMBIA, pitfall trap, 19 Dec 2006, R. Guerrero, coll., (ICN); 1w, Magdalena, Santa Marta, Vereda Mosquito, 11 10 23.6 N 74 10 45 W 96 m, COLOMBIA, manual collection; 03 Jan 2008, R. Guerrero, coll., (CEUM).

2.3. Measurements and Indexes. Measurements were taken with micrometer ocular to 40x–80x attached to a stereoscope. All measurements are expressed in mm. The measurements and indexes used were the following:

HL: head length, in full-face view, the maximum length of the head capsule,

HW: head width, in full-face view, the maximum width of the head capsule above the eyes,

EL: eye length, the maximum length of the eye in full-face view,

EW: eye width, the maximum width of the eye in full-face view,

SL: scape length, the length of the scape from the apex to the basal flange, not including the basal condyle,

WL: Weber's length, measured in perfect lateral view of the mesosoma, diagonally from the posteroventral corner of the mesosoma to the farthest point on anterior face of the pronotum, excluding the neck.

Indexes

CI: Cephalic Index = HW × 100/HL.

SI: Scape Index = SL × 100/HL.

REL: Relative Length of the Eye = EL × 100/HL.

OI: Ocular Index = EW × 100/EL.

TLI: Thorax Length Index = WL × 100/HL.

Holotypes will be deposited in IAvH, ICN and paratypes in CASC, CEUM, IFML, and MZSP. All the species recorded were re-described based in all castes (worker, gyne, and male) when material was available.

Male terminology follows Ward [7].

3. Results

3.1. Synopsis. Genus *Dorymyrmex* Mayr, 1866 [1].

Type species: *Dorymyrmex flavescens*, by monotypy.

Region: Neotropical, Nearctic.

Dorymyrmex Mayr (1866a: 494 [1]).

Psammomyrma as subgenus of *Dorymyrmex*: Forel, 1912: 43 [8]. Type species: *Dorymyrmex planidens*, by subsequent designation of Wheeler, 1913: 82 [9]. Kempf, 1972: 100 [10].

Psammomyrma as junior synonym of *Dorymyrmex*: Forel, 1913: 350 [11]; Santschi, 1922: 365 [12]; Wheeler, W. M. 1922: 689 [13]; Snelling and Hunt, 1976: 93 [14]; Shattuck, 1992: 77 [15]; Bolton, 1994: 27 [16]; Bolton, 2003: 86 [17].

Conomyrma as subgenus of *Dorymyrmex*: Forel, 1913: 350 [11]. Type species: *Prenolepis pyramica*, by subsequent designation of Santschi, 1922: 365 [12]; Forel, 1917: 248 [18]; Wheeler, W. M., 1922: 689 [13]; Gallardo, 1930: 147 [19]; Smith, M. R., 1951: 837 [20]; Smith, M. R., 1958: 140 [21].

Conomyrma as a genus: Kusnezov, 1952: 429 [22]; Kusnezov, 1959: 51 [23]; Kusnezov, 1964: 66 [24]; Kempf, 1972: 78 [10]; Snelling, 1973: 1 [25]; Smith, D. R., 1979: 1419 [26]; Holldöbler and Wilson, 1990: 17 [27]; Jaffé, 2004: 9 [28].

Conomyrma as junior synonym of *Dorymyrmex*: Brown Jr., 1973: 179 (provisional) [29]; Shattuck, 1992: 77, [15]; Bolton, 2003: 86, [17].

Araucomyrmex as genus: Gallardo, 1919: 249 [30]. Type species: *Dorymyrmex tener*, by original designation; Wheeler, 1922 [13]: 689; Kusnezov, 1956: 28 [31]; Kusnezov, 1959: 51 [23]; Kusnezov, 1964: 66 [24]; Kempf, 1972: 25 [10]; Snelling, 1975: 9 [32]; Snelling and Hunt, 1976: 93 [14]; Dlussky and Fedoseeva, 1988: 77 [33].

Araucomyrmex as junior synonym of *Conomyrma*: Snelling, 1981: 402 [34].

Araucomyrmex as junior synonym of *Dorymyrmex*: Brown Jr., 1973: 178 (provisional) [29]; Shattuck,1992: 77 [15]; Bolton, 2003: 87 [17].

Ammomyrma as a subgenus of *Dorymyrmex*: Santschi, 1922: 365 [12]. Type species: *Dorymyrmex exanguis*, by original designation. Gallardo, 1930: 147 [19]; Kempf, 1972: 100 [10].

Ammomyrma as junior synonym of *Araucomyrmex*: Snelling and Hunt, 1976: 93 [14].

Ammomyrma as junior synonym of *Dorymyrmex*: Shattuck, 1992: 77 [15]; Bolton, 2003: 87 [17].

Biconomyrma as a subgenus of *Conomyrma*: Kusnezov, 1952: 429 [22]. Type species: *Dorymyrmex pyramicus* var. *brunneus* (now *Dorymyrmex brunneus*), by subsequent designation of Kusnezov, 1959: 51 [23].

Biconomyrma as genus: Kusnezov, 1959: 51 [23]; Kusnezov, 1964: 67 [24].

Biconomyrma as junior synonym of *Conomyrma*: Smith, M. R., 1958: 140 [21]; Kempf, 1972: 78 [10].

Biconomyrma as junior synonym of *Dorymyrmex*: Shattuck, 1992: 78 [15]; Bolton, 2003: 87 [17].

Spinomyrma as subgenus of *Dorymyrmex*: Kusnezov, 1952: 429 [22]. Type species: *Dorymyrmex alboniger*, by subsequent designation of Kusnezov, 1959: 51 [23]; Kempf, 1972: 100 [10].

Spinomyrma as genus: Kusnezov, 1956: 30 [31] (in key); Kusnezov, 1959: 51 [23]; Kusnezov, 1964: 66 [24].

Spinomyrma as junior synonym of *Dorymyrmex*: Kempf, 1972: 100 [10]; Snelling and Hunt, 1976: 93 [14]; Shattuck, 1992: 78 [15]; Bolton, 1994: 26 [16]; Bolton, 2003: 87 [17].

The characters used here to identify *Dorymyrmex* are based on the diagnosis proposed by Shattuck [15, page 78], with some differences. Characters mentioned below, with , are redefined and based in the Shattuck proposal; characters with are new.

We have not used the length of curved hairs placed in the dorsal clypeal margin proposed by Shattuck [15], because it is quite variable along the genus. Some species have these setae shorter, not reaching the distal edge of closed mandibles.

3.2. Diagnostic Characters Common to All Castes. Apical teeth of mandible elongate, at least twice longer than preapical . This character was used by Shattuck [15] only for workers but is also a constant in all known queens and males. Psammophore is present as a discrete group of elongated hairs, uniform in length, arranged in a definite pattern, on the ventral face of head . Third segment of the maxillar palp elongate, longer than segments 4 + 5 + 6 joined together.

3.3. Worker Diagnosis. Monomorphic to slightly polymorphic ants. Mandibles with 5-6 teeth and 2–4 denticles on masticatory margin and several denticles on basal margin . Dorsal surface of mandible longitudinally striated . Pair of erect setae on the dorsal face of pronotum present or absent . A well-defined spine, cone, or tubercle always present between dorsal and declivitous faces of propodeum .

3.4. Queen Diagnosis. Forewing with close radial cell . Forewing with 1-2 cubital cell and 0-1 discoidal cells . Hindwing with only 0–3 closed cells placed in the basal part of the wing .

3.5. Male Diagnosis. Antennal scape relatively short, at most only slightly longer than the length of funicular segments 1 + 2 + 3 . Second funicular segment with a lateral bend . Mandible with 2–4 teeth (sometimes with 2 or more denticles) . Forewing with close radial cell .

4. Dorymyrmex in Colombia

Only four species of *Dorymyrmex* have been mentioned in the most recent list of Neotropical ants [35] in Colombia. We record 9 species, two new records and three new for science: *Dorymyrmex amazonicus* n. sp., *Dorymyrmex tuberosus* n. sp., and *Dorymyrmex xerophylus* n. sp.

Table 1: Major characters differing among worker, queen, and male of *Dorymyrmex* and *Forelius*.

Character	*Dorymyrmex*	*Forelius*
Psammophore	Present	Absent
Third maxillary palp segment	Elongated	Subequal in length to the remaining segments
Apical tooth of mandible	Greatly elongated	Slightly larger than the subapical
Queen and male forewing	With a close radial cell	With an open radial cell

Major characters used to separate *Dorymyrmex* from *Forelius,* the closest Dolichoderinae ant genus found in South America are given in Table 1.

4.1. *List of Dorymyrmex in Colombia*

D. amazonicus n. sp. Cuezzo & Guerrero
D. bicolor Wheeler, 1906 [36]
D. biconis Forel, 1912 [8]
D. brunneus Forel, 1908 [37]
D. goeldii Forel, 1904 [38]
D. insanus (Buckley, 1866) [39]
D. pyramicus Roger, 1863 [40]
D. tuberosus n. sp. Cuezzo & Guerrero
D. xerophylus n. sp. Cuezzo & Guerrero.

4.2. Key to Dorymyrmex Workers in Colombia. This key is based on worker caste of all valid species of *Dorymyrmex* found in Colombia.

(1) Mesosomal profile with two well-developed tubercles, one on the posterodorsal margin of mesonotum and the other on the dorsal face of propodeum (Figures 3(b) and 11(b)) . . . (2).

(1) Mesosomal profile lacking a mesonotal tubercle (Figures 1(b), 8(b), and 9(d)); in some specimens, we can see an angle in the posterior end of mesonotum (Figures 2(b), 7(b), 7(d), 9(b), and 12(b)) but never a well-differentiated knob (= tubercle). Mesosomal profile bearing only a well-developed tubercle placed between the dorsal and declivitous faces of propodeum. . . . (3).

(2) Body concolorous light reddish brown to yellowish. Pubescence sparse. Dorsal face of propodeum, anterior to the tubercle, convex. Propodeal tubercle stout and higher than the promesonotal profile in lateral view (Figure 3(b)) . . . *D. biconis.*

(2) Body concolorous dark brown, pubescence dense. Dorsal face of propodeum, anterior to the tubercle, straight. Propodeal tubercle thin and lower than or at the same level than the promesonotal profile in lateral view (Figure 11(b)) . . . *D. tuberosus* n. sp.

(3) Body bicolored, head and mesosoma always yellow-reddish, gaster dark brown to black; some specimens could be lighter but always with the gaster darker than the rest of the body . . . (4).

(3) Body concolorous orange or medium to dark brown . . . (5).

(4) Promesonotal profile continuous (Figure 9(d)). Propodeal tubercle pointed backward. Petiolar scale short, sharp apically, forward directed. Subpetiolar process feebly developed, convex, and covering all the ventral surface of petiole . . . *D. pyramicus.*

(4) Promesonotal profile interrupted in posterior end of mesonotum, forming an angle and determining a clear mesosomal dorsal and declivitous face (Figure 2(b)). Petiolar scale tall, rounded apically, upward directed. Subpetiolar process not well developed, only conspicuous in the ventral end of petiole . . . *D. bicolor.*

(5) Posterior end of mesosoma, in lateral view, forming an angle but not a tubercle (Figures 7(b), 7(d), 9(b), 12(b), and 12(c)) . . . (6).

(5) Posterior end of mesosoma straight, without a differentiated dorsal and declivitous face (Figures 1(b) and 8(b)) . . . (8).

(6) Small ants, TLI: <117. Scape short, not surpassing the posterior margin of head more than twice its maximum diameter (Figure 12(a)). Posterior margin of head strongly convex . . . *D. xerophylus* n. sp.

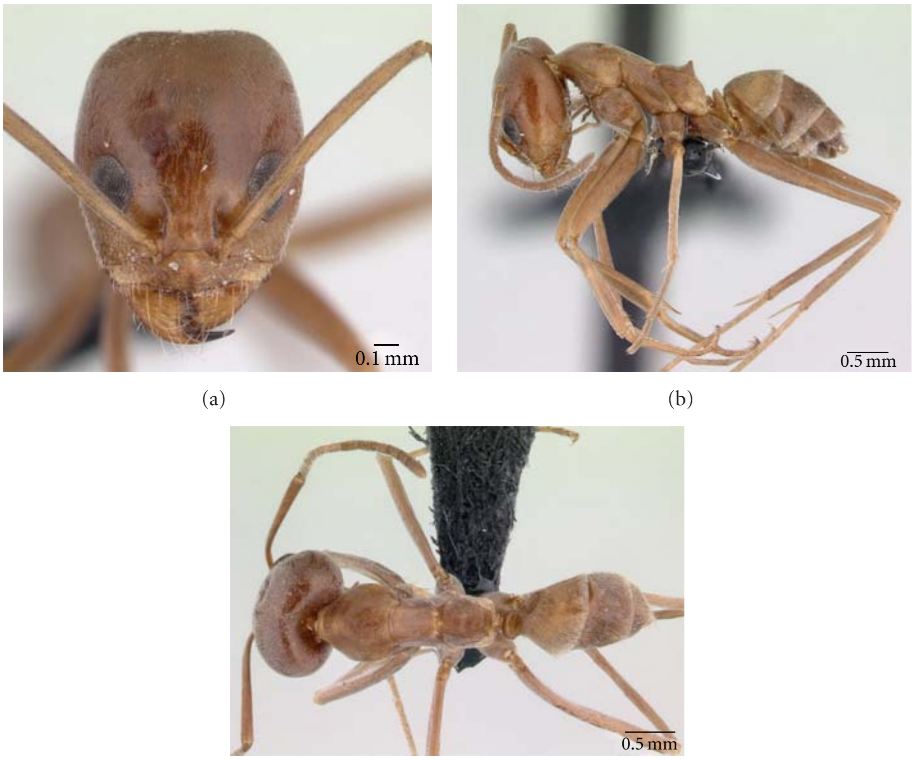
(6) TLI >117. Scape longer, surpassing the posterior margin of the head more than three times its maximum diameter (Figures 7(a), 7(c), and 9(a)). Posterior margin of head straight to concave in the middle but never convex . . . (7).

(7) Posterior margin of head always medially concave (Figure 9(a)). Promesonotal profile uniformly convex. Dorsal face of propodeum, anterior to the tubercle, straight (Figure 9(b)) . . . *D. insanus.*

(7) Posterior margin of head straight to slightly concave in the middle. Promesonotal profile straight to feebly convex. Dorsal face of propodeum, anterior to the tubercle, sinuous (Figures 7(b) and 7(d)) . . . *D. brunneus.*

(8) Lateral margin of head, in full-face view, strongly convex, with compound eyes placed far inside the head capsule (Figure 1(a)). Posterior margin of head concave in the middle. Propodeal tubercle well developed and upward directed (Figure 1(b)). . . . *D. amazonicus* n. sp.

(8) Lateral margin of head slightly convex (Figure 8(a)). Posterior margin of head strongly convex (Figure 8(a)). Propodeal tubercle poorly developed (Figure 8(b)) . . . *D. goeldii.*



(a)

(b)

(c)

Figure 1: *Dorymyrmex amazonicus* n. sp. worker, holotype. (a) Head in full-face view; (b) body in lateral view; (c) body in dorsal view (CASENT0192703). Pictures and labels of localities of each photographed specimen are available at http://www.antweb.org/.

5. Species Account

5.1. *Dorymyrmex amazonicus* Cuezzo & Guerrero n. sp. *(Figures 1(a)–1(c) and 13)*

5.1.1. *Diagnosis*

Worker. Large ant, TLI: 133–135. Head with lateral margins broadly convex and posterior margin of head concave medially. Short scape not surpassing the posterior margin of the head more than three times its apical width.

5.1.2. *Description*

Worker

Measurements. Holotype (Paratypes = 2). HL: 1.00 (1.02–1.04). HW: 0.92 (0.94–0.96). EL: 0.30 (0.28–0.30). EW: 0.22 (0.22). SL: 1.06 (1.06–1.08). WL: 1.32 (1.36–1.40). CI: 92 (92). SI: 106 (104). REL: 30 (27–29). OI: 73 (73–79). TLI: 132 (133–135).

Head and scapes reddish-brown; lateral clypeal region and dorsal face of mandibles testaceous yellow; masticatory mandibular margin dark brown; mesosoma, legs, petiole, and gaster yellowish-brown. Whitish, short, and appressed pubescence covering all the body tagma. *Head* (Figure 1(a)): head slightly longer than wide, with lateral margins strongly convex and posterolateral corners rounded. Posterior margin of the head concave in the middle. Mandibles strongly striate, with apical tooth four times longer than others. Masticatory margin with four denticles. Compound eye well developed and placed far inside the head capsule. Psammophore with short hairs disposed in a semicircle; the hairs on the top line are close to the foramen magnum and not reaching the oral cavity. Scape short (SI = 104–106) not surpassing the posterior margin of the head more than three times its apical width. *Mesosoma* (Figure 1(b)): dorsal face of pronotum with no erected setae, pronotum and mesonotum in profile forming a continuous line, not interrupted (Figure 1(b)), metanotal suture not impressed. Dorsum of propodeum weakly sinuate. Propodeal cone acute, upward directed with wide base. Apical point of the propodeal cone reaches the same level of the highest point of pro-mesonotum in lateral view. Declivitous face of propodeum convex. *Metasoma*: petiolar scale wide, thin and rounded in the apex.

Queen and Male. Unknown.

Examined Material. Type series.

Geographic Distribution. Colombia, Amazon rainforest. Only known from its type locality (Figure 13).

Etymology. The name *amazonicus* refers to the apparently unusual distribution of this species, the Amazon rainforest in Colombia. It is a noun in apposition and invariant.

(a)

(b)

(c)

Figure 2: *Dorymyrmex bicolor* worker. (a) Head in full-face view; (b) body in lateral view; (c) body in dorsal view (CASENT0179517). Pictures and labels of localities of each photographed specimen are available at http://www.antweb.org/.

Natural History. The type series was collected in the vicinity of an Amazonian forest relict, outside Leticia (Colombia). All the specimens were collected in open deforested habitat, probably this is an indication of the preference of this species to nest in highly anthropic or disturbed environments.

5.1.3. Comments. At first view, this species could be confused with *D. brunneus,* but a greater TLI, shorter scapes, eyes placed deep inside the head capsule, and a continuous mesosomal profile in *D. amazonicus* are the best characters to separate it from *D. brunneus*. Other *Dorymyrmex* species found in Colombia share with *D. amazonicus* the shape of mesonotal profile (i.e., *D. pyramicus*), but all the characters, given in the key and in the diagnosis above, are useful to separate *D. amazonicus* from other species of *Dorymyrmex* found in Colombia.

5.2. *Dorymyrmex bicolor* Wheeler, 1906 [36] *(Figures 2(a)–2(c), 6(a), and 13)*

Dorymyrmex pyramicus var. *bicolor* Wheeler, 1906: 342 [36]. Description of worker.

Dorymyrmex pyramicus var. *bicolor* Wheeler: Gallardo, 1916: 63 [41]. Description of queen.

Conomyrma (*Biconomyrma*) *bicolor* (Wheeler): Kusnezov, 1952: 430 [22].

Conomyrma bicolor Wheeler: Snelling, 1973: 4 [25]; Johnson, 1989: 192 [42].

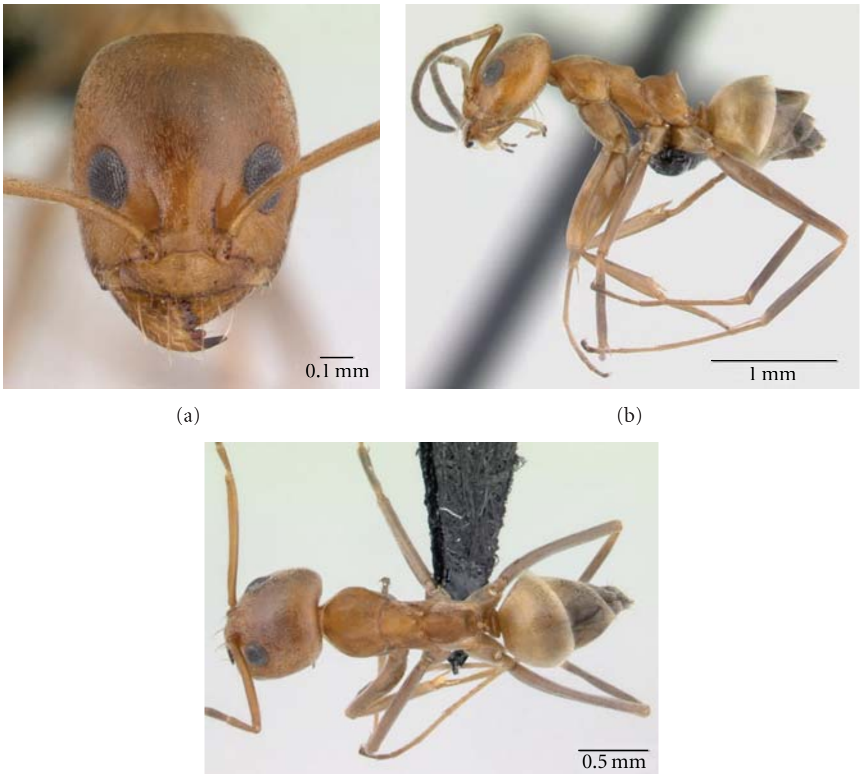
Dorymyrmex bicolor Wheeler: Cole Jr., 1957: 130 [43]; Crozier, 1970: 114 (karyotype) [44]; Shattuck, 1992: 85 [15]; Shattuck, 1994: 75 [45]; Snelling, 1995: (key) [4]; Bolton et al. 2006 (catalog) [46].

5.2.1. Diagnosis

Worker. CI equal or over 90. Worker bicolored: head, mesosoma, and petiole, dark reddish; gaster black (Figures 2(b) and 2(c)). Same pattern of color is found in queen. Posterior margin of the head slightly concave in frontal view. Dorsal face of pronotum with no erect setae. Mesonotal profile continuous with pronotum, with a distinct dorsal and declivitous face before mesopropodeal suture.

Queen. Head slightly wider than long with the posterior margin of head strongly concave (Figure 6(a)). Maximum diameter the head behind of compound eyes.

Male. Unknown.



(a) (b)

(c)

Figure 3: *Dorymyrmex biconis* worker. (a) Head in full-face view; (b) body in lateral view; (c) body in dorsal view (CASENT0179483). Pictures and labels of localities of each photographed specimen are available at http://www.antweb.org/.

5.2.2. Descriptions

Worker

Measurements. ($n = 25$): HL: 0.78–1.1; HW: 0.7–1; EL: 0.18–0.28; EW: 0.15–0.2; SL: 0.78–1.05; WL: 1.25–1.53; CI: 90-91; SI: 105–111; REL: 23–25; OI: 73–86; TLI: 139–161.

Worker bicolored: head, mesosoma, and petiole, dark reddish; gaster black. Funicle and legs darker than rest of the body in some specimens. *Head* (Figure 2(a)): square in frontal view, almost as wide as long, sides slightly convex. Posterior margin of head feebly convex medially. Scape short (SI: 105–111). Psammophore with short hairs disposed in a triangle, far from the foramen magnum, slightly reaching the oral cavity. *Mesosoma* (Figures 2(b) and 2(c)): promesonotum in profile, forming a continuous convexity; end of mesonotum with well-differentiated dorsal and declivitous faces, anterior to metanotal suture. Propodeal tubercle short, upward directed, with wide base. *Metasoma*: petiolar scale forward directed.

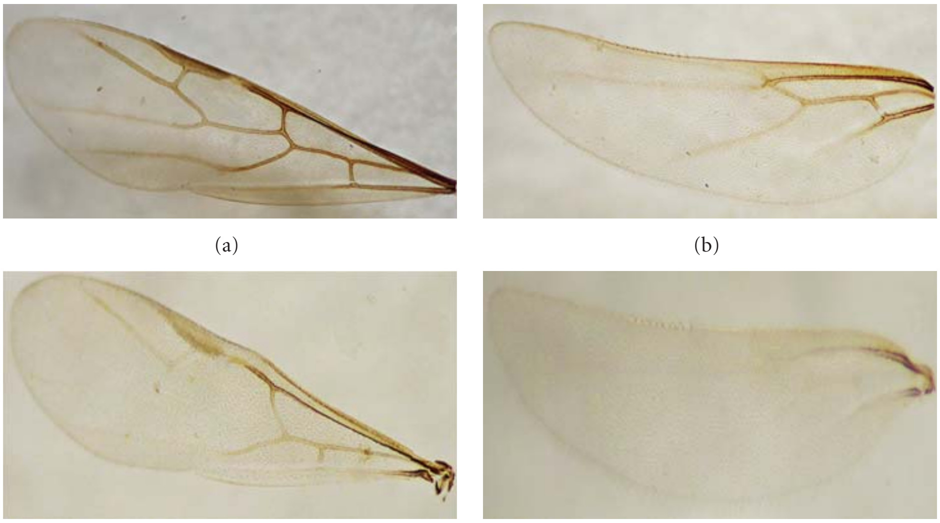
Queen

Measurements. ($n = 7$): HL: 1.18–1.23; HW: 1.25–1.33; EL: 0.38–0.4; EW: 0.18–0.23; SL: 1.08–1.13; WL: 2.43–2.6; CI: 106–108; SI: 91-92; REL: 32-33; OI: 47–56; TLI: 206–212.

Similar to worker in color. Whitish pubescence covering all body tagma. *Head*: Wider than long, with convex sides, in frontal view. Posterolateral corner rounded, posterior margin of head slightly concave (Figure 6(a)). Masticatory margin of mandible with six teeth and two or three denticles; basal margin completely dentate with a well-differentiated angle between both margins. Scape surpassing posterior margin of the head by more than twice its maximum diameter. *Mesosoma*: Parapsidal furrow well developed, diverging forward, axilla not divided. Anepisternum and katepisternum incompletely divided by a short pleural suture. Wings: forewing with only one close radial cell, one cubital cell, and no discoidal cell; pterostigma well developed, longer than wide. Hindwing with three cells closed in basal area; hamuli with 12 hooks. *Metasoma*: petiolar scale tall, stout, forward directed, and rounded apically. Ventral face of petiole slightly convex. Gaster with dark brown tergites and covered with whitish pubescence.

Male. Unknown.

Examined Material. COLOMBIA: La Guajira, Riohacha, Corregimiento Camarones, SFF Los Flamencos, 1w (CASC), 4w (CEUM); Magdalena, 1w (ICN), 1w (LACM) (see Figure 12).



(a) (b)

(c) (d)

Figure 4: Wings of *Dorymyrmex biconis.* (a) Queen forewing; (b) queen hindwing; (c) male forewing; (d) male hindwing.

Additional Examined Material. Outside COLOMBIA: Syntypes and no type material: USA (Western Texas to Southern Nevada, and California), Mexico, Belize, El Salvador, Grenada, Honduras, Jamaica, and Perú. MEXICO: Acapulco, 2w (USNM); Chihuahua, 1w, (LACM); Cordoba, 1w, (USNM); Guerrero, 2w, (USNM); Ixtapa, 8w, (LACM); Revolcadero, 4w, (USNM); Zihuatanejo, 4w, (LACM); Uruapan, 2w, (USNM); San Blas, Playa Nayarit, 2w (LACM); Sinaloa, 30.5mi N. Los Mochis, 1w, (LACM); Guaymas, 11w, (LACM); Nogales, 4w, (USNM); Rio Yaqui, 1w, (LACM); San Bernardo, 3w, (LACM); Tecamachalco, 7 mi. NW Puebla, 2w, (LACM); Veracruz, 2 mi. S. Mocambo, 3w, (USNM); Veracruz, Boca del Rio, 2w, (USNM); Cordoba, 1w, (USNM); Veracruz, Fortin, 3w, (USNM); Jalapa, 3w, (USNM); Itze ChiChen, 1w, (USNM); BELIZE: 9w, (USNM); EL SALVADOR: San Salvador, 2w, (USNM); GRENADA: BWI, St. George's, 8w, (USNM); HONDURAS: Tegucigalpa, 1w, (USNM); JAMAICA: no further data, 1w, (USNM); PERÚ: Lima, 10w, (USNM).

Geographic Distribution. Southwest of USA to Peru.

Etymology. The name of *bicolor* is referred to the particular pattern of colors found in all known castes (worker and queen).

Natural History. Nest, briefly described by Wilson [47], has a small entrance hall with more regularly formed craters than *D. insanus*. *D. insanus* and *D. pyramicus* are sympatric in the northern part of its distributional range. Both species mentioned above are very active in open areas between 11:00 a.m. and 3:30 p.m and share similar habits of foraging according wilson's observations [47].

5.2.3. Comments. Several species of *Dorymyrmex* (*D. pyramicus, D. thoracicus,* etc.) have the same pattern of colors and could be confused with *D. bicolor* s. str. In some papers, *D. bicolor* was confused with *D. pyramicus*, because of its pattern of colors (orange head, mesosoma and petiole with dark gaster), but two main characters are useful to identify and to differentiate both species: head width (larger in workers and queens of *D. bicolor*) and mesonotum interrupted in lateral view, with a well-defined dorsal and declivitous faces, often descending vertically or nearly so, into mesopropodeal suture, (as described below, *D. pyramicus* has a promesonotal profile continuous, convex in lateral view). Apparently, *D. bicolor* belongs to a complex of species, as observed by Forel [48]. The identity of this complex could be solved with a more detailed and extensive research, specially comparing nest series from the west part of USA.

5.3. Dorymyrmex biconis Forel, 1912 [8] *(Figures 3(a)–3(c); 4(a)–4(d); 5(a)–5(d); 6(c)-6(d); 13)*

Dorymyrmex biconis Forel, 1912: 37 [8]. Description of worker.

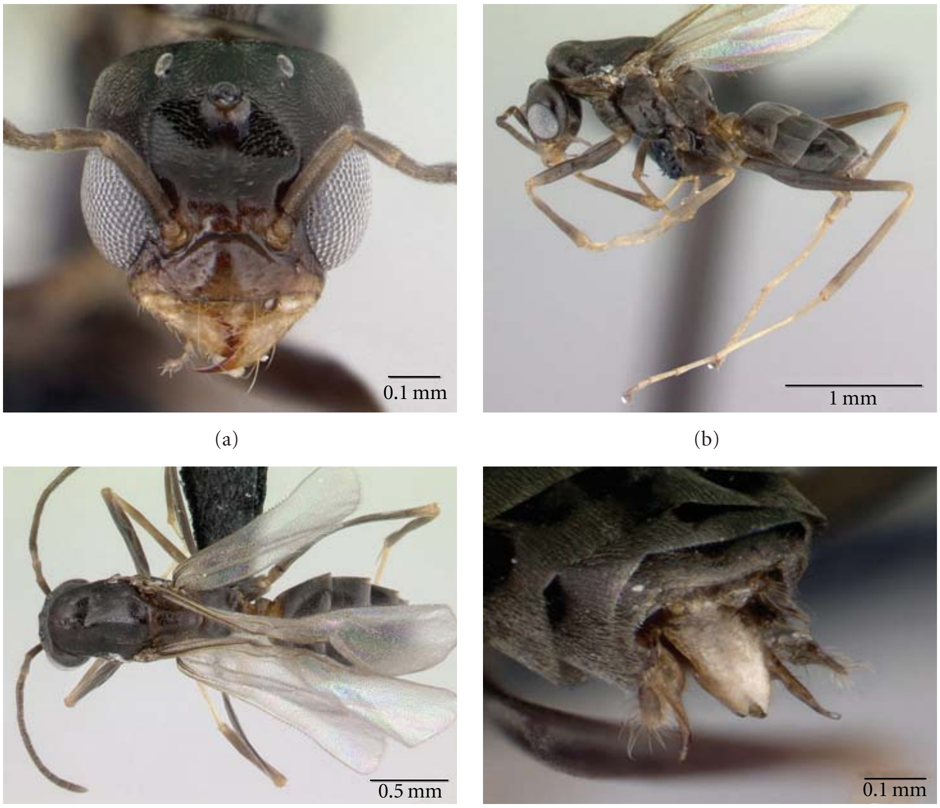
Conomyrma (Biconomyrma) biconis Forel: Kusnezov, 1952: 430 [22].

Dorymyrmex biconis Forel: Shattuck, 1992: 85, [15]; Shattuck, 1994: 75 [45]; Bolton et al. 2006 [46] (catalog).

5.3.1. Diagnosis

Worker. Concolorous reddish brown. CI: 84–107. Posterior margin of head straight to slightly convex. Mesosomal profile interrupted by the presence of two tubercles: one stout short metanotal tubercle, posteriorly directed, and another placed in apical corner of the propodeum, dorsally directed.

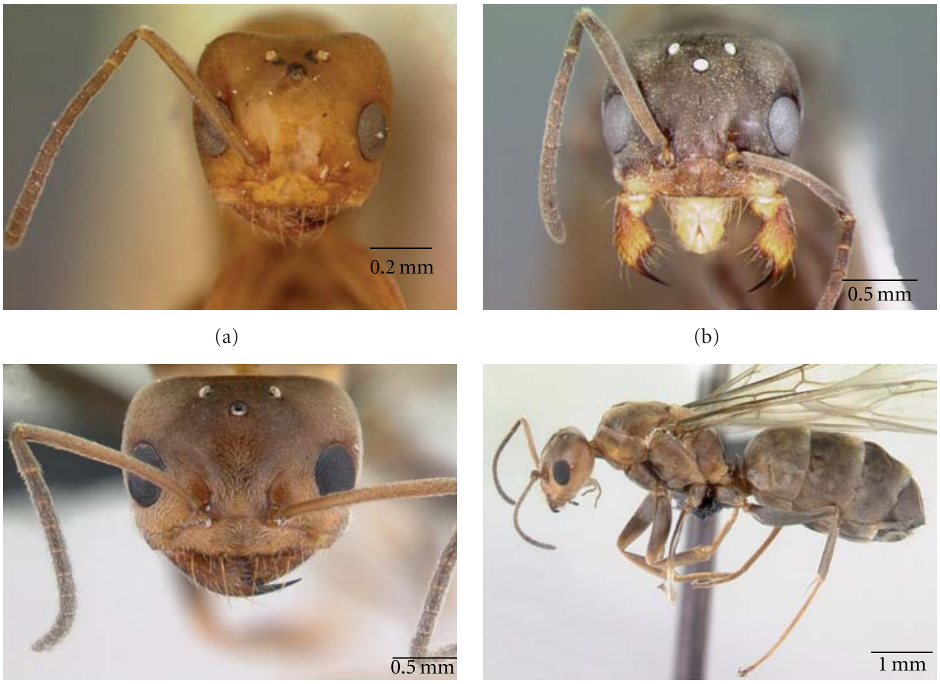
Queen. Color similar to worker but darker. Head subquadrate with a straight posterior margin. Compound eyes



(a) (b)

(c) (d)

Figure 5: *Dorymyrmex biconis* male. (a) Head in frontal view; (b) profile of mesosoma; (c) dorsal view; (d) male genitalia in dorsal view (CASENT0192695). Pictures and labels of localities of each photographed specimen are available at http://www.antweb.org/.



(a) (b)

(c) (d)

Figure 6: Queens of three *Dorymyrmex* species. (a) and (b) Heads of (a) *Dorymyrmex bicolor*; (b) *Dorymyrmex brunneus*; (c)-(d) *Dorymyrmex biconis*: (c) head and (d) body profile.

(a) (b) (c) (d)

Figure 7: *Dorymyrmex brunneus* workers. (a) and (c) Head in full-face view; (b) and (d) body in lateral view. (a)-(b) CASENT0192705; (c)-(d) CASENT0192698. Pictures and labels of localities of each photographed specimen are available at http://www.antweb.org/.

notably developed, longer than wide, placed in middle of lateral margin of head.

Male. Mandible thin, falcate, with only three teeth: one long apical tooth, one subapical, and one denticle. Masticatory and basal margin well differentiated, basal margins completely devoid of teeth or denticles.

5.3.2. Descriptions

Worker

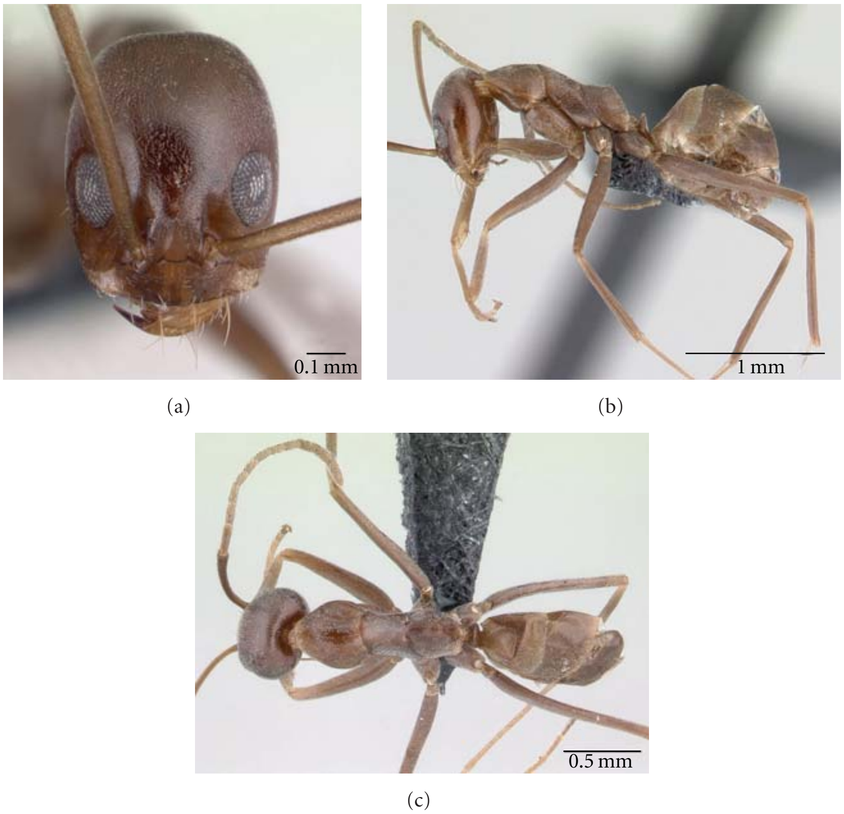
Measurements. ($n = 62$): HL: 0.56–1.16; HW: 0.62–1.20; EL: 0.18–0.34; EW: 0.16–0.32; SL: 0.78–1.10; WL: 1.00–1.12; CI: 84–107; SI: 93–127; REL: 24–33; OI: 55–88; TLI: 128–191.

Concolorous reddish brown, whitish pubescence covering all body tagma. Some specimens have some segments of gaster darker than rest of the body. Worker length 2.8–3.0 mm. *Head* (Figure 3(a)): subquadrate, longer than wide, with lateral sides straight to slightly convex, posterior margin of the head straight to slightly convex. Scape surpassing the posterior margin of head by no more than 1/3 of its length. Compound eyes placed far from posterior clypeal margin but in the first half of the head. Psammophore with short hairs disposed in a triangle; the hairs in the top line are near to the foramen magnum and do not reach the oral cavity. *Mesosoma*: mesonotum with a stout cone, rounded apically, and shorter than propodeal tubercle. Mesonotal tubercle directed posteriorly. Metanotal suture well developed and located inside a very pronounced concavity posterior to mesonotal tubercle (Figure 3(b)). Dorsal face of propodeum anterior to tubercle sinuate (Figure 3(b)). *Metasoma*: petiolar scale directed dorsally.

Queen (Figures 6(c) and 6(d))

Measurements. ($n = 7$): HL: 1.10–1.16; HW: 1.18–1.20; EL: 0.40–0.46; EW: 0.28–0.32; SL: 1.06–1.12; WL: 2.04–2.32; CI: 102–107; SI: 93–102; REL: 36–40; OI: 61–76; TLI: 179–200.

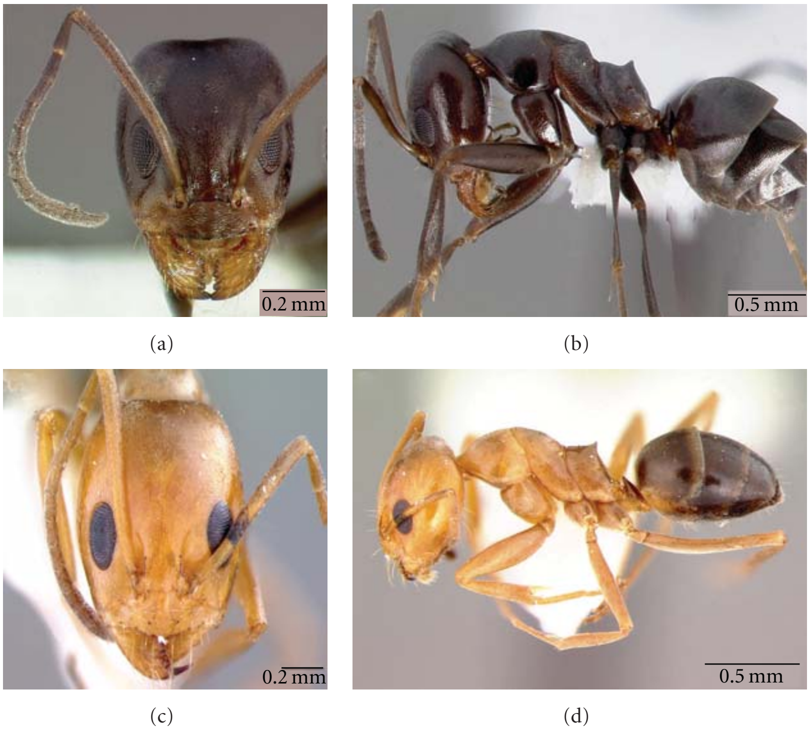
Body reddish brown, darker than worker. Pubescence dense, with long, decumbent hairs covering all body tagma. *Head*: subquadrate. Head capsule with lateral margins parallel to slightly convex, especially in their posterior half. Posterior margin of head straight, with occipital corners rounded. Mandible with a long and sharp apical tooth, three additional teeth and four denticles along the masticatory margin; basal margin completely denticulate without any



(a) (b)

(c)

Figure 8: *Dorymyrmex goeldii* worker. (a) Head in full-face view; (b) body in lateral view; (c) body in dorsal view (CASENT0192699). Pictures and labels of localities of each photographed specimen are available at http://www.antweb.org/.



(a) (b)

(c) (d)

Figure 9: *Dorymyrmex* workers. (a) and (c) Heads of (a) *Dorymyrmex insanus*; (c) *Dorymyrmex pyramicus*; (b) and (d) body profiles of (b) *Dorymyrmex insanus*; (d) *Dorymyrmex pyramicus.*

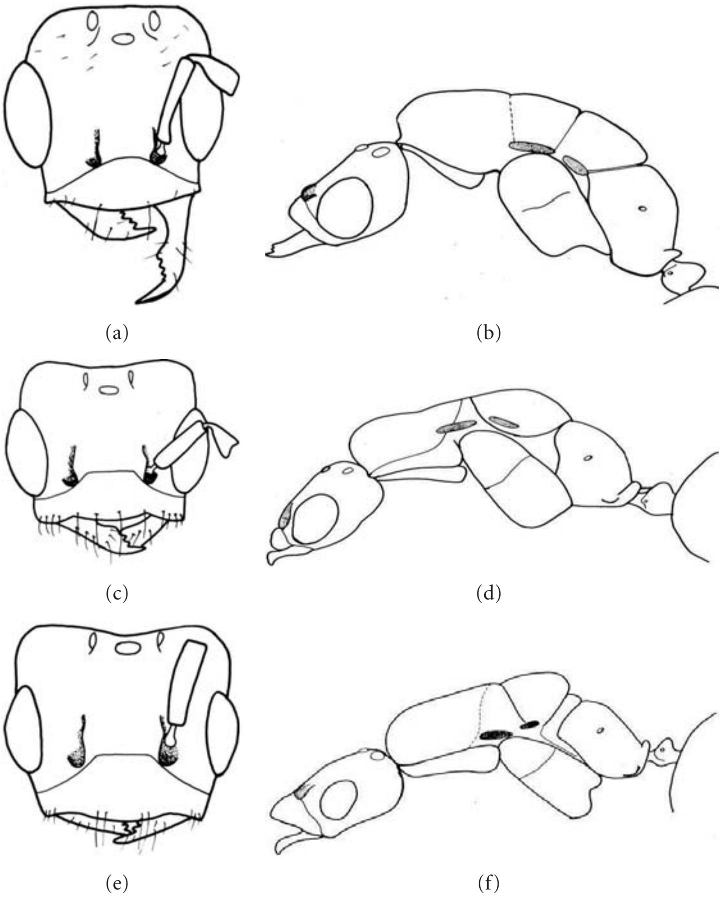

(a) (b)
(c) (d)
(e) (f)

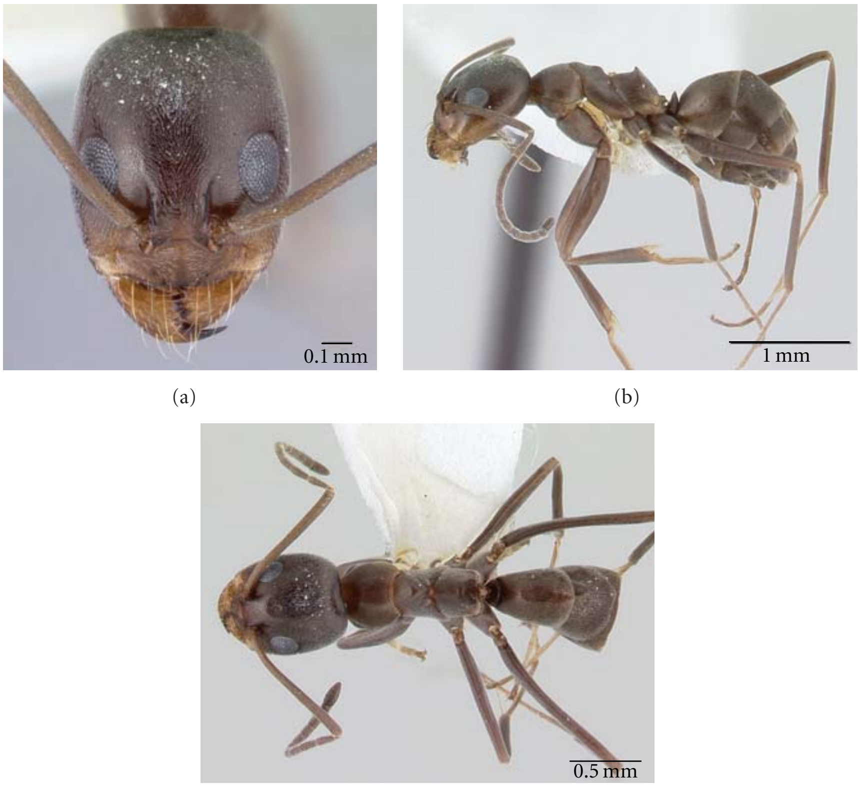
Figure 10: Males of three *Dorymyrmex* species. (a), (c), and (e) Heads of (a) *Dorymyrmex brunneus*; (c) *Dorymyrmex insanus*; (e) *Dorymyrmex pyramicus*; (b), (d), and (f) body profiles of (b) *Dorymyrmex brunneus*; (d) *Dorymyrmex insanus*; (f) *Dorymyrmex pyramicus.*

angle between both margins. Compound eyes notably large, longer than wide, placed in the middle of lateral sides. Scape surpassing the posterior margin of head by twice its maximum diameter. *Mesosoma*: parapsidal furrow slightly developed, visible in dorsal view as a tenuous line reaching posterior half of pronotum, diverging forwards, axilla not divided. Anepisternum and katepisternum incompletely divided by a short pleural suture. Pleural suture with long and abundant hairs (better observed in specimens preserved in EtOH). Wings (Figures 4(a) and 4(b)): forewing with one close radial cell, only one cubital cell, no discoidal cell; pterostigma well developed, longer than wide. Hindwing with three closed cells, hamuli with 12 hooks. *Metasoma*: petiolar scale tall, directed dorsally, and apically obtuse. Petiolar ventral face straight with posterior end slightly convex. Gastral tergites dark brown, especially in posterior 2/3; sternite 1 and 2 lighter than the rest of the body.

Male (Figures 5(a)–5(d))

Measurements. ($n =$ 5): HL: 0.56–0.60; HW: 0.58–0.62; EL: 0.30–0.34; EW: 0.24–0.28; SL: 0.22–0.24; WL: 1.24–1.36; CI: 100–107; SI: 38–41; REL: 50–59; OI: 75–88; TLI: 217–234.

Body dark brown to black, mandibles yellowish brown except masticatory margin which is reddish brown; legs, except femora, lighter than rest of the body. Head and mesosoma strongly pointed. Pilosity with dense, decumbent, thin, and whitish hairs covering all tagma. Katepisternum and metapleural area with only a few hairs. Anterior face of petiolar scale with 2-3 long hairs. *Head* (Figure 5(a)): square. Posterior margin of head weakly concave medially; occipital corners rounded; dorsal face of head with a weak, middle furrow. Mandible thin and falcate, with parallel sides; one long apical tooth, three times longer than subapical one, one denticle, and a diastema before the angle with the basal margin. Masticatory and basal margin well differentiated; basal margins completely devoid of teeth or denticles. Posterior part of clypeus wide and reaching the toruli; anterior clypeal margin convex, with a subclypeal border thin, anteromedial part of clypeus straight. Antenna with exposed condyle; long scape (< to EL) reaching posterior margin of compound eye; pedicel as long as each flagellomere. Compound eye large, maximum length more than 2/3 of cephalic length. Median ocellus hyaline, well developed; lateral ocelli close to posterior margin of head. *Mesosoma* (Figure 5(b)): pronotum long, comprises more than a half of mesosoma, projecting forward as an



(a) (b)

(c)

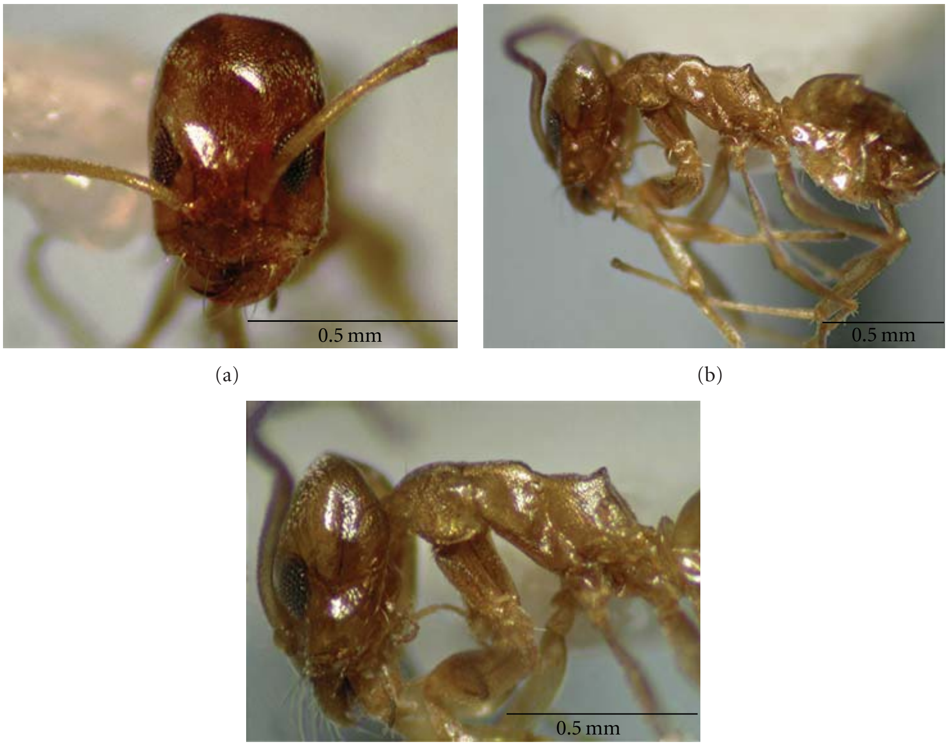
Figure 11: *Dorymyrmex tuberosus* n. sp. worker. holotype. (a) Head in full-face view; (b) body in lateral view; (c) body in dorsal view (CASENT0179518). Pictures and labels of localities of each photographed specimen are available at http://www.antweb.org/.

elbow with a strong depression medially; parapsidal furrows running parallel, reaching the middle part of pronotum, placed inside the depression. Mesonotum twice longer than wide. Anepisternum and katepisternum completely divided by a mesopleural sulcus. Dorsal face of propodeum not well differentiated form posterior face, with a strong declivitous face; propodeal spiracles strongly protruded. Wings (Figures 4(c) and 4(d)): forewing with close radial cell, no close cubital nor discoidal cell. Hindwing without closed cells, hamuli with 12 hooks. *Metasoma*: petiolar scale low and apically rounded, without ventral petiolar process. Pygostyle stout and short, well developed; paramere stout, covered with long dark setae; digitus curved ventrally, longer than volsella (Figure 5(d)); aedeagus serrate ventrally.

Examined Material. COLOMBIA: Atlántico: Puerto Colombia, 1w (IAvH). Bolívar: Zambrano, Hda. Monterrey, 15w (IAvH); same locality above, 8w (IAvH); same locality above, 3w (IAvH-E 90487); same locality above, 3w (IAvH-E 90486); same locality above, 3w (IAvH-E 90485); same locality above, 3w (IAvH-E 90484). Boyacá: Moniquirá, 8w (IFML); Ráquira, Desierto de la Candelaria, 10w (IAvH); Villa de Leyva—Plaza central, 4w (IAvH and IFML). Caldas: Mpio. Aguadas, La Nubia, 7w (IAvH); Mpio. Aguadas, La Nubia, Cañón Río Arma, 3w (IAvH). Cesar: Chiriguaná, 10w (CEUM). Córdoba: Ciénaga de Oro, 2w (IAvH). Cundinamarca: Fusagasugá, 1w (IAvH). Huila: Altaminar [Altamira], 1w (ICN-MHN # 2847); Altamira, 1w (IAvH); 10 Km. N San Agustín, 2w (IAvH); 10 Km. W Palermo, 1w (IAvH). La Guajira: Cabo de la Vela, 4w (CEUM, ICN); Maicao, 6w (LACM); Riohacha, 24w (LACM); SFF Los Flamencos, 6w (CEUM, ICN). Magdalena: Ciénaga, 1w (LACM); PNN Tayrona, Sector Neguanje, 131w and 15q (CAS, IAvH and IFML); Pivijay, 7w (IAvH); Santa Marta, San Antonio, 2w (IAvH), Santa Marta, Valenera, 9w (LACM), Santa Marta, 4w (LACM); Santa Marta, 5m (ICN).

Additional Examined Material. Outside COLOMBIA: Brazil, Peru and Venezuela. BRAZIL: Bahia, Planalto Casimiro Andrade, 10w (MZSP); ES, Santa Tereza, 2w (MZSP); PA, Pindobal, 2w (MZSP). PERU: Puerto Pizarro: #1091, 5w (MZSP). VENEZUELA: Lara: Barquisimeto, 2w (IFML).

Geographic Distribution. Brazil (Bahia, Pará, and Espírito Santo States), Colombia (Atlántico, Bolívar, Boyacá, Caldas, Córdoba, Cundinamarca, Huila, La Guajira, Magdalena, and Valle del Cauca Departments), Perú (Puerto Pizarro), Venezuela (Lara State: Barquisimeto).



(a) (b) (c)

Figure 12: *Dorymyrmex xerophylus* n. sp. worker. (a) Head in full-face view; (b) and (c) body in lateral view; (c) body in dorsal view. These pictures were made by RJG using Nikon Coolpix digital camera and COMBINE Z5 software.

Etymology. The name of this species refers to the main diagnostic character of *D. biconis*: the presence of a pair of tubercles interrupting the mesosomal profile (Figure 3(b)).

Natural History. In Colombia, *Dorymyrmex biconis* is spread throughout, from sea level to more than 2300m. It is more common in lowlands (i.e., Colombian Caribbean region, North of Colombia) and quite common in anthropic environments, with higher abundance in urban places. Nevertheless, workers of *D. biconis* have been collected in primary dry forests and in mangroves. *D. biconis* builds nests in soil devoid of vegetation, in very warm areas. Exceptions are arid but extremely cold places such as Boyacá, Colombia. As in other species of *Dorymyrmex*, nests are superficial, with simple architecture, and no more than 10–15 cm in depth. Excavated nests by RJG in Santa Marta (Magdalena, Colombia) share a similar architecture: only one circular entrance (no more than 5 mm in diameter) surrounded by a mound of sand or other soil particles with a diameter of 9-10 cm. The nest consist of one chamber with queens and males, a second one with larvae and worker pupae, and a third chamber with food and insects remains, such as several Bruchidae (Coleoptera). In one nest, RJG collected some dead Thysanoptera in the food storage camera.

One nest of *D. biconis* can keep between 10 to 15 alate queens, 8 to 10 males and several tens of workers. Sometimes there are no more than 100 to 200 workers in a single nest. No dealate queens have been found in explored nests. Colonies of *D. biconis* are probably polydomous, and queen may fly outside of its colony to build satellite nests. In some cases, RJG has found two or three nests in an area of 10 m^2; only one of these nests had queens.

5.3.3. Comments. The first description of *D. biconis* was based in workers collected in San Antonio (St. Antonio), Santa Marta, Colombia [8]. Three species of *Dorymyrmex* (*D. bituber*, *D. pulchellus*, and *D. tuberosus* n. sp.) share a few characters with *D. biconis*. This is a group of species easy to recognize by the presence of two well-developed mesosomal tubercles: one in the last part of the metanotum and the other one between the dorsal and declivitous faces of propodeum. Considering its geographical distribution, *D. biconis* seems to be confined to the north and central parts of South America, from Venezuela to Peru. This species was included in the subgenus “*Biconomyrma*” [19] based on characters of wing venation of queen.

5.4. *Dorymyrmex brunneus* Forel, 1908 [37] *(Figures 6(b); 7(a)–7(d); 10(a)-10(b); 13)*

Dorymyrmex pyramicus var. *brunnea* Forel, 1908: 385 [37]. Description of worker.

Dorymyrmex pyramicus subsp. *brunneus* Forel: Forel, 1911: 306 [48]. Description of queen.

Dorymyrmex pyramicus subsp. *brunnea* Forel: Emery, 1913: 37 [49].

Dorymyrmex (*Conomyrma*) *pyramicus* race *brunneus* Forel: Forel, 1913: 244 [50].

Dorymyrmex pyramicus subsp. *brunneus* Forel: Santschi, 1912: 53 [51], Gallardo 1916: 59 [41] (queen redescribed).

Dorymyrmex (*Conomyrma*) *brunneus* var. *spurious* Forel: Santschi, 1929: 305 [52].

Conomyrma (*Biconomyrma*) *brunnea* (Forel): Kusnezov, 1952: 430 [22].

Conomyrma brunnea (Forel): Kempf, 1975: 375 [6].

Dorymyrmex brunneus Forel: Shattuck, 1992: 85 [15]; Shattuck, 1994: 77 [45]; Bolton et al. 2006 (catalog) [46].

5.4.1. Diagnosis

Worker. Head slightly longer than wide. Posterior margin of head straight to feebly concave medially (Figure 7(a)). Psammophore with short hairs disposed in a triangle, not reaching the posterior end of hypostome. Pro-mesonotum depressed in lateral view, always lower than the apex of propodeal tubercle. Mesonotal profile with a well-defined dorsal and declivitous face in the posterior end. Metanotal suture well impressed forming a concavity anterior to the propodeum.

Queen. Maximum diameter of head behind the compound eyes. Posterior margin of head feebly concave medially. Forewing with only one close cubital cell.

Male. Dark brown. Scape long, reaching the posterior margin of compound eyes. Mandible with only three teeth. Forewing with no discoidal and no cubital cells, hindwing with only two closed cells. Pygostyle poorly developed, paramere stout and covered with long hairs.

5.4.2. Descriptions

Worker

Measurements. Lectotype: HL: 0.95; HW: 0.8; EL: 0.23; EW: 0.125; SL: 0.875; WL: 1.175; CI: 84; SI: 92; REL: 24; OI: 54; TLI: 124.

Other Examined Material. w (*n* = 98): HL: 0.70–1.04; HW: 0.64–0.92; EL: 0.22–0.30; EW: 0.10–0.20; SL: 0.80–1.14; WL: 1.00–1.46; CI: 83–117; SI: 98–129; REL: 24–34; OI: 45–77; TLI: 122–171.

Concolorous dark brown; whitish pubescence covering all body tagma. 0–2 erected setae on the dorsum of pronotum. *Head* (Figures 7(a) and 7(c)): subquadrate, with lateral margins strongly convex, maximum head width at the compound eye level. Mandibles strongly striate, reddish brown. Compound eyes in central 1/3 of the head as seen in frontal view. Scape long (SI: 92–129), surpassing the posterior margin of head by more than twice its maximum width. Posterior margin of head usually straight but sometimes feebly concave in the middle. Psammophore with a few extremely short hairs disposed in a triangle, the hairs in the top line are near to the foramen magnum and do not reach the oral cavity. Upper setae of psammophore close to the anterior margin of foramen magnum. *Mesosoma*: promesonotal profile sinuate to straight and, in lateral view, always lower than the apex of propodeal tubercle (Figures 7(b) and 7(d)). Posterior end of mesonotum forming two faces, one dorsal and one declivitous but not conforming a well-developed tubercle (Figures 7(b) and 7(d)). Propodeal tubercle stout, with wide base, and slightly directed dorsally. Declivitous face straight to slightly convex (Figure 7(d)). *Metasoma*: petiole forward directed, included in a concavity placed in the anterior face of the first gastral segment. Scale apically thin and rounded.

Queen

Measurements. (*n* = 5): HL: 1.13; HW: 1.15; EL: 0.38; EW: 0.18; IOD: 0.78; SL: 1.1; WL: 2.3.

Color and pubescence as in worker; *head*: subquadrate, maximum diameter after the compound eyes (Figure 6(b)). Clypeal sides lighter than the rest of the head; scape surpassing the posterior margin of head by more than twice its maximum width; mandibles striated with four teeth and two denticles; posterior margin of head feebly concave medially. *Mesosoma*: parapsidal furrows well developed, parallel, axilla not divided. A short, incomplete suture divides anepisternum from katepisternum. Forewing with only one closed cubital cell; radial cell long and close. *Metasoma*: low and stout petiole, apically rounded.

Male (First Description)

Measurements. (*n* = 3): HL: 0.58–0.6; HW: 0.58–0.63; EL: 0.28–0.33; EW: 0.15–0.2; SL: 0.25; WL: 1.3–1.38.

Color of the body similar to worker and queen; *head* (Figure 10(a)): subquadrate with round occipital corner; mandibles thin with only three teeth, the apical more than twice longer than the others. Scape long, reaching the posterior margin of compound eyes. *Mesosoma*: parapsidal furrows parallel, axilla not divided medially; forewing with one close radial cell and no cubital nor discoidal cell. Hindwing with only two closed cells. *Metasoma*: petiolar scale (Figure 10(b)) low, round, and stout, ventral process round, feebly developed. Pygostyle poorly developed; paramere stout covered with long, erected setae; aedeagus serrate ventrally.

Examined Material. COLOMBIA: Amazonas: Araracuara, 9w (IAvH). Antioquia: Sonsón, Quebrada La Violeta, 6w (IAvH-E 90491); same data as above, 1w (IAvH-E 90502); same locality, 3w (IAvH-E 90476); same locality, 2w (AvH-E 90492). Boyacá: El Infiernito, 14w (IAvH); Ráquira, Desierto de la Candelaria, 10w (IAvH), one of these specimens was photographed; Arcabuco, 1w (IAvH). Caldas: Aguadas, 2w (IAvH); Aguadas, Arenillas, 9w (IAvH); same data, #CES292, 3w (IAvH-E 90503), same data, #CES292, 3w (IAvH-E 90496); same data, #CES292, 3w (IAvH-E 90461); Aguadas, Puente Albania, 1w (IAvH-E 90501); Aguadas, Cañón Río Arma, 3w (IAvH); same data, #CES069, 12w (IAvH), same data, #CES068, 1w (IAvH-E 90504); Aguadas, Quebrada Pito, 1w (ICN-MHN 022550); Manizales, Vereda El Dorado, Finca El Placer, 2w (IAvH); La Nubia, 7w (IAvH). Cauca: Mercaderes, Mojarras, rivera del río Guachicano, 7w + 1 queen (CEUM). Caquetá: Puerto Solano, PNN Chiribiquete, río Curañé-Amú, 1w (IAvH). Cundinamarca: Fusagasugá, 2w (ICN); Nariño: RN La Planada, 6w (IAvH). Meta: 7w (LACM); 65 Km. E Puerto López, 2w (LACM). Quindío: Circasia, Vereda Buena Vista, Finca Calamar, 12w (IAvH); Calarcá, Vereda Pradera Baja, Finca La Holanda, 3w (IAvH); same data, 9w [2w (IAvH-E 90473), 2w (IAvH-E 90474), 3w (IAvH-E 90470), 2w (IAvH-E 90472)]. Risaralda: La Virginia, Finca Miralindo, 6w (CEUM). Santander: Barrancabermeja, [2w (IAvH-E 90490), 2w (IAvH-E 90498), 2w (IAvH-E 90493)]; Socorro, Vereda Altos de Reina, Finca San Luis, [1w (IAvH 25099), 1w (IAvH 25097), 1w (IAvH 25098)]; same locality, Finca El Clavelino, [1w (IAvH 25162), 1w (IAvH 25163)]. Tolima: locality not recorded, 8w (LACM). Valle del Cauca: Buenaventura, Bajo Anchicayá, [1w (IAvH-E 90499), 1w (IAvH-E 90500)]. Vichada: Cumaribo, Selva de Matabén, 7w (IAvH).

Additional Examined Material. Outside COLOMBIA: Several series from Argentina, Bolivia, Brazil, Guatemala, and Paraguay. ARGENTINA: Chaco: Las Palmas, #989, 6m, (MACN); Entre Ríos, 5w, (MACN); Misiones: Esperanza, 5w and 1m, (MZSP); San Luis2w, (MZSP); #236, C. Bruch coll, identified as "cotypus", 2w, (MACN). BOLIVIA: Cochababma, 10w, #9479, 4w, (IFML); Depto. Santa Cruz, Prov. Andrés Ibáñez, 12 km E Santa Cruz, 5w, (IFML). BRASIL: BA: Bom Jesus da Lapa, 6w, (CEPEC); MT: Araguai, 2w, (MZSP); Cáceres, 1w, (MZSP); Campo Grande, 6w, 1q (MZSP); Carmo da Cachoeira, 5w, 1q, (MZSP); same loc, 3w, (MZSP); Colonia Vicentina, Dourados, 1w, (MZSP); 3w, (MZSP); Cuiabá, 22w, 2m, (MZSP); Chapada, 8w, (MZSP); same loc, 2w, (MZSP); Diamarum, Parque Nac. Xingu, 12w, (MZSP); Fátima, 7w, (MZSP); Faz. Beija Flor, 4w, (MZSP); Faz. Sta. Blanca, Corumbá, 4w, (MZSP); Itaum, 1w, (MZSP); Jardim, 9w, (MZSP); Mons. Paulo, V. dos Santos, 6w, (MZSP); Paconé, 8w, (MZSP); same loc, 3w, (MZSP); same loc, 5w, (MZSP); Porto Murtinho, 4w, (MZSP); Rondonópolis, 2w, (MZSP); same loc, 3w, (MZSP); Santa Bárbara, 2w, (MZSP); Serra Caraça, 16w, (MZSP); same loc., 4w, (MZSP); Serra do Urucum-Corumbá, 24w, (MZSP); S. Lourenço, 1w, (MZSP); Tiradentes, 1w, (MZSP); Três Lagoas, 4w, (MZSP); Utiariti, Río Papagaio, 6w, (MZSP); same loc, 3w, (MZSP); PE: Caruara, 2w, (MZSP); Diapoque, 5w, (MZSP); João Pessoa, 9w, (MZSP); Prado, Recife, 3w, (MZSP); Recife, 4w, (MZSP); same loc, 3w, (MZSP); Tapera, 2w, (MZSP); PR: Castro, 3w, (MZSP); Foz do Iguazú, Cataratas, 4w, (MZSP); Marienthal, 2w, (MZSP); Rio Negro, 3w, (MZSP); same loc, 1w, (MZSP); Rolandia, 3w, (MZSP); RD: Assis, 2w, (MZSP); RGS: Erechim, Campinas, 14w, (MZSP); Três Arroios, 5w, 2m, (MZSP); RJ: Fábrica Nacional de Motores, 2w, (MZSP); Itaipava, 2w, (MZSP); Jardim Primavera, 2w, (MZSP); Macaé, 4w, (MZSP); Marambaia, 2w, (MZSP); Rio de Janeiro, 5w, (MZSP); RS: Morretes, 6w, (MZSP); SC: Blumenau, 1w, (MZSP); Camboriu, 12w, (MZSP); Canoinhas, 3w, (MZSP); Forquilhinha, 5w, (MZSP); Ituporanga, 3w, (MZSP); Poço Grande, 3w (MZSP); Rio do Sul, 9w, (MZSP); Rodeio, 1w, (MZSP); SP: Agudos, 14w, (IFML); Amparo, 3w, (MZSP); Anhembi, 11w, 2q, (MZSP); Assis, Rd 333, km 44, 2w, (MZSP); Avaré, 5w, (MZSP); Barueri, 31w, (MZSP); Butantan, 1w, (MZSP); Campinas, 5w, (MZSP); Campo dos Jordão, 6w, 3m (MZSP); Campo Limpo, 1w, (MZSP); Caraguatatuba (Res. Flor. 40m), 4w, (MZSP); Curitiba, 6w, (MZSP); Embú, 1w, (MZSP); Faz. Itaqueri, Rôa Esperança do Sul, 18w, (MZSP); Alhambra, 6w, (MZSP); Ilha da Vitória, 16w, 5q, 8m, (MZSP); Ilha dos Buzios, 1w, (MZSP); Interlagos, 12w (cotype), (MZSP); Monte Mor, 7w, 2m, (MZSP); Piracicaba, 12w, (MZSP); Rio Claro, Bairro Saudade, 9q, (MZSP); Rio Claro, Horto Forestal, 3w, (MZSP); Rod. S.Paulo-Curitiba, Km 300, M.Iporanga, 15w, (MZSP); S.Sebastião, 4w, (MZSP); Teod. Sampaio, 2W, (MZSP); Ubatuba, 2w, (MZSP); Venceslau, 3w, (MZSP); 20 km W Conchas, 4w, (MZSP); Boraceia, 6w, (MZSP); Piracicaba, 9w, (MZSP); S. Sebastião, Bairro S. Francisco, 4w, (MZSP); Orlândia, 3w, (MZSP); Holambra, 6w, (MZSP); Praia Grande 3w, (MZSP); Interlagos, 12w, (MZSP); Anhembi, Faz. B. Rico, MANAUS, Amazonas, 4w, (IFML); PARAGUAY: Caacupé, 3w, (IFML); Pastoreo, 5w, (MZSP); GUATEMALA: Antigua, 3w, (USNM).

Geographic Distribution. Argentina, Bolivia, Brazil, Colombia (Amazonas, Antioquia, Boyacá, Caldas, Caquetá, Cundinamarca, Nariño, Meta, Quindío, Santander, Tolima, Valle del Cauca, Vichada), French Guyana, Guyana, Panama, Guatemala, Paraguay, and Surinam.

Etymology. The name "*brunneus*" means dark brown. It is the main color of worker, queen, and male.

Natural History. D. brunneus is mainly restricted to arid environments of the Andean region of Colombia, at elevations above 1000 m. Some lowland populations live in dry forests of western Colombia (Valle del Cauca, 400–500 m), savannas in eastern plains (Vichada, 240 m), and in Colombian Amazon basin (Amazonas, 200–300 m).

Like *Dorymyrmex biconis, D. brunneus* is well adapted to anthropic environments. Most of the specimens studied here have been collected in areas transformed by humans, mainly in open areas with low vegetation (stubble), coffee plantations (shade coffee culture), wooded areas for cattle grazing, and urban areas.

5.4.3. Comments. D. brunneus is one of the most variable species of *Dorymyrmex* with the widest distributional range. This species was found from Panama (Canal Zone) up to the central part of Argentina. This species is the most frequently collected in Brazil, from sea level to more than 2000 m. As suggested by the variability observed in specimens from Figures 7(a)–7(d), *D. brunneus* may be a species complex. More detailed studies are needed based on series of specimens collected from same nest and different localities from all over its distributional range.

The shape of the mesosomal profile was one of the most frequently characters used to separate species of *Dorymyrmex* but is almost unusable to identify *D. brunneus*. Local populations of this species have strong differences in the profile of mesosoma (Figures 7(b) and 7(d)) and scape length. There are morphological variations among Colombian populations which seem to be stable: only workers with broad head (CI: 90–107) have a strong mesonotal depression making a sort of tubercle at the middle of mesonotum (different from *D. biconis*), with a deep and wide metanotal groove. Besides, workers have a median ocellus and, sometimes, two tiny lateral ocelli (populations from Boyacá, Colombia). The shape of queen head in frontal view (Figure 6(b)), mandibles with only three teeth in male and the number of closed cells in forewings have proved to be useful to separate *D. brunneus* from other *Dorymyrmex* species.

5.5. *Dorymyrmex goeldii* Forel, 1904 [38] *(Figures 8(a)–8(c); 13)*

> *Dorymyrmex Göldii* Forel, 1904: 41 [38].
>
> *Dorymyrmex (Ammomyrma) goeldii* Forel: Kusnezov, 1952: 429 [22].
>
> *Conomyrma goeldii* (Forel): Kempf, 1972: 79 [10].
>
> *Dorymyrmex goeldii* Forel: Shattuck, 1992: 85 [15]; Bolton et al. 2006 (catalog) [46].

5.5.1. Diagnosis

Worker. Concolours, light brown. Head longer than wide, with the posterior margin of head strongly convex, scape long (SI: more than 115), long mesosoma, in profile.

Queen and Male. Unknown.

5.5.2. Descriptions

Worker

Measurements. ($n = 30$): HL: 0.70–0.86; HW: 0.55–0.72; EL: 0.20–0.26; EW: 0.10–0.18; SL: 0.85–1.00; WL: 1.05–1.36; CI: 77–84; SI: 116–160; REL: 29–32; OI: 50–69; TLI: 147–163.

Concolours, light brown. Sculpture reticulated, widely spaced. Pubescence whitish and dense. Pilosity brownish. *Head* (Figure 8(a)): psammophore triangular with short setae, the hairs in the top line close to the foramen magnum and do not reach the oral cavity. Uppermost setae of psammophore close to the lower margin of foramen magnum. Scape surpassing occipital margin by more than twice its apical width. Posterior margin of head slightly straight. *Mesosoma* (Figures 8(b) and 8(c)): 0–2 pronotal erected setae; propodeal tubercle round and short tubercle, directed dorsally; declivitous face of propodeum straight to feebly convex. *Metasoma*: low petiolar scale.

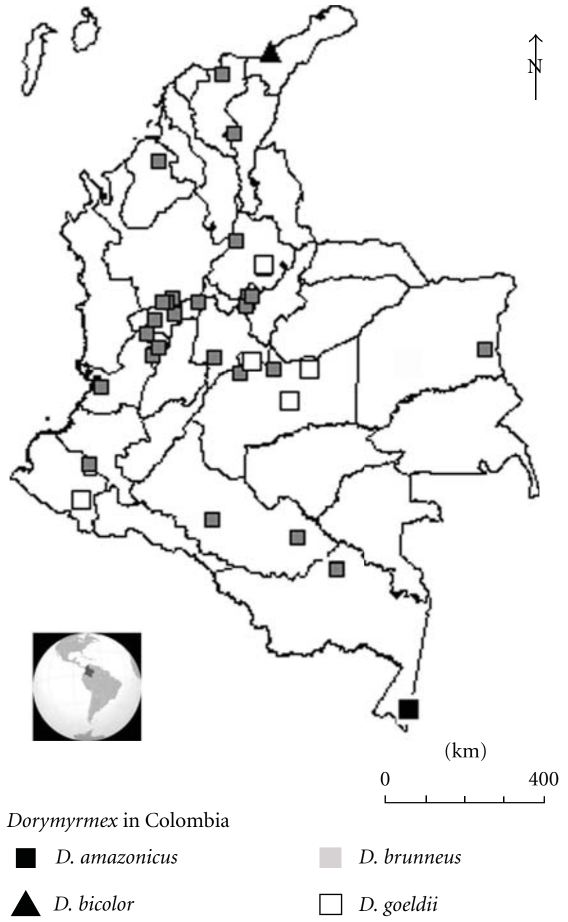


Figure 13: Geographic distribution of *Dorymyrmex amazonicus* n. sp., *Dorymyrmex bicolor*, *Dorymyrmex brunneus*, and *Dorymyrmex goeldii* in Colombia.

Queen and Male. Unknown.

Examined Material. COLOMBIA: Meta: Puerto López, 6w (IAvH); PNN Sierra de la Macarena, Caño Curía, Sendero Cachicaos, 29w (IAvH); same locality, 29w (IAvH); same locality, 25w (IAvH); Cumaral, 5w (LACM). Nariño: R.N. La Planada, 1w (IAvH). Santander: Socorro, Vereda Alto de Reinas, Finca San Luis, 1w (IAvH).

Additional Examined Material. Outside COLOMBIA: BOLIVIA: Ignacio de Velasco, 3w (MZSP). BRAZIL: MT: Rondonópolis, 11w (MZSP). PE: Araripina, 9w (MZSP). PI: 5 km E Oeiras, Faz. Talhada, 10w (MZSP); 10 km N. Corrente, Faz. Maracujá, 2w (MZSP); Canto do Buriti, 2w (MZSP). SP: Agudos, 9w (MZSP); same locality, 11w (IFML).

Geographic Distribution. Bolivia, Brazil, and Colombia (Meta, Nariño and Santander). Figure 13 shows distribution of *D. goeldii* in Colombia.

Etymology. Named in honor of Emilio Goeldi.

Natural History. Geographical distribution of *D. goeldii* has a strong disjunction in Colombia: some populations are found in the Andean region (Deptartment of Santander and Nariño) at high altitude, between 1700 a 1900 m; other colonies, where *D. goeldii* is more common, prefer open areas of an isolated chain of mountains in the La Macarena National Park; in this area, specimens were collected at 493 m.

5.5.3. Comments. Characters given in the diagnosis are enough to differentiate this species from all other *Dorymyrmex* found in Colombia.

5.6. *Dorymyrmex insanus* (Buckley, 1866) [39] *(Figures 9(a)-9(b); 10(c)-10(d); 14)*

Formica insana Buckley, 1866: 165 [39].

Dorymyrmex insanus: McCook, 1880: 185-186 [53].

Dorymyrmex pyramicus (as senior synonymy of *D. insanus*): Mayr, 1886: 433 [1]; Emery, 1895: 331 [54]; W. M. Wheeler, 1902: 6-7, [55]; W. M. Wheeler, 1906: 342 [36]; Creighton, 1950: 346–349 [56].

Dorymyrmex pyramicus v. *insana*: Santschi, 1920: 381 [57] (revived from synonymy as variety of *D. pyramicus*).

Dorymyrmex (*Conomyrma*) *pyramicus*: Smith, 1951: 837 [20]; Gregg, 1963: 432–434 [58] (in part).

Conomyrma insana: Snelling, 1973 [25] (in part), Johnson, 1989: 185 [42] (Senior synonym of *D. medeis* and *D. reginicula*).

Dorymyrmex insanus (Buckley): Shattuck, 1992: 85 [15]; Shattuck, 1994: 84 [45]; Snelling, 1995: [4]; Bolton et al. 2006 [46].

5.6.1. Diagnosis

Worker. Medium brown to dark. Head longer than wide, lateral sides parallel and slightly convex. Posterior margin of head with a weak median emargination. Pronotum with 0–2 erect setae. Pro-mesonotum slightly convex with a weak subangle behind, forming a feeble tubercle in the same line of propodeum in profile.

Queen. Maximum cephalic width at the level of compound eyes, weakly narrow behind.

Male. Dark brown to black. Maximum head width after level of eyes. Posterior margin of head feebly concave in the middle; only three teeth present on the masticatory margin of the mandible. Forewing with no discoidal nor cubital cells.

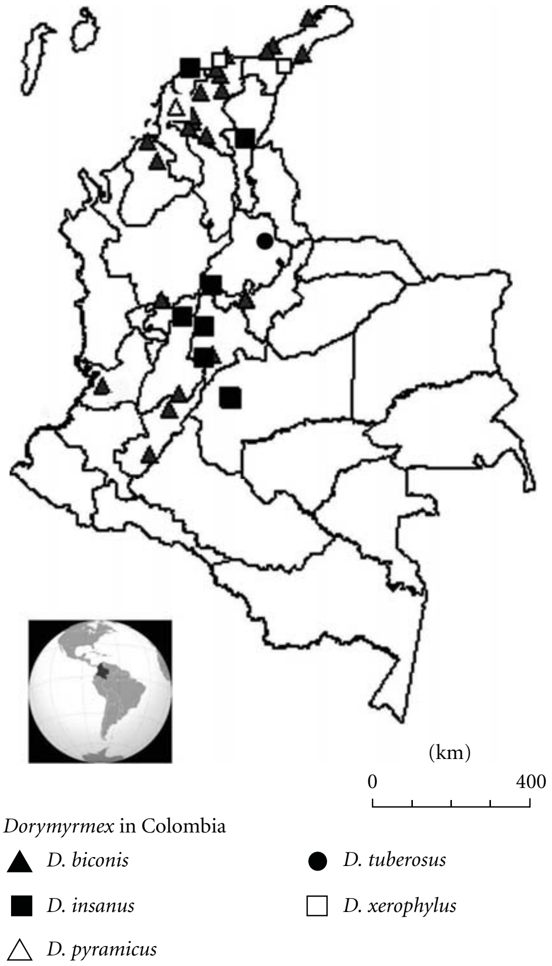


Figure 14: Geographic distribution of *Dorymyrmex biconis*, *Dorymyrmex insanus*, *Dorymyrmex pyramicus*, *Dorymyrmex tuberosus* n. sp., and *Dorymyrmex xerophylus* n. sp. in Colombia.

5.6.2. Descriptions

Worker

Measurements. ($n = 55$): HL: 0.78–1.16; HW: 0.70–1.00; EL: 0.22–0.57; EW: 0.15–0.22; SL: 0.80–1.12; WL: 1.08–1.44; CI: 79–96; SI: 74–119; REL: 25–71; OI: 26–82; TLI: 125–147.

Head, mesosoma, and gaster medium brown to dark; some specimens are almost black. Head and dorsal part of mesosoma covered with a dense and whitish pubescence but lighter than in *D. brunneus*. *Head* (Figure 9(a)): subquadrate, convex laterally. Compound eyes placed in first cephalic third. Scape surpassing the posterior margin of head by 1/3 of its length. Posterior margin of head concave medially. Psammophore with short setae, disposed in a double file, forming a semicircle; the hairs in the top line are disposed far from the foramen magnum and do not reach the oral cavity. *Mesosoma* (Figure 9(b)): profile interrupted in the middle, promesonotal profile higher than apical summit of propodeal tubercle. Mesonotal sclerite, in profile, forming an angle defining two faces, one dorsal and one posterior but not forming a real tubercle. In profile, the dorsal face of propodeum is feebly sinuate. *Metasoma*: petiolar scale directed dorsally. No ventral petiolar process.

Queen. Well described by Snelling [4].

Male (First Description)

Measurements. ($n = 4$): HL: 0.55–0.6; HW: 0.58–0.63; EL: 0.25–0.28; EW: 0.15; SL: 0.25–0.28; WL: 1.08–1.23.

Body dark brown, mandibles yellowish brown except masticatory margin which is reddish brown. Whitish pubescence covering all the body. *Head* (Figure 10(c)): square with round occipital corner; posterior margin of head feebly concave in the middle. Mandible falcate, with subparallel inner and outer sides, with only three teeth: apical tooth three times longer than the preapical one; there is no well differentiated angle between masticatory and basal margins; basal margin completely devoid of tooth or denticles. Posterior margin of clypeus wide, reaching torulus; anterior margin of clypeus convex. Scape long (> or = to EL) surpassing posterior margin of compound eye; pedicel as long as each flagellomere. Compound eye large, exceeding the lateral margin of head. Hyaline ocelli well developed; lateral ocelli placed close to the posterior cephalic margin. *Mesosoma* (Figure 10(d)): pronotum projected forwards as an elbow; parapsidal furrows strongly divergent, reaching the middle part of pronotum. Mesonotum twice longer than wide in lateral view. Anepisternum and katepisternum completely divided by a mesopleural suture. Profile of propodeum continuous, dorsal and declivitous faces not well defined. Forewing with no discoidal nor cubital cell. Hindwing with 0–3 closed cells. Hamuli with 12 hooks. *Metasoma*: petiole low; scale apically rounded in lateral view; ventral petiolar process short. Pygostyle short, stout and covered with white, erect setae. Stout paramere, differentiated from volsella by a sulcus; digitus curved surpassing the volsellae in length, no cuspis present; aedeagus ventrally serrate.

Examined Material. COLOMBIA: Atlántico: Barranquilla, Km. 6 vía Puerto Colombia, 5w (CEUM). Boyacá: Puerto Boyacá, Puerto Romero, Vereda La Fiebre, Finca El Golfo, 1w (ICN). Cesar: Chiriguaná, 14w (CEUM). Cundinamarca: Fusagasugá, Rio Cuja, [1w (ICN-022530), 1w (ICN-022467), 1w (ICN 022468), 1w (ICN-022534), 1w (ICN-022529), 1w (ICN-022533), 1w (ICN-022536), 1w (ICN-022531), 2w (ICN-CORD78)]; Villeta, Buenos Aires, [1w (ICN-022538), 1w (ICN-022537)]. Meta: Vereda el Cocuy, 3 19 7.68 N 73 54 21.96 W 467 m, 23 Apr 1978, [1w (ICN-022542), 1w (ICN-022543)]; San Juan de Arama, Vereda Monserrate, PNN Sierra de la Macarena, 1w (ICN-F86M159); Meta, loc. not recorded, 2w (LACM). Tolima: Municipio Fresno, Vereda Colombia, Finca Las Perlas, 1w (IAvH).

Additional Examined Material. (Outside of COLOMBIA): USA: Arizona: Cochise Co., Portal, 33w (LACM); same locality, 2w, 2m, 2q (LACM); 4 mi. N. Sedona, Oak Co., 2w (LACM). California: Glamis, Riverside Co., 9w (LACM); 3.5 mi NW Glamis, Algodones Dunes, Imperial Co., 5w; La Jolla, San Diego Co., 4w (LACM). Kansas: Anthony City Lake, Harper Co., 5w, 1m, 1q (LACM).

Geographic Distribution. Colombia (Boyacá, Cesar, Cundinamarca, Meta and Tolima), Costa Rica, El Salvador, Honduras, Panama, USA (Arizona, California and Kansas).

Etymology. Insanus means mad, probably because of the crazy movement of foraging workers on the ground.

Natural History. In Colombia, *Dorymyrmex insanus* is commonly found in lowlands. This species nests close to the sea level (75 m.) in anthropic sub-xerophytic deciduous forests and in temporal cultivated areas. Some populations are restricted to arid and open areas of central Colombia, between 400 and 700 m, where small herbs cover the ground.

5.6.3. Comments. Taxonomical limits of this species are here clearly defined. In the past, the names of *D. pyramicus* and *D. insanus* were used as synonyms, in a sort of confusion, considering both species as one with a wide distributional range (from Texas, USA, to Argentina). Snelling [4] was the first to recognize this mistake and to propose a clear description of *D. insanus*, designating a neotype worker (Figures 9(a) and 9(b)) and neoparatypes. According to him, *D. insanus* can be found from Central Texas to Kansas and westward to Northern California. In the same paper, Snelling [4] says that the southern limit of its range is unclear in part due to inadequate collecting. With new material examined from Central and South America, we can confirm the presence of *D. insanus* in Central America and in the north part of South America. For more information, see comments of *D. pyramicus* below. Another interesting data is that *D. insanus* was considered as a vulnerable species by de IUNC Red List as fitting the "D2" criteria of the vulnerable (VU) category in the "1994 Categories & Criteria," meaning the population has an acute restriction in its area of occupancy (typically less than 100 km^2) or in the number of locations (typically less than five). With the distributional data provided here, this species can be considered to exceed the above criteria and, therefore, should be removed from the list of endangered species.

5.7. *Dorymyrmex pyramicus* Roger, 1863 [40] *(Figures 9(c)-9(d); 10(e)-10(f); 14)*

Prenolepis pyramica Roger, 1863: 160 [40]. Description of worker.

Dorymyrmex pyramicus (Roger): Mayr, 1870 : 947 [59]; Mayr, 1870b: 394 [60].

Dorymyrmex pyramicus: Emery, 1888: 362 [3]. Description of male.

Dorymyrmex (*Conomyrma*) *pyramicus* (Roger): Forel, 1913: 350 [11].

Dorymyrmex pyramicus (Roger): Gallardo, 1916: 54 [41] (w, q, m redescribed).

Dorymyrmex (Conomyrma) pyramicus (Roger): Santschi, 1925: 244 [61].

Dorymyrmex (Conomyrma) pyramicus G. C. Wheeler & J. Wheeler, 1951: 83 [62] (description of larvae).

Conomyrma (Conomyrma) pyramica (Roger): Kusnezov, 1952: 430 [22]; Snelling, 1973: 4 [25]; Goñi et al. 1984: 366 [63] (karyotype).

Dorymyrmex pyramicus (Roger): Shattuck, 1992: 85 [15]; Shattuck, 1994: 85 [45]; Bolton et al. 2006 [46] (catalog).

5.7.1. Diagnosis

Worker. Promesonotal profile continuous, strongly convex. Head, mesosoma, and legs reddish-yellow with gaster dark brown to black. Psammophore reaches the posterior margin of hypostoma.

Queen. Head subquadrate, maximum width at level of compound eyes; scape surpassing the posterior margin of head by no more than its maximum width; mandibles feebly striated with four teeth and two denticles on the masticatory margin; posterior margin of head straight. Forewing with only one large cubital cell.

Male. Head wider than long; posterior margin of head medially concave; scape long, surpassing the level of compound eyes, pygostyle poorly developed.

5.7.2. Descriptions

Worker

Measurements. (n = 10): HL: 0.78–0.88; HW: 0.73–0.78; EL 0.20–0.25; EW: 0.1–0.13; SL: 0.78–0.85; WL: 1.18–1.20; CI: 89–94; SI: 97–100; REL: 26–29; OI: 50–52; TLI: 137–152.

Head, mesosoma, and petiole concolorous reddish yellow; gaster always darker than the rest of the body, frequently dark brown to black. Whitish and sparse pubescence covering all body tagma. *Head* (Figure 9(c)): posterior margin of head feebly emarginated medially. Psammophore with short hairs forming a triangle; the hairs in the top line are dispose near to the foramen magnum and do not reach the oral cavity. Upper seta line of psammophore close to anterior margin of foramen magnum. *Mesosoma* (Figure 9(d)): pronotum with two subdecumbent short setae. Promesonotal profile strongly convex. Mesonotum not angulated, as in *D. insanus*. Propodeal tubercle well developed and directed dorsally. Declivitous face of propodeum, straight. *Metasoma*: petiolar scale pointing dorsally.

Queen

Measurements. (n = 2): HL: 1.15–1.18; HW: 1.18–1.2; EL: 0.33–0.4; EW: 0.13–0.15; IOD: 0.73; SL: 0.93–0.95; WL: 1.93–1.95; CI: 102-103; SI: 80-81.

Color and pubescence as in worker. *Head*: subquadrate; scape surpassing the posterior margin of head by no more than its maximum width; mandibles feebly striated, four teeth and two denticles on the masticatory margin; posterior margin of head straight; external margin of compound eye included in head surface in frontal view; ocelli hyaline, close to the posterior margin of head. *Mesosoma*: parapsidal furrows not well developed but parallels, axilla not divided medially. Anepisternum incompletely separated from katepisternum by a short suture. Forewing with only one close cubital cell; radial cell open. *Metasoma*: petiolar scale low, stout, and rounded apically.

Male

Measurements. (n = 2): HL: 0.6–0.64; HW: 0.7–0.75; EL: 0.2–0.26; EW: 0.13–0.14; SL: 0.34; WL: 1.48–1.50.

Body color similar to worker and queen. *Head* (Figure 10(e)): subquadrate, wider than long; lateral side of clypeus feebly projected forward; mandibles thin, with four teeth, apical tooth more than twice longer than the others; scape long, surpassing posterior margin of compound eyes. *Mesosoma* (Figure 10(f)): parapsidal furrows present and parallel, axilla not divided medially; forewing with one close radial cell and no cubital nor discoidal cell. Hindwing with two basal cells. *Metasoma*: petiole stout and low, directed dorsally, ventral process round, feebly developed. Pygostyle poorly developed; gonystylus stout covered with few erect setae; digitus short and no cuspis. Aedeagus with serrate ventral border.

Examined Material. COLOMBIA: Bolivar, Zambrano, 1w (IaVH), no more data available.

Additional Examined Material. Outside Colombia: ARGENTINA: La Rioja: Guayapa, 17w (IFML). Salta: PN El Rey, 2w (IFML); Campo Quijano, 19w (IFML). Tucumán: Salinas, 12w (IFML); Villa Nougués, 123w, 37q, 21m (IFML); Tucumán, 2w (MZSP). BRAZIL: Bahia: Rodelas, 2w (CEPEC); Domingos, Ilhéus, 1w (CEPEC); Simões Filho, 1w (CEPEC); Planalto, 1w (CEPEC). ES: Cda. Barra, 1w (CEPEC); REG-Linh, 1w (CEPEC); Itaúnas, Cord. De Antonia. 1w (MZSP); Rio de Janeiro: Macaé, 2w (MZSP); MT: Rondonopolis, 1w (MZSP); Tres Lagoas, 4w (MZSP); RS: Tramandaí, 49w (MZSP); Porto Alegre, 2w (MZSP). SC: Florianópolis, Praia da Joaquina, 1w (MZSP). CUBA: Guavia Cave, 3w (LACM). GUATEMALA: Escuintla, 20w (USNM); PARAGUAY: Central, Areguá, 3w (IFML); URUGUAY: Carmelo, 2w (LACM).

Geographic Distribution. Central and South America. Cuba, Guatemala, Colombia (literature records), Brazil (Bahía, Espírito Santo, Mato Grosso, Rio de Janeiro, Rio Grande and Santa Catarina States), Uruguay, Paraguay, Argentina (La Rioja, Salta, and Tucumán Provinces).

Etymology. The name of *pyramicus* refers to the typical tubercle or cone on propodeum present in all species of *Dorymyrmex*, giving to the propodeal angle an appearance of pyramid. Several *Dorymyrmex* species are known as "pyramid ants."

5.7.3. Comments. This species was described by Roger [40] as *Prenolepis pyramica* from one worker collected in Bahia, Brazil, and transferred to *Dorymyrmex* by Mayr [59]. Unfortunately, Wheeler [55] erroneously stated that *Formica insana* Buckley [39] (*Dorymyrmex insanus*) was an "undoubtedly synonym" of *D. pyramicus*. Originally, *Formica insana* was described from Texas and southern states of the United States. Workers of *D. insanus* are concolorous black to dark brown, as Snelling [25] says (see Figures 8(a) and 8(b)), differing from workers of *D. pyramicus* that are typically bicolored, as we describe above. Nevertheless, this mistake persisted, authors having considered *D. pyramicus* as a species with a very large distribution, from the south part of the United States throughout the Caribbean area to the north of Argentina. We only found one worker of *D. pyramicus* in Colombia, but there are bibliographic records that confirm its presence in this country [35]. Apparently, *D. insanus* and *D. pyramicus* are only sympatric in Central America (Cuba and Guatemala) and in the north part of South America (Colombia, Venezuela, and Northern Brazil). Beside color, *D. pyramicus* and *D. insanus* can be differentiated by the shape of head in full-face view and the shape of the promesonotal profile (continuous in *D. pyramicus*, interrupted at its end in *D. insanus*).

5.8. *Dorymyrmex tuberosus* Cuezzo & Guerrero n. sp. *(Figures 11(a)–11(c); 14)*

5.8.1. Diagnosis

Worker. Dark brown; whitish pubescence in all tagma; scape long; posterior margin of head concave in the middle; mesonotal profile interrupted by a short but distinct tubercle, besides a thin tubercle directed dorsally between dorsal and declivitous faces of propodeum.

5.8.2. Description

Worker

Measurements. Holotype (paratype): HL: 0.88 (0.93); HW: 0.80 (0.88); EL: 0.24 (0.25); EW: 0.20 (0.23); SL: 1.04 (0.98); COD: 0.18 (0.2); WL: 1.18 (1.20); CI: 90 (95); SI: 105 (106); REL: 27 (28); OI: 83 (90); TLI: 134 (131).

Concolorous, dark brown with the lateral corners of the clypeus reddish brown. Whitish and dense pubescence covering the all body. *Head* (Figure 10(a)): longer than wide. Compound eye placed in the middle of the lateral part of cephalic capsule, not surpassing the lateral margins. Psammophore with short hairs disposed in a triangle; the hairs on the top line are close to the foramen magnum and not reach the oral cavity. Scape long, surpassing the posterior margin of head. Mandibles strongly striate, with five teeth and at least two denticles along the masticatory margin and numerous denticles along the basal margin. Posterior margin of head with a feeble medial emargination. *Mesosoma* (Figures 11(b) and 11(c)): in profile with two tubercles, one in the posterior end of the mesonotum and one between the dorsal and the declivitous faces of the propodeum. *Metasoma*: petiolar scale directed dorsally, thin apically.

Queen and Male. Unknown.

Examined Material. Type series.

Geographic Distribution. COLOMBIA: (Bolivar: San Juan Nepomuceno, Santander: Bucaramanga, type localities).

Etymology. The name *tuberosus* refers to the presence of two tubercles on the dorsal face of both mesonotum and propodeum.

Natural History. Known only from museum collections. Specimens of Santander were collected in the campus of the Industrial University of Santander and those deposited in LACM have a label saying: "ex-Manihot," probably referred to be collected in a cultivate place. According to this data, *D. tuberosus* prefers, as several species of *Dorymyrmex,* disturbed habitats.

Examined Material. Type series.

5.8.3. Comments. Two well-developed tubercles on the mesosoma, along with whitish pubescence, and general dark color can be useful to differentiate *D. tuberosus* from the other species of *Dorymyrmex* found in Colombia. This species could be confused with *D. brunneus* by color but differs by the following characters: shape of the head, slightly wider after compound eyes and always with an emargination in the middle of posterior margin. Pro-mesosomal profile always at level or higher than the apex of propodeal cone. In contrary to *D. brunneus, D. tuberosus* has well-developed tubercles on the mesonotum.

5.9. Dorymyrmex xerophylus Cuezzo & Guerrero n. sp. (Figures 12(a)–12(c); 14)

5.9.1. Diagnosis

Worker. Small ants, TLI: <117. Head oval in full-face view, lateral margins parallel, and posterior margin strongly convex. Compound eyes not surpassing the sides of cephalic capsule. Propodeal tubercle short, stout, and lower than mesonotum. Pubescence dense and golden.

5.9.2. Description

Worker

Measurements. Holotype (Paratype): HL: 0.60 (0.62). HW: 0.44 (0.46). EL: 0.18 (0.18). EW: 0.12 (0.12). SL: 0.52 (0.54). WL: 0.70 (070). CI: 73 (74). SI: 87 (87). REL: 41 (39). OI: 67 (67). TLI: 117 (113).

Concolorous, light brown; only tergites 2 and 4 of gaster, darker. *Head* (Figure 11(a)): longer than wide. Mandibles feebly striate (only seen at more than 100x), with 4 teeth and 2 denticles. Compound eye well-developed in the first part of head in full-face view. Psammophore with only few hairs disposed in the central part of ventral cephalic face, not reaching the oral cavity; those hairs are equidistant between the foramen magnum and the oral cavity. Scapes short (SI = 87). *Mesosoma* (Figures 12(b) and 12(c)): dorsal face of pronotum with two erect hairs lengthless than the greatest width of the antennal scape. Mesonotum straight in profile, lower than pronotum, only interrupted in its posterior end, forming a declivitous face continuous with propodeum. *Metasoma*: petiolar scale wide, thin and rounded apically.

Queen And Male. Unknown.

Examined Material. Type series.

Geographic Distribution. COLOMBIA (La Guajira and Magdalena, type localities).

Etymology. The specific name is in apposition, refers to the extremely arid environments where *D. xerophylus* usually nests.

Natural History. Ants of Magdalena were collected with sausage baits, between 10:00 and 11:00 a.m. Apparently, *D. xerophylus* prefers, like other *Dorymyrmex*, open areas of dry forests in lowlands. Specimens were found in dry forest of Sierra Nevada de Santa Marta, dominated by Poaceae. This habitat is subjected to occasional human disturbances resulting from logging. Ants collected in La Guajira live in restored areas of opencast coal mines, abandoned 10 years ago.

5.9.3. Comments. *D. xerophylus* is close to *D. goeldii* but differ by size, pubescence, and color. In Colombia, only this two species have the posterior margin of head strongly convex and head more than twice longer than wide (CI: 73-74 and 77–40 for *D. xerophylus* and *D. goeldii*, resp.).

Acknowledgments

The authors are indebted to Mónica Ospina, Diego Perico (IAvH), Carlos Sarmiento (ICN), Inge Armbrecht and her students (Universidad del Valle), Yamileth Domínguez and Larry Fontalvo (Universidad del Atlántico), Vivian Sandoval (Universidad Nacional de Colombia), Roy Snelling (LACM), Carlos Roberto F. Brandão (MZSP), and Ted Schultz (USNM) for the loan of indispensable material for this study. Thanks to Brian Fisher and his team (http://www.antweb.org/) for excellent images of several species of *Dorymyrmex* shown in this paper. R. J. Guerrero is indebted to Leonardo D. Granados and Mayron E. Escárraga (Grupo Insectos Neotropicales, Universidad de Magdalena) for their help with ant measurements. These findings are a part of the research project Composition and Distribution of the Subfamily Dolichoderinae (Hymenoptera: Formicidae) in Colombia, funded by COLCIENCIAS-Unimagdalena (Agreement no. 122). Part of this research was funded by CONICET and CIUNT 26/G413 Projects granted to the first author. In accordance with section 8.6 of the ICZNs International Code of Zoological Nomenclature, printed copies of the edition of Psyche containing this article are deposited at the following six publicly accessible libraries: Green Library (Stanford University), Bayerische Staatsbibliothek, Library—ECORC (Agriculture & Agri-Food Canada), Library—Bibliotheek (Royal Belgium Institute of Natural Sciences), Koebenhavns Universitetsbibliotek, University of Hawaii Library.

References

[1] G. Mayr, *Myrmecologische Beiträge*, vol. 53 of *Sitzungsberichte der Koenigliche Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe*, 1866.

[2] P. S. Ward, S. G. Brady, B. L. Fisher, and T. R. Schultz, "Phylogeny and biogeography of dolichoderine ants: effects of data partitioning and relict taxa on historical inference," *Systematic Biology*, vol. 59, no. 3, pp. 342–362, 2010.

[3] C. Emery, "Formiche della provincia di Rio Grande do Sûl nel Brasile, raccolte dal dott. Hermann von Ihering," *Bolletino della Societa Entomologica Italiana*, vol. 19, pp. 352–366, 1888.

[4] R. R. Snelling, "Systematics of Nearctic ants of the genus *Dorymyrmex* (Hymenoptera: Formicidae)," *Contribution in Science*, vol. 454, pp. 1–14, 1995.

[5] J. C. Trager, "A revision of *Conomyrma* (Hymenoptera: Formicidae) from the southeastern United States, especially Florida, with keys to the species," *Florida Entomologist*, vol. 71, no. 1, pp. 11–29, 1988.

[6] W. W. Kempf, "Miscellaneous studies on Neotropical ants. VI. (Hymenoptera, Formicidae)," *Studia Entomológica*, vol. 18, pp. 341–380, 1975.

[7] P. S. Ward, "The ant genus *Leptanilloides*: discovery of the male and evaluation of phylogenetic relationships based on DNA sequence data," in *Advances in Ant Systematics (Hymenoptera: Formicidae): Homage to E. O. Wilson – 50 Years of Contributions*, R. R. Snelling, B. L. Fisher, and P. S. Ward, Eds., vol. 80 of *Memoirs of the American Entomological Institute*, pp. 637–649, 2007.

[8] A. Forel, "Formicides néotropiques. Part V. 4me sous–famille dolichoderinae forel," *Mémoires de la Société Entomologique de Belgique*, vol. 20, pp. 33–58, 1912.

[9] W. M. Wheeler, "Corrections and additions to "List of type species of the genera and subgenera of Formicidae"," *Annals of New York Academy of Science*, vol. 23, pp. 77–83, 1913.

[10] W. W. Kempf, "Catálogo abreviado das formigas da região Neotropical (Hymenoptera: Formicidae)," *Studia Entomológica*, vol. 15, pp. 3–344, 1972.

[11] A. Forel, "Formicides du Congo Belge récoltés par MM. Bequaert, Luja, etc.," *Revue de Zoolgie Africaine*, vol. 2, no. 1—4, pp. 306–351, 1913.

[12] F. Santschi, "Myrmicines, dolichodérines et autres formicides néotropiques," *Bulletin de la Societé Vaudoise des Sciences Naturelles*, vol. 54, pp. 345–378, 1922.

[13] W. M. Wheeler, "Ants of the American Museum Congo expedition. A contribution to the myrmecology of Africa," *Bulletin of American Museum of Natural History*, vol. 45, article 1, pp. 1–1004, 1922.

[14] R. R. Snelling and J. H. Hunt, "The ants of Chile (Hymenoptera: Formicidae)," *Revista Chilena de Entomología*, vol. 9, pp. 63–130, 1976.

[15] S. O. Shattuck, "Generic revision of the ant subfamily Dolichoderinae (Hymenoptera: Formicidae)," *Sociobiology*, vol. 21, no. 1, pp. 1–181, 1992.

[16] B. Bolton, *Identification Guide to the Ant Genera of the World*, Harvard University Press, Cambridge, Mass, USA, 1994.

[17] B. Bolton, "Synopsis and classification of Formicidae," *Memoirs of the American Entomological Institute*, vol. 71, 370 pages, 2003.

[18] A. Forel, "Cadre synoptique actuel de la faune des fourmis," *Bulletin de la Société Vaudoise des Sciences Naturelles*, vol. 51, pp. 229–253, 1917.

[19] A. Gallardo, "Sobre el género *Dorymyrmex* Mayr en la Argentina," *Revista Chilena de Historia Natural*, vol. 34, pp. 143–148, 1930.

[20] M. R. Smith, "Family Formicidae," in *Hymenoptera of America North of Mexico Synoptic Catalogue*, C. F. Muesebeck, K. V. Krombein, and H. K. Townes, Eds., pp. 778–875, United States Department of Agriculture, Washington, DC, USA, 1951.

[21] M. R. Smith, "Family Formicidae," in *Hymenoptera of America North of Mexico*, K. V. Krombein, Ed., first supplement, Synoptic Catalog, pp. 108–162, 1958.

[22] N. Kusnezov, "El estado real del grupo *Dorymyrmex* Mayr (Hymenoptera, Formicidae)," *Acta Zoologica Lilloana*, vol. 10, pp. 427–448, 1952.

[23] N. Kusnezov, "Die dolichoderinen–gattungen von sud–amerika (Hymenoptera, Formicidae)," *Zoologische Anzeiger*, vol. 162, pp. 38–51, 1959.

[24] N. Kusnezov, "Zoogeografía de las hormigas en Sudamérica," *Acta Zoológica Lilloana*, vol. 19, pp. 25–186, 1964.

[25] R. R. Snelling, "The ant genus *Conomyrma* in the United States (Hymenoptera: Formicidae)," *Contribution in Science*, vol. 238, pp. 1–6, 1973.

[26] D. R. Smith, "Formicidae," in *Catalog of Hymenoptera in America north of Mexico*, K. V. Krombein, P. D. Hurd, D. R. Smith, and B. D. Burds, Eds., pp. 1323–1467, Smithsonian Institute Press, Washington, DC, USA, 1979.

[27] B. Holldöbler and E. O. Wilson, *The Ants*, Harvard University Press, Cambridge, Mass, USA, 1990.

[28] K. Jaffé, *El mundo de las Hormigas*, Editorial Equinoccio, Universidad Simón Bolivar, Maracay, Venezuela, 2004.

[29] W. L. Brown Jr., "A comparison of the Hylean and Congo-West African rain forest ant faunas," in *Tropical Forest Ecosystems in Africa and South America: A Comparative Review*, B. J. Meggers, E. S. Ayensu, and W. D. Duckworth, Eds., pp. 161–185, Smithsonian Institution Press, Washington, DC, USA, 1973.

[30] A. Gallardo, "Hormigas de Neuquén y Río Negro," *Anales del Museo Nacional de Historia Natural de Buenos Aires*, vol. 30, pp. 243–254, 1919.

[31] N. Kusnezov, *Claves Para la Identificación de las Hormigas de la Fauna Argentina*, vol. 104-105, IDIA, Ministerio de Agricultura y Ganadería de la Argentina, Buenos Aires, Argentina, 1956.

[32] R. R. Snelling, "Descriptions of new Chilean ant taxa (Hymenoptera: Formicidae)," *Contributions in Science*, vol. 274, pp. 1–19, 1975.

[33] G. M. Dlussky and E. B. Fedoseeva, "Origin and early stages of evolution in ants," in *Cretaceous Biocenotic Crisis and Insect Evolution*, A. G. Ponomarenko, Ed., pp. 70–144, Nauka Press, Moscow, Russia, 1988.

[34] R. R. Snelling, "Systematics of social Hymenoptera," in *Social Insects*, H. R. Hermann, Ed., vol. 2, pp. 369–453, Academic Press, New York, NY, USA, 1981.

[35] F. Fernández and S. Sendoya, "List of Neotropical ants (Hymenoptera: Formicidae)," *Biota Colombiana*, vol. 5, no. 1, pp. 3–93, 2004.

[36] W. M. Wheeler, "The ants of the Grand Cañon," *Bulletin of American Museum of Natural History*, vol. 22, pp. 329–345, 1906.

[37] A. Forel, "Ameisen aus Sao Paulo (Brasilien), Paraguay etc. gesammelt von Prof. Herm. v. Ihering, Dr. Lutz, Dr. Fiebrig, etc.," *Verhandlungen der Zoologisch–Botanischen Gesellschaft in Wien*, vol. 58, pp. 340–418, 1908.

[38] A. Forel, "Miscellanea myrmécologiques," *Revue Suisse de Zoologie*, vol. 12, pp. 1–52, 1904.

[39] S. B. Buckley, "Descriptions of new species of North American Formicidae," *Proceedings of the Entomological Society of Philadelphia*, vol. 6, pp. 152–172, 1866.

[40] J. Roger, "Die neu aufgeführten Gattungen und Arten meines Formiciden–Verzeichnisses nebst Ergänzung einiger früher gegebenen Beschreibungen," *Berliner Entomologische Zeitschrift*, vol. 7, pp. 131–214, 1863.

[41] A. Gallardo, "Las hormigas de la República Argentina. Subfamilia Dolicoderinas," *Anales del Museo Nacional de Buenos Aires*, vol. 28, pp. 1–130, 1916.

[42] C. Johnson, "Taxonomy and diagnosis of *Conomyrma insana* (Buckley) and *C. flava* (McCook) (Hymenoptera: Formicidae)," *Insecta Mundi*, vol. 3, pp. 179–194, 1989.

[43] A. C. Cole Jr., "Notes on western ants (Hymenoptera: Formicidae)," *Journal of New York Entomological Society*, vol. 65, pp. 129–131, 1957.

[44] R. H. Crozier, "Karyotypes of twenty-one ant species (Hymenoptera; formicidae), with reviews of the known ant karyotypes," *Canadian Journal of Genetics and Cytology*, vol. 12, no. 1, pp. 109–128, 1970.

[45] S. O. Shattuck, *Taxonomic catalog of the ant subfamilies Aneuretinae and Dolichoderinae (Hymenoptera: Formicidae)*, vol. 112, University of California, Berkeley, Calif, USA, 1994.

[46] B. Bolton, G. Alpert, P. Ward, and P. Naskrecki, *Bolton's Catalogue of the Ants of the World: 1758–2005*, Harvard University Press, Cambridge, Mass, USA, 2006.

[47] E. O. Wilson, "Sympatry of the ants *Conomyrma bicolor* (Wheeler) and *C. pyramica* (Roger)," *Psyche*, vol. 64, no. 2, p. 75, 1957.

[48] A. Forel, "Ameisen des Herrn Prof. v. Ihering aus Brasilien (Sao Paulo usw.) nebst einigen anderen aus Südamerika und Afrika (Hym.)," *Deutsche Entomologische Zeitschrift*, pp. 285–312, 1911.

[49] C. Emery, "Hymenoptera. Fam. Formicidae. Subfam. Dolichoderinae," *Genera Insectorum*, vol. 137, pp. 1–50, 1913.

[50] A. Forel, "Fourmis d'Argentine, du Brésil, du Guatémala & de Cuba reçues de M. M. Bruch, Prof. v. Ihering, Mlle Baez, M. Peper et M. Rovereto," *Bulletin de la Société Vaudoise des Sciences Naturelles*, vol. 49, pp. 203–250, 1913.

[51] F. Santschi, "Quelques fourmis de l'Amérique australe," *Revue Suisse de Zoologie*, vol. 20, pp. 519–534, 1912.

[52] F. Santschi, "Nouvelles fourmis de la République Argentine et du Brésil," *Anales de la Sociedad Científica Argentina*, vol. 107, pp. 273–316, 1929.

[53] H. C. McCook, "Formicariae," in *Report upon Cotton Insects*, J. H. Comstock, Ed., pp. 182–189, Government Printing Office, Washington, DC, USA, 1880.

[54] C. Emery, "Beiträge zur Kenntniss der nordamerikanischen Ameisenfauna. (Schluss)," *Zoologische Jahrbücher Abteilung für Systematik Ökologie und Geographie der Tiere*, vol. 8, pp. 257–360, 1895.

[55] W. M. Wheeler, "A consideration of S. B. Buckley's "North American Formicidae"," *Transactions of the Texas Academy of Science*, vol. 4, pp. 17–31, 1902.

[56] W. S. Creighton, "The ants of North America," *Bulletin of the Museum of Comparative Zoology of Harvard College*, vol. 104, pp. 1–585, 1950.

[57] F. Santschi, "Formicides africains et américains nouveaux," *Annales de la Société Entomologique de France*, vol. 88, pp. 361–390, 1920.

[58] R. E. Gregg, *The Ants of Colorado with Reference to Their Ecology, Taxonomy, and Geographic Distribution*, University of Colorado Press, Boulder, Colo, USA, 1963.

[59] G. Mayr, "Neue formiciden," *Verhandlungen der Zoologisch–Botanischen Gesellschaft in Wien*, vol. 20, pp. 939–996, 1870.

[60] G. Mayr, "Formicidae novogranadenses," *Sitzungsberichte der Kais. Akademie der Wissenschaften. Wien Mathematisch.–Naturwissenschaftlichen. Klasse. Abteilung I*, vol. 61, pp. 370–417, 1870.

[61] F. Santschi, "Nouvelles fourmis brésiliennes," *Annales de la Société Entomologique de Belgique*, vol. 64, pp. 5–20, 1925.

[62] G. C. Wheeler and J. Wheeler, "The ant larvae of the subfamily Dolichoderinae," *Proceedings of the Entomological Society of Washington*, vol. 53, pp. 169–210, 1951.

[63] B. Goñi, L. C. de Zolessi, and H. T. Imai, "Karyotypes of thirteen ant species from Uruguay (Hymenoptera, Formicidae)," *Caryologia*, vol. 36, pp. 363–371, 1984.

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 960475, 12 pages
doi:10.1155/2012/960475

Research Article

Effects of the Heterogeneity of the Landscape and the Abundance of *Wasmannia auropunctata* on Ground Ant Assemblages in a Colombian Tropical Dry Forest

Rafael Achury,[1] Patricia Chacón de Ulloa,[1] and Ángela Arcila[2]

[1] *Grupo de Investigación en Biología, Ecología y Manejo de Hormigas, Departamento de Biología, Universidad del Valle, Calle 13 No. 100-00, AA 25360 Cali, Colombia*
[2] *Corporación Colombiana de Investigación Agropecuaria (Corpoica), E.E Caribia, Km 6 vía Sevilla, Zona Bananera, Magdalena, Colombia*

Correspondence should be addressed to Rafael Achury, rafaelachury@gmail.com

Received 2 May 2011; Accepted 8 August 2011

Academic Editor: Jonathan D. Majer

To evaluate the response of the ant assemblages to different management practices in the tropical dry forests of southwestern Colombia, 10 sites that conserve forest fragments surrounded by pastures and sugarcane crops were sampled. Tuna-fish baits placed on the ground in the three habitats captured 100 ant species (41 genera). The greatest number of species was found in the forests in contrast with a significant loss of richness and diversity in the productive habitats, the pastures being richer than the cane fields. Species richness was negatively correlated with the abundance of the little fire ant *Wasmannia auropunctata*. Ant species composition was related to soil temperature and percent ground cover, as well as being partially determined by location and the abundance of *W. auropunctata*. The forests had a significantly different species composition from the other two habitats, but there were no consistent differences between the pastures and the cane fields.

1. Introduction

The commonest consequence of converting tropical forests on a large scale is a mosaic of fragments of relictual vegetation surrounded by productive habitats such as pastures for cattle, sugarcane crops, and oil palm plantations [1, 2]. Modifications of the natural habitat generally result in loss of species and changes in the composition and diversity of different animal groups [3–6] including insects [7–9]. To understand the effects of transforming the natural habitat, it is important to examine how the richness and composition of species change in areas that contain different-sized fragments as part of one large disturbed matrix [10].

The tropical dry forest is one of the most transformed and threatened ecosystems in the world [11, 12]. Of the 519,597 km^2 of remnants of this forest distributed throughout the Americas, half the area (51%) is found in South America [13], where conversion to agriculture represents a substantial risk to the highly fragmented patches of dry forest [14]. Of the 30,713 km^2 of dry forest existing in Colombia today, 1977 km^2 [13], are found in the geographic valley of the Cauca River, spread out in more than 1600 fragments with an average size of 6 ha [15]. This situation is the consequence of the expansion of the sugarcane monocrop and pastures [16].

Given the urgency of determining the biodiversity in the relictual forests of the Cauca River Valley, studies have been conducted on ants and Staphylinidae (Coleoptera) [17], highlighting the need for obtaining information about the structure and dynamics of the biotic communities in these forest remnants and their adjacent matrixes.

Ants have a large number of attributes, offering many possibilities for monitoring, inventorying, and basic ecology [18, 19]. In addition to their high diversity and dominance in terms of biomass and numbers, particularly in tropical forests [20, 21], the ground-foraging ant assemblage is especially sensitive to impacts due to transformation of the habitat [22], because of this, they have been widely used as indicator species [23]. Many studies report that such disturbances promote changes in the structure and composition of the ant assemblages [24, 25], loss of species richness [26], reduced density of nests within the fragments [27, 28], and a high number of tramp species in fragments as compared with continuous forests [29].

In the dry forests of southwestern Colombia, where some 200 ant species have been recorded [17], the forest fragments conserve greater species richness than their adjacent matrixes [30]. Moreover, the richest forests have a greater number of rare species [31], and the richness and relative frequency of some groups (e.g., legionary or army ants) are correlated positively with the area [32]. Although the actual composition of ant species varies significantly among sampling sites [33], the little fire ant (*Wasmannia auropunctata* R.) is numerically dominant; thus, it has been proposed as an indicator of low diversity in the dry forest [34].

This study compared the richness and composition of the ground ant community at 10 sites in the three different habitats: forest fragments, pastures for cattle-raising, and sugarcane crops. The objective was to determine the effect of the different sites and habitats on the richness and composition of ant species, taking into account a gradient of disturbance and environmental and biotic variables. In addition, the study aimed to determine whether the changes in species richness and composition were conditioned by the presence of dominant ants. Finally, based on the results, a broader view for conserving forest fragments and using sustainable management practices for the associated habitats can now be provided.

2. Materials and Methods

2.1. Study Area. Located in southwestern Colombia, the area corresponds to the inter-Andean floodplain formed by the upper watershed of the Cauca River, with an area 230 km long by 10–20 km wide and at an altitude of 900–1100 m. The climate is typical of a tropical dry forest, with an average annual temperature of 24 C and 1000–2000 mm of rainfall, distributed in two periods (April-May and October-November), during which 70% of the total annual rainfall occurs [35].

Ten sites were selected, distributed from South to North, covering three states in southwestern Colombia (Table 1). Each site comprises a forest fragment whose arboreal vegetation reaches a canopy of 30 m, with prominent species of wild cashew (*Anacardium excelsum*), *Xylopia ligustrifolia*, *Laetia americana*, cow or wild fig (*Ficus glabrata*), *Cecropia* sp., and kapok (*Ceiba petandra*) [36], frequently mixed with clumps of *Guadua angustifolia* (Tribe Bambuseae). The forest fragments differ in shape, area, and type of matrix [37], in which pastures for cattle raising (36% of the area) and intensive sugarcane production (52%) predominate [15].

2.2. Sampling of Ants. Sampling was performed during the rainy season, from October to December, 2005 and February to May, 2006. Three habitats were identified at each site: forest, sugarcane fields, and pastures. All the pastures and cane fields surveyed were adjacent to the forest. Linear transects were marked off at random in each habitat, and 40 sampling stations were placed every 20 m to guarantee independence of the samples based on the ants' foraging distances [38]. All transects were placed parallel to the forest edges at a minimum distance of 50 m. At each sampling station, coordinates were taken (GPS Garmín 12XL); and four variables were measured: soil moisture, soil pH (Kelway meter), soil temperature (Weksler thermometer), and canopy cover (spherical concave densitometer, Forestry Suppliers, Inc.).

The ants were collected using tuna-fish baits, one per sampling station. This method is useful for estimating the composition and richness of the ant fauna that forage actively on the ground [39] and has been widely used in dry forests [30, 31, 34]. The baits, previously evaluated by Achury et al. [33], consisted of a piece (4 × 4 cm) of white bond paper, on which was placed an average of 9 g (± 1.7) of tuna fish conserved in oil. They were then put on the ground and left there for 3 hours. The ants that were found directly on the tuna fish were collected, and the rest of the bait, including part of the soil beneath, was also picked. This was done because on underside of the paper, there were often very small or less aggressive ant species.

The samples were cleaned in the laboratory and conserved in ethanol at 80%. Their identification was done to the genus level according to Palacio and Fernández [40] and Bolton [41]. At the species level, Longino's key [42] was used, as well as to comparing ants with specimens from the Museum of Entomology at the Universidad del Valle (MEUV) and the Museum of Zoology at the Universidade de São Paulo (MZUSP). The reference collection was deposited in the MEUV.

2.3. Data Analyses. For each sample (1 tuna-fish bait), the number of morphospecies of ants that were attracted to the bait and their respective abundances were counted. A descriptive analysis was done of the percent occupation of the baits by the different subfamilies, genera, and certain species.

To determine the differences with respect to ant richness and composition, two scales were analyzed: sites (total 10) and habitats (total 3, represented by forests, cane fields, and pastures). Correlations were sought between species richness per site versus three variables: latitude, total number of captures, and abundance of the commonest species (*W. auropunctata*). A correlation was also run between latitude and abundance of *W. auropunctata*. The richness per habitat was compared using rarefaction curves based on samples [43, 44], using the Estimates S program v. 8.2 [45]. Data on species density were used because they provide a better indicator of the differences in structure within the habitats [24].

The three habitats were compared with respect to four variables: abundance of ants per bait (natural logarithm), species richness per bait, the Shannon diversity index, and the numeric dominance index (ratio between number of workers of the most abundant species and total abundance of all species in the habitat). A one-way analysis of variance (the Kruskal-Wallis test) was applied, and multiple comparisons

Table 1: Description of the location and characteristics of the sites within fragments of tropical dry forest in the upper watershed of the Cauca River; sites ordered geographically from North to South.

Site	Adjacent matrix	Municipality and state	Coordinates	Altitude (masl)	Area (ha)
Miralindo I	Pastures	La Virginia, Risaralda	4 54 19.89 N 75 51 30.5 W	900	6.7
Aguas Claras	Pastures and sugarcane	Pereira, Risaralda	4 53 23.1 N 75 55 56.6 W	940	13.0
Alejandría	Pastures	La Virginia, Risaralda	4 49 58.6 N 75 53 2.4 W	900–940	15.3
Las Pilas	Pastures	Zarzal, Valle	4 26 25.7 N 75 59 23.1 W	1000	12.4
El Medio	Sugarcane	Zarzal, Valle	4 20 13.8 N 76 5 0.1 W	950	13.1
Las Chatas	Pastures and sugarcane	Buga, Valle	3 51 20.8 N 76 20 5.35 W	950	10.8
El Vínculo	Pastures	Buga, Valle	3 50 2.38 N 76 17 19.7 W	980–1150	15
El Hatico	Pastures and sugarcane	El Cerrito, Valle	3 38 34.48 N 76 19 40.52 W	980	12.6
Colindres	Pastures and sugarcane	Jamundí, Valle	3 16 25.8 N 76 29 31 W	975	10.0
San Julián	Pastures and sugarcane	Santander de Quilichao, Cauca	3 06 38.8 N 76 31 41.2 W	950	3.5

were made using the Tukey test and Bonferroni correction [46].

Species composition was described using the data on frequency of capture for all the species, and the similarity among the sampled sites was determined by means of hierarchical cluster analysis [47]. Then, the PC-ORD program v. 4 [48] was used to compare the groups formed, using the nonparametric multivariate technique MRPP (Multiresponse permutation procedure), which tests the null hypothesis of there being no difference between two or more groups of entities, based on previously defined groups [47, 49]. This technique was also used to compare the ant assemblages among habitats.

To examine whether the environmental variables (soil moisture, pH, temperature, and percent ground cover) and biotic variables (species richness and abundance of *W. auropunctata*) are related to the ant assemblage structure (frequency of capture per habitat), a canonical correspondence analysis (CCA) [48] was performed, followed by the Monte Carlo significance test (999 permutations). These analyses were done with the PC-ORD program v. 4.

3. Results

3.1. General Data on Ants Collected. Of the 1062 baits placed, 93.03% scored positive for ants, with an average per site of 92.83% (± 6.41) (Table 2). A total of 194,347 ants were attracted to the tuna-fish baits, classified into 100 species, 41 genera and 8 subfamilies (see the appendix). Myrmicinae was the subfamily with the most genera and species (24 and 66, resp.), followed by Dolichoderinae (5 genera, 7 species), Formicinae (4, 16), Ponerinae (2, 4), Ecitoninae (2, 2) Ectatomminae (2, 2), Pseudomyrmecinae (1, 2), and Heteroponerinae (1, 1). The richest genera were *Pheidole* (19 species), *Crematogaster* (9), *Solenopsis* (8), and *Camponotus* (4). The dominant species in the study were *W. auropunctata* (130,757 workers) and *Solenopsis geminata* (29,565), together representing 82.5% of the captures.

3.2. Richness and Abundance. The average number of ant species per site was 30.4 (minimum 17, maximum 46), with higher values toward the North of the study area (Table 2). Except for two sites (Colindres and San Julián), where the pastures or cane fields, respectively, had the greatest species richness, more species were recorded in the forest habitat (Figure 1). The rarefaction curves showed that the forests had the greatest richness compared with the pastures and cane fields ($F_{2,12} = 789.34$; $P < 0.001$), which had the lowest number of species (Figure 2).

A highly significant positive correlation was found between richness and latitude ($r = 0.8453$; df = 8; $P = 0.002$). In contrast, a highly significant negative correlation was found between abundance of *W. auropunctata* and latitude ($r = -0.9581$; df = 7; $P < 0.001$). Species richness per site varied inversely with the total captures of *W. auropunctata* ($r = -0.8062$; df = 7; $P = 0.008$) and its respective abundance ($r = -0.8569$; df = 7; $P = 0.003$).

Significant differences were found among the habitats for the variables ant abundance per bait ($F_{2,985} = 12.31$; $P < 0.0001$) and species richness per bait ($H = 25.86$; df = 2, $n = 988$; $P < 0.001$), as well as for the Shannon diversity index ($F_{2,22} = 21.13$; $P < 0.001$). Abundance was greater in the cane fields and the forest than in the pastures (Tukey: $P < 0.001$) (Figure 3(a)), while richness was greater

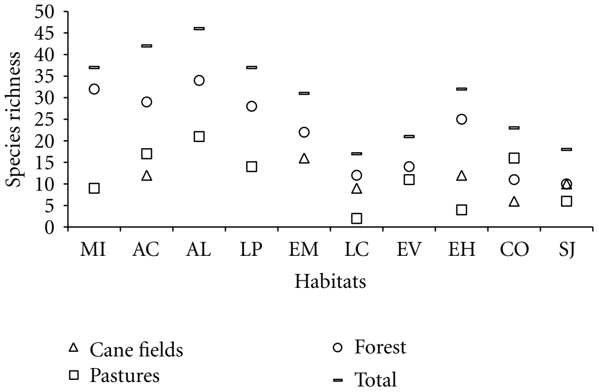


Figure 1: Richness of ant species broken down by habitat at 10 sites ordered geographically from North to South. MI (Miralindo), AC (Aguas Claras), AL (Alejandría), LP (Las Pilas), EM (El Medio), LC (Las Chatas), EV (El Vínculo), EH (El Hatico), CO (Colindres), and SJ (San Julián).

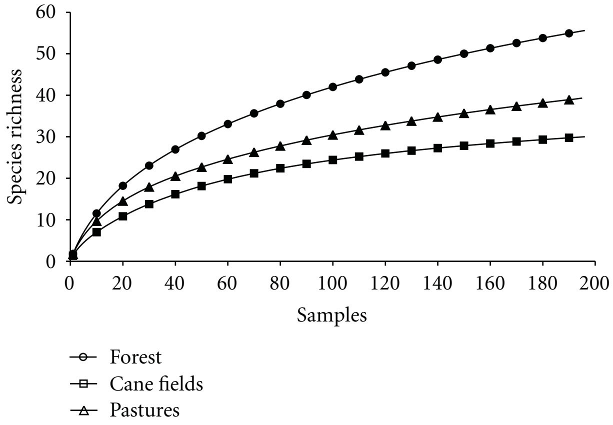


Figure 2: Rarefaction curves, based on the Coleman method, for species of ants captured at tuna-fish baits in three habitats within the tropical dry forest region. For purposes of clarity, the confidence intervals (95%) and the SD are omitted in the figure.

in the pastures and forest (Bonferroni correction: $P < 0.001$) (Figure 3(b)). The diversity index was significantly greater in the forest (Tukey: $P < 0.001$) (Figure 3(c)). No significant differences were found for the dominance index ($F_{2,19} = 0.13$; $P = 0.87$) given that in the three habitats it was higher than 60% (Figure 3(d)). *Wasmannia auropunctata* ant was dominant in the forest and cane fields, whereas in the pastures its index was low (36%), the dominant species being *S. geminata*.

Table 2: Effectiveness of tuna-fish baits and total richness of ant genera and species in the study area.

Site	Bait attraction (%)	No. of genera	No. of species
North			
Miralindo	95.6	23	37
Aguas Claras	96.8	21	42
Alejandría	87.2	22	46
Las Pilas	96.7	18	37
Midzone			
El Medio	97.5	15	31
Las Chatas	86.7	13	17
El Vínculo	78.9	15	21
Hatico	95.0	21	32
South			
Colindres	95.0	17	23
San Julián	98.7	12	18
Average ± SD	92.8 ± 6.41	17.7 ± 3.92	30.4 ± 10.24

3.3. Species Composition. Based on the dendrogram, four groups were differentiated with a level of retention of over 50% (Figure 4). There were significant differences in ant composition among sites (MRPP: $A = 0.129$; $T = -4.408$; $P = 0.0002$), which were determined by geographic location and the abundance of *W. auropunctata*. The first group was formed by the four sites in the North, which also had the lowest abundance of *W. auropunctata* (Aguas Claras, Alejandría, Miralindo, and Las Pilas). In Las Chatas, which was separate from the other sites, no *W. auropunctata* ants were captured. The third group covered the midzone of the geographic valley of the Cauca River (El Hatico, El Vínculo, and El Medio). Lastly, the fourth group was formed by the two sites in the South (Colindres and San Julián), where the greatest abundance of *W. auropunctata* was found.

The CCA showed that the habitats formed separate groups that varied with respect to the composition of ants (Figure 5), which was significant globally (MRPP: $A = 0.116$; $T = -5.847$; $P = 0.0001$). However, the differences were between the forest and pastures (MRPP: $A = 0.124$; $T = -6.263$; $P = 0.0003$) and the forest and cane fields (MRPP: $A = 0.067$; $T = -3.475$; $P = 0.007$); but not between the pastures and cane fields (MRPP: $A = 0.052$; $T = -1.757$; $P = 0.063$). Moreover, the canonic regression (Table 3) shows that that there is a strong relationship between the community structure and the variables soil temperature, percent ground cover, abundance of *W. auropunctata*, and richness of ant species, of which the first three were strongly associated with the second axis, while the last one was associated with the first axis. The variables pH and soil moisture had weak relationships with the composition of ants. The proper values (eigenvalues) for the first two axes explained the highest percent of cumulative variance (21.7%) and were significant (Table 3).

4. Discussion

Sampling methods in this study did not include collecting litter, so it would be expected that species richness would not be as high; however, the 100 ant species collected with the tuna-fish baits in the 10 dry forest fragments represent 50% of the species recorded in the study area [17]. Myrmicinae was the most diverse subfamily, with five times more genera

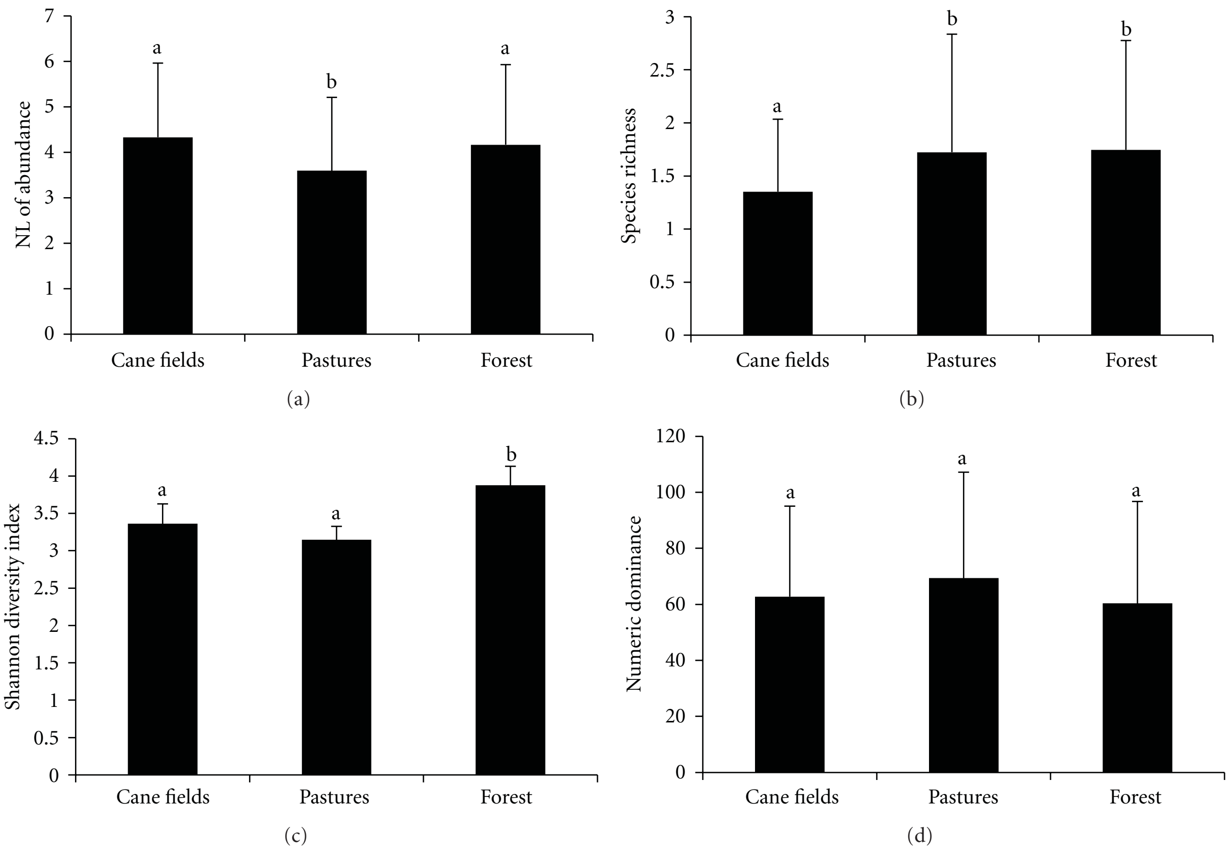


Figure 3: Average values and SD for (a) natural logarithm of the abundance of ants per bait; (b) species richness per bait; (c) shannon diversity index, and (d) numeric dominance of the most abundant species in each habitat. Bars with different letters are statistically different.

Table 3: Summary of the CCA statistics for each axis and the Monte Carlo significance test for the proper values (eigenvalues) based on 999 permutations.

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.538	0.319	0.233
Monte Carlo probability test	0.001	0.006	0.015
% cumulative variance in species data	13.7	21.7	27.6
Variables of the canonic multiple regression			
Soil moisture	– 0.038	0.104	– 0.172
pH	0.080	– 0.170	– 0.141
Soil temperature	– 0.141	0.314	– 0.086
% ground cover	0.304	– 0.480	– 0.784
Abundance of *W. auropunctata*	0.170	– 0.268	0.984
Species richness	0.713	0.787	0.482

and four times more species than the other subfamilies. This preeminence can be explained by the great adaptive radiation, range of foraging behaviors, nesting habits, and colony structure of this subfamily [20], which includes the genus *Pheidole*, which had the greatest richness (19 species) and which is represented by 651 species in the New World [50].

In the study area, agricultural intensification has occurred from the edges of the Cauca River in the flatlands toward the foothills [16]. Species' richness increased toward the North of the study area (Figure 1), where the sampled sites are found close to the foothills of the central and western Andean mountain ranges; by contrast, the sites in the South are found in the flatlands closer to the edge of the Cauca River. Arcila-Cardona et al. [37] showed that the sites located to the North are more interconnected than the midzone and South of the geographic valley and are surrounded by gallery forests and patches of *Guadua angustifolia*, which increases

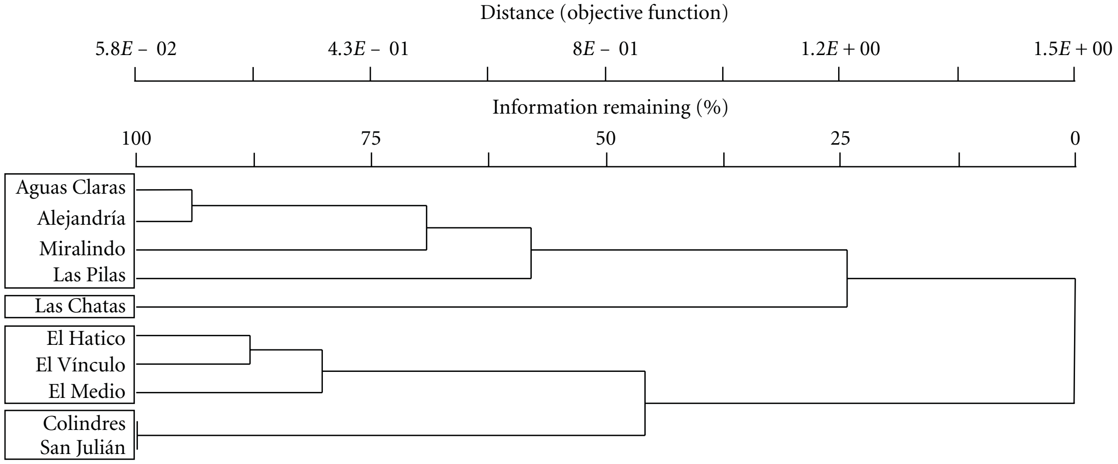


Figure 4: Clustering of the ant assemblages at the 10 sampled sites, based on the Sorensen (Bray-Curtis) index of dissimilarity and the Beta-flexible clustering method ($b = -0.25$). Percent concatenation: 10%.

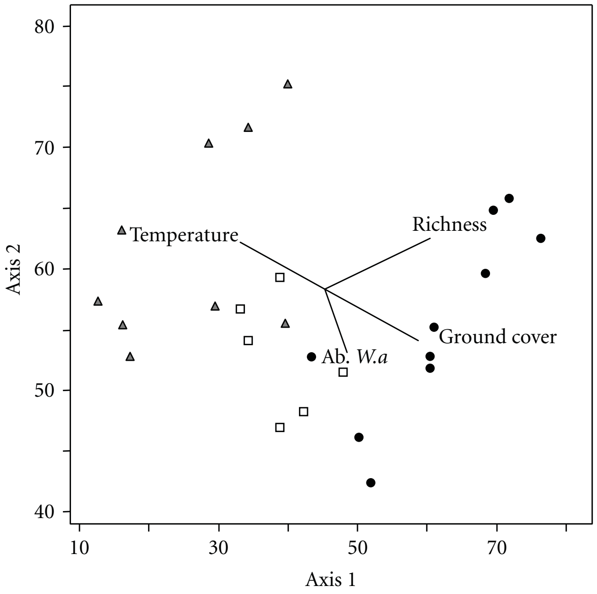


Figure 5: Canonical correspondence analysis (CCA) of the composition of ants in three habitats (●: Forest; ▲: Pastures; □: Cane fields). The lines show the direction and strength of the relationship of the environmental and biotic variables with respect to the structure of the ant assemblage per habitat.

the heterogeneity of the landscape and favors the movement of ant species among sites. This result is related to what Cook et al. found [51], where small or isolated fragments maintain high species richness due to the availability of colonizers from adjacent heterogeneous matrixes. Another phenomenon that can affect the species richness of ground ants is the periodic flooding that affects the sites in the South with greater frequency [16]. This stochastic event could alter the availability and quality of the habitat dramatically [22], resulting in a reduction in the richness of ants [52] when they are forced to move their nesting sites regularly [53].

The inverse correlation between species richness and the abundance of *W. auropunctata* reinforces the idea that the little fire ant can be used as an indicator of low diversity in ant assemblages [34]. This species is 10 times more abundant toward the South of the region sampled, where the process of fragmentation has been more aggressive [16]. Under these circumstances, *W. auropunctata* has largely displaced the ant fauna in some areas of the tropical forest in southwestern Colombia, accounting for up to 84% of the total captures. The increase in invasive or aggressive species is one of the effects of fragmentation that has been reported with greatest frequency [28, 29, 54–56] and has had negative effects on the native fauna, decreasing the utilization of resources for other species of ants and other arthropods, thereby affecting plants and associated arthropods, either directly or indirectly [22]. Although *W. auropunctata* is a very common native species of neotropical forests that does not usually dominate entire assemblage [57–59], in disturbed areas such as agricultural and forestry systems, as well as in regions outside its native range, the little fire ant commonly has enormous populations [60, 61] and is capable of exterminating ant populations over large areas [20]. That result is in agreement with those found in this study.

In agreement with the rarefaction curve (Figure 2), there are significant differences in the number of species per habitat, which shows that management has an important effect on the ant fauna in these tropical dry forests. Species richness is greatest in the forests and lowest in the cane fields. The comparison among habitats indicates a significant loss of species between the forest and productive habitats, given that the forests have 51 species that were not recorded in either the cane fields (only 3 exclusive species) or the pastures (8 species). This pattern of species richness is common in tropical zones [24, 27, 62], where the richness declines along a gradient of succession or disturbance. Majer et al. [63] showed that the permanent transformation of forests to crops dramatically reduces species richness. Perfecto et al. [64] reviewed 22 studies, of which 18 reported that ant diversity decreased with the intensification of agriculture. In

Table 4: List of ant species sampled and their abundance at baits along a tropical dry forest region of southwestern Colombia.

Species	Forest	Cane fields	Pastures	Total abundance	% occupation of baits
Dolichoderinae					
Azteca instabilis	1324	26	0	1350	5.36
Azteca sp. 1	29	0	0	29	0.10
Dolichoderus bispinosus	1279	0	0	1279	3.74
Dorymyrmex brunneus	0	0	1	1	0.10
Linepithema iniquum	135	14	1	150	1.32
Linepithema sp. 1	66	0	0	66	0.61
Tapinoma melanocephalum	3	0	1	4	0.40
Ecitoninae					
Eciton burchelli	5	0	0	5	0.10
Labidus coecus	774	228	294	1296	0.91
Ectatomminae					
Ectatomma ruidum	0	8	42	50	3.24
Gnamptogenys annulata	1	0	0	1	0.10
Formicinae					
Acropyga exsanguis	1	0	0	1	0.10
Brachymyrmex heeri	0	1	57	58	1.52
Brachymyrmex sp. 1	7	0	8	15	0.51
Brachymyrmex sp. 2	11	0	0	11	0.61
Brachymyrmex sp. 3	5	0	2	7	0.20
Brachymyrmex sp. 4	0	0	1	1	0.10
Brachymyrmex sp. 5	11	0	73	84	0.91
Brachymyrmex sp. 6	4	0	0	4	0.20
Camponotus claviscapus	0	5	0	5	0.10
Camponotus novogranadensis	248	2	9	259	4.25
Camponotus sp. 1	0	2	45	47	2.63
Camponotus sp. 2	1	0	0	1	0.10
Nylanderia fulva	390	0	0	390	1.72
Paratrechina longicornis	0	3	1	4	0.20
Paratrechina sp. 1	19	4	7	30	1.42
Paratrechina sp. 2	11	11	20	42	1.62
Heteroponerinae					
Heteroponera sp. 1	1	0	0	1	0.10
Myrmicinae					
Acromyrmex octospinosus	3	0	0	3	0.10
Apterostigma pilosum	1	0	0	1	0.10
Atta cephalotes	27	0	0	27	0.81
Cardiocondyla minutior	0	2	42	44	1.42
Cardiocondyla obscurior	0	3	131	134	1.92
Carebara brevipilosa	31	0	0	31	0.10
Cephalotes minutus	0	0	1	1	0.10
Crematogaster carinata	6994	0	0	6994	5.26
Crematogaster curvispinosa	343	0	0	343	0.61
Crematogaster distans	172	0	0	172	0.20
Crematogaster erecta	0	0	57	57	0.10
Crematogaster evallans	4922	35	0	4957	2.63
Crematogaster limata	284	0	51	335	1.01

Table 4: Continued.

Species	Forest	Cane fields	Pastures	Total abundance	% occupation of baits
Crematogaster nigropilosa	448	0	0	448	0.71
Crematogaster sotobosque	3751	0	0	3751	3.04
Crematogaster sp. 1	178	0	0	178	0.51
Cyphomyrmex costatus	1	0	0	1	0.10
Cyphomyrmex rimosus	5	0	2	7	0.71
Hylomyrma reitteri	3	0	0	3	0.10
Megalomyrmex sp. 1	4	0	0	4	0.10
Megalomyrmex wallacei	3	0	0	3	0.10
Monomorium florícola	88	992	197	1277	3.04
Mycocepurus smithii	3	0	0	3	0.30
Myrmycocrypta sp. 1	3	0	0	3	0.20
Myrmycocrypta sp. 2	19	0	0	19	0.30
Octostruma balzani	2	0	0	2	0.20
Octostruma sp. 1	4	0	0	4	0.10
Pheidole radoszkowskii	0	0	27	27	0.20
Pheidole rugiceps	57	0	0	57	2.33
Pheidole sabella	79	534	4	617	2.43
Pheidole scalaris	359	19	132	510	8.20
Pheidole sp. 1	228	0	0	228	0.10
Pheidole sp. 2	0	325	80	405	0.40
Pheidole sp. 3	4	0	0	4	0.20
Pheidole sp. 4	1124	0	7	1131	4.15
Pheidole sp. 5	4	0	0	4	0.20
Pheidole sp. 6	354	0	0	354	0.40
Pheidole sp. 7	1	407	5	413	0.91
Pheidole sp. 8	778	9	0	787	0.61
Pheidole sp. 9	52	0	0	52	0.20
Pheidole sp. 10	3	0	0	3	0.10
Pheidole sp. 11	4	0	0	4	0.30
Pheidole sp. 12	4	0	0	4	0.10
Pheidole sp. 13	0	0	3	3	0.10
Pheidole subarmata	5	0	151	156	0.91
Pheidole susannae	507	518	38	1063	7.09
Pheidole synarmata	644	71	0	715	2.43
Pyramica denticulata	22	0	1	23	0.51
Rogeria belti	1	0	0	1	0.10
Solenopsis geminata	2087	11653	15825	29565	18.02
Solenopsis picea	259	0	0	259	0.30
Solenopsis pollux	1592	469	54	2115	10.53
Solenopsis sp. 1	6	0	0	6	0.10
Solenopsis sp. 2	16	0	0	16	0.30
Solenopsis sp. 3	67	0	2	69	0.30
Solenopsis sp. 4	37	0	5	42	1.72
Solenopsis sp. 5	40	36	25	101	2.13
Strumigenys sp. 1	1	0	0	1	0.10

Table 4: Continued.

Species	Forest	Cane fields	Pastures	Total abundance	% occupation of baits
Strumigenys trieces	1	0	0	1	0.10
Temnothorax subditivus	0	470	0	470	0.30
Tetramorium bicarinatum	0	147	21	168	0.51
Tetramorium simillimum	0	1	4	5	0.20
Trachymyrmex opulentus	1	0	0	1	0.10
Trachymyrmex sp. 1	2	0	0	2	0.20
Tranopelta gilva	0	0	138	138	0.20
Wasmannia auropunctata	101864	22718	6176	130758	38.36
Ponerinae					
Hypoponera sp. 1	12	0	0	12	0.40
Hypoponera sp. 2	0	7	0	7	0.10
Pachycondyla constricta	25	0	0	25	0.91
Pachycondyla impressa	5	0	0	5	0.51
Pseudomyrmecinae					
Pseudomyrmex boopis	7	0	0	7	0.71
Pseudomyrmex sp. 1	0	0	20	20	1.82

Species sharing the resource with the little fire ant (*W. auropunctata*).

the tropics, a large part of the anthropogenic disturbance is due to pastures for cattle raising [22], and this intensification can result in the loss of richness, especially of cryptic or specialized predator species [65]. The habitat with the lowest number of species was the cane fields, which can be related to common cultural practices in this monocrop, such as burning, application of agrochemicals, and removal of litter from the ground [66]. These factors, in contrast with management of the pastures, impact species richness more intensely by eliminating nesting and food resources.

In this study, the composition of the ant assemblage at the scale of the site and habitat could be partially structured by the abundance of *W. auropunctata*. Some studies provide evidence that the dominant species is a key factor in structuring the ant assemblages [25, 67], given that such species partially control the competitive interactions in tropical forests [33, 68].

Significant differences were found in ant composition among habitats. The forests are more diverse (Figure 3(c)) and have a composition separate from the other two habitats. In the study area, some mechanisms that explain the changes in species composition are related to microenvironmental variables, such as soil temperature and percent ground cover (Table 3). The loss of arboreal vegetation has a significant effect on the assemblage of ants, given that it changes microclimatic conditions, including temperature regimes and relative humidity gradients [22]. These disturbances and conversions to productive agroecosystems limit the nesting sites, generating changes in species composition [69]. For example, *W. auropunctata* is the dominant species in the forest and cane fields, whereas in the pastures *S. geminata* dominates (Figure 3(d)). The pastures have a higher temperature and little ground cover in the form of litter and pieces of bark, conditions that are adverse for the nesting of *W. auropunctata*. In contrast, *S. geminata* dominates sites where the intensification of agriculture has generated open systems with high solar radiation [70]. Although there is a clear distinction between the assemblages of ants associated with the cane fields and pastures, the differences were not significant ($P = 0.063$). One possible reason is that the cane fields in the study area are adjacent to the pastures, so there could be a movement of species between habitats. Our results agree with other studies conducted in tropical forests [24], which found that in a regeneration gradient, soil generalists ant fauna can move between adjacent areas with low complexity. Thus, they propose the existence of spatial self-correlation as an explanation, given that low-complexity habitats most likely present a more traversable surface at the scale of a foraging ant.

5. Conclusions

The results obtained confirm that the structure and composition of the ground ant assemblage in the tropical dry forest of southwestern Colombia differ at both site and habitat levels. These changes are related to the abundance of dominant species (primarily *W. auropunctata*), as well as to geographic position, microclimatic conditions, and the complexity of the habitats and sampling sites. Moreover, it is important to take into account the conditions of each site and the gradient of isolation and disturbance that there is from South to North. The sites in the South, in contrast with those from the North, are more isolated and have been submitted to greater disturbance (e.g., cattle entering the forest fragments, cutting down trees, and greater use of agrochemicals in the cane crops).

Moreover, it is hypothesized that the indirect effect of loss of species due to isolation and fragmentation can favor colonization by species such as *W. auropunctata*, which takes advantage of the freeing up of resources and niches due to the disappearance of other species and manages to build up a high population density. Given that agricultural conversion has favored the excessive abundance of *W. auropunctata* to the detriment of the diversity of ants associated with the dry forest, it is important to maintain the heterogeneity of the landscape. Despite the aggressive transformation of the dry forest for agriculture, these relicts conserve a large number of species whose composition depends on the site. Consequently, the loss of some of the forest fragments would theoretically mean the disappearance of some species at the local and regional scale, resulting in the homogenization of the ant fauna. Accordingly, it would be important to increase the structural connectivity between sites, which would also serve to prevent the continued degradation of the forest and improve management of the matrixes. Finally, in line with other studies [71, 72], this work reinforces the idea of how vulnerable ant assemblages are to environmental disturbance.

Appendix

For more details, see Table 4.

Acknowledgments

Rodrigo Feitosa and Carlos Roberto Brandão, from the Museu de Zoologia da Universidade de São Paulo (MZUSP), collaborated in determining some ant species. María del Pilar López, Paloma Bejarano, Néstor Zúñiga, and Christian Bermúdez helped with the fieldwork. The Alexander von Humboldt Institute for Research on Biological Resources provided financial aid under Agreement no. 192 with the University of the Valley. The following owners and administrators of the forests gave us permission to work on their properties: Hilda Sanint (Alejandría), Carlos Ávila (El Medio), Luis Carlos Sadovnik (San Julián), and the Institute for the Research and Preservation of the Cultural and Natural Heritage of the Cauca Valley (INCIVA—El Vínculo). The evaluators' revisions were fundamental for improving the final version of this paper.

References

[1] C. Gascon, W. F. Laurance, and T. E. Lovejoy, "Forest fragmentation and biodiversity in central Amazonia," in *How Landscape Changes*, G. A. Bradshaw and P. A. Marquet, Eds., Ecological Studies, pp. 33–48, Springer, Berlin, Germany, 2003.

[2] W. F. Laurance and M. Goosem, "Impacts of habitat fragmentation and linear clearings on Australian rainforest biota," in *Living in a Dynamic Tropical Forest Landscape*, N. E. Stork and S. M. Turton, Eds., pp. 295–306, Blackwell, Oxford, UK, 2008.

[3] C. A. Peres, "Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates," *Conservation Biology*, vol. 15, no. 6, pp. 1490–1505, 2001.

[4] W. F. Laurance and H. L. Vasconcelos, "Ecological effects of habitat fragmentation in the tropics," in *Agroforestry and Biodiversity Conservation in Tropical Landscapes*, G. Schroth, G. A. B. da Fonseca, C. A. Harvey, G. Gascon, H. L. Vasconcelos, and A. M. Izac, Eds., pp. 33–49, Island Press, Washington, DC, USA, 2004.

[5] D. B. Lindenmayer, R. B. Cunningham, C. F. Donnelly, H. Nix, and B. D. Lindenmayer, "Effects of forest fragmentation on bird assemblages in a novel landscape context," *Ecological Monographs*, vol. 72, no. 1, pp. 1–18, 2002.

[6] G. Gascon, G. A. B. da Fonseca, W. Sechrest, K. A. Billmark, and J. Sandenson, "Biodiversity conservation in deforested and fragmented tropical landscapes: an overview," in *Agroforestry and Biodiversity Conservation in Tropical Landscapes*, G. Schroth, G. A. B. da Fonseca, C. A. Harvey, G. Gascon, H. L. Vasconcelos, and A. M. Izac, Eds., pp. 15–32, Island Press, Washington, DC, USA, 2004.

[7] R. G. Davies, "Feeding group responses of a neotropical termite assemblage to rain forest fragmentation," *Oecologia*, vol. 133, no. 2, pp. 233–242, 2002.

[8] O. Barbosa and P. A. Marquet, "Effects of forest fragmentation on the beetle assemblage at the relict forest of Fray Jorge, Chile," *Oecologia*, vol. 132, no. 2, pp. 296–306, 2002.

[9] D. A. Driscoll and T. Weir, "Beetle responses to habitat fragmentation depend on ecological traits, habitat condition, and remnant size," *Conservation Biology*, vol. 19, no. 1, pp. 182–194, 2005.

[10] W. F. Laurance, T. E. Lovejoy, H. L. Vasconcelos et al., "Ecosystem decay of Amazonian forest fragments: a 22-year investigation," *Conservation Biology*, vol. 16, no. 3, pp. 605–618, 2002.

[11] D. Janzen, "Tropical dry forests. The most endangered major tropical ecosystem," in *Biodiversity*, E. O. Wilson, Ed., pp. 130–137, National Academy of Sciences/Smithsonian Institution, Washington, DC, USA, 1988.

[12] J. M. Hoekstra, T. M. Boucher, T. H. Ricketts, and C. Roberts, "Confronting a biome crisis: global disparities of habitat loss and protection," *Ecology Letters*, vol. 8, no. 1, pp. 23–29, 2005.

[13] C. A. Portillo-Quintero and G. A. Sánchez-Azofeifa, "Extent and conservation of tropical dry forests in the Americas," *Biological Conservation*, vol. 143, no. 1, pp. 144–155, 2010.

[14] L. Miles, A. C. Newton, R. S. DeFries et al., "A global overview of the conservation status of tropical dry forests," *Journal of Biogeography*, vol. 33, no. 3, pp. 491–505, 2006.

[15] A. M. Arcila-Cardona, C. Valderrama-Ardila, and P. C. de Ulloa, "Análisis de la fragmentación del bosque seco de la cuenca alta del río Cauca, Colombia," in *III Congreso Internacional de Ecosistemas Secos*, M. Rodríguez, G. E. Guerra, B. S. Reyes, and R. K. Banda, Eds., p. 62, Fundación Ecosistemas Secos, Bogotá, Colombia, 2008.

[16] I. Armbrecht, I. Tischer, and P. Chacón, "Nested subsets and partition patterns in ant assemblages (Hymenoptera, Formicidae) of Colombian dry forest fragments," *Pan-Pacific Entomologist*, vol. 77, no. 3, pp. 196–209, 2001.

[17] P. C. de Ulloa and I. Armbrecht, "Las hormigas del bosque seco tropical," in *Informe sobre el Avance en el Conocimiento y la Información de la Biodiversidad 1998–2004*, M. E. Chávez and M. Santamaría, Eds., pp. 345–351, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia, 2006.

[18] S. P. Yanoviak and M. Kaspari, "Community structure and the habitat templet: ants in the tropical forest canopy and litter," *Oikos*, vol. 89, no. 2, pp. 259–266, 2000.

[19] L. E. Alonso and D. Agosti, "Biodiversity studies, monitoring, and ants: an overview," in *Ants: Standard Methods for Measuring and Monitoring Biodiversity*, D. Agosti, J. Majer, L. Alonso,

and T. Schultz, Eds., pp. 1–8, Smithsonian Institution Press, Washington, DC, USA, 2000.

[20] B. Hölldobler and E. O. Wilson, *The Ants*, Harvard University Press, Cambridge, Mass, USA, 1990.

[21] H. L. Vasconcelos, "Effects of forest disturbance on the structure of ground-foraging ant communities in central Amazonia," *Biodiversity and Conservation*, vol. 8, no. 3, pp. 409–420, 1999.

[22] S. M. Philpott, I. Perfecto, I. Armbrecht, and C. L. Parr, "Ant diversity and function in disturbed and changing habitats," in *Ant Ecology*, L. Lach, C. L. Parr, and K. L. Abbott, Eds., pp. 137–156, Oxford University Press, Oxford, UK, 2010.

[23] A. D. Gove, J. D. Majer, and V. Rico-Gray, "Ant assemblages in isolated trees are more sensitive to species loss and replacement than their woodland counterparts," *Basic and Applied Ecology*, vol. 10, no. 2, pp. 187–195, 2009.

[24] R. R. Silva, R. S. M. Feitosa, and F. Eberhardt, "Reduced ant diversity along a habitat regeneration gradient in the southern Brazilian Atlantic forest," *Forest Ecology and Management*, vol. 240, no. 1–3, pp. 61–69, 2007.

[25] X. Arnan, M. Gracia, L. Comas, and J. Retana, "Forest management conditioning ground ant community structure and composition in temperate conifer forests in the Pyrenees Mountains," *Forest Ecology and Management*, vol. 258, no. 2, pp. 51–59, 2009.

[26] R. R. Dunn, "Managing the tropical landscape: a comparison of the effects of logging and forest conversion to agriculture on ants, birds, and lepidoptera," *Forest Ecology and Management*, vol. 191, no. 1–3, pp. 215–224, 2004.

[27] K. S. Carvalho and H. L. Vasconcelos, "Forest fragmentation in central Amazonia and its effects on litter-dwelling ants," *Biological Conservation*, vol. 91, no. 2-3, pp. 151–157, 1999.

[28] C. A. Brühl, T. Eltz, and K. E. Linsenmair, "Size does matter—effects of tropical rainforest fragmentation on the leaf litter ant community in Sabah, Malaysia," *Biodiversity and Conservation*, vol. 12, no. 7, pp. 1371–1389, 2003.

[29] A. V. Suarez, D. T. Bolger, and T. J. Case, "Effects of fragmentation and invasion on native ant communities in coastal southern California," *Ecology*, vol. 79, no. 6, pp. 2041–2056, 1998.

[30] I. Armbrecht and P. C. de Ulloa, "Composición y diversidad de hormigas en bosques secos relictuales y sus alrededores, en el Valle del Cauca, Colombia," *Revista Colombiana de Entomología*, vol. 23, no. 1-2, pp. 45–50, 1997.

[31] I. Armbrecht and P. Ulloa-Chacón, "Rareza y diversidad de hormigas en fragmentos de bosque seco colombianos y sus matrices," *Biotropica*, vol. 31, no. 4, pp. 646–653, 1999.

[32] F. H. Lozano-Zambrano, P. Ulloa-Chacón, and I. Armbrecht, "Hormigas: relaciones especies-área en fragmentos de bosque seco tropical," *Neotropical Entomology*, vol. 38, no. 1, pp. 44–54, 2009.

[33] R. Achury, P. C. de Ulloa, and A. M. Arcila, "Composición de hormigas e interacciones competitivas con *Wasmanniaauropunctataen* fragmentos de bosque seco tropical," *Revista Colombiana de Entomología*, vol. 34, no. 2, pp. 209–216, 2008.

[34] I. Armbrecht and P. Ulloa-Chacón, "The little fire ant *Wasmanniaauropunctata* (Roger) (Hymenoptera: Formicidae) as a diversity indicator of ants in tropical dry forest fragments of Colombia," *Environmental Entomology*, vol. 32, no. 3, pp. 542–547, 2003.

[35] M. Álvarez, F. Escobar, F. Gast, H. Mendoza, A. Repizzo, and H. Villareal, "Bosque seco tropical," in *Informe Nacional sobre el Estado de la Biodiversidad 1997*, M. E. Chávez and N. Arango, Eds., pp. 56–72, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia, 1998.

[36] R. M. I. Salazar, T. Gómez, G. Vargas, M. Reyes, L. E. Castillo, and W. Bolívar, *Bosques Secos y Muy Secos del Departamento del Valle del Cauca-Colombia*, Corporación Autónoma Regional del Valle del Cauca (CVC), Santiago de Cali, Colombia, 2002.

[37] A. Arcila-Cardona, A. M. Osorio, C. Bermúdez, and P. C. de Ulloa, "Diversidad de hormigas cazadoras asociadas a los elementos del paisaje del bosque seco," in *Sistemática, Biogeografía y Conservación de las Hormigas Cazadoras de Colombia*, E. Jiménez, F. Fernández, T. M. Arias, and F. H. Lozano-Zambrano, Eds., pp. 531–552, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia, 2007.

[38] M. M. Byrne, "Ecology of twig-dwelling ants in a wet lowland tropical forest," *Biotropica*, vol. 26, no. 1, pp. 61–72, 1994.

[39] B. T. Bestelmeyer, D. Agosti, L. E. Alonso et al., "Field techniques for the study of ground-dwelling ants," in *Ants: Standard Methods for Measuring and Monitoring Biodiversity*, D. Agosti, J. Majer, L. Alonso, and T. Schultz, Eds., pp. 122–144, Smithsonian Institution Press, Washington, DC, USA, 2000.

[40] E. E. Palacio and F. Fernández, "Clave para las subfamilias y géneros," in *Introducción a las Hormigas de la Región Neotropical*, F. Fernández, Ed., pp. 233–260, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia, 2003.

[41] B. Bolton, *Identification Guide to the Ant Genera of the World*, Harvard University Press, Cambridge, Mass, USA, 1994.

[42] J. T. Longino, "Ants of Costa Rica," 2009, http://www.evergreen.edu/ants/AntsofCostaRica.html.

[43] N. J. Gotelli and R. K. Colwell, "Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness," *Ecology Letters*, vol. 4, no. 4, pp. 379–391, 2001.

[44] R. K. Colwell, X. M. Chang, and J. Chang, "Interpolating, extrapolating, and comparing incidence-based species accumulation curves," *Ecology*, vol. 85, no. 10, pp. 2717–2727, 2004.

[45] R. K. Colwell, "EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples, v. 8.2," 2009, http://viceroy.eeb.uconn.edu/estimates.

[46] N. J. Gotelli and A. M. Ellison, *A Primer of Ecological Statistics*, Sinauer Associates, Sunderland, Mass, USA, 2004.

[47] B. McCune and J. B. Grace, *Analysis of Ecological Communities*, MjM Software Design, Gleneden Beach, Ore, USA, 2002.

[48] B. McCune and M. J. Mefford, *PC-ORD: Multivariate Analysis of Ecological Data, v. 4*, MjM Software Design, Gleneden Beach, Ore, USA, 1999.

[49] G. M. Zimmerman, H. Goetz, and P. W. Mielke Jr., "Use of an improved statistical method for group comparisons to study effects for prairie fire," *Ecology*, vol. 66, no. 2, pp. 606–611, 1985.

[50] J. T. Longino, "Pheidole Working Group," 2009, http://academic.evergreen.edu/projects/ants/pheidoleworkinggroup/deployedkey/key.htm.

[51] W. M. Cook, K. T. Lane, B. L. Foster, and R. D. Holt, "Island theory, matrix effects and species richness patterns in habitat fragments," *Ecology Letters*, vol. 5, no. 5, pp. 619–623, 2002.

[52] A. Ballinger, P. S. Lake, and R. MacNally, "Do terrestrial invertebrates experience floodplains as landscape mosaics? Immediate and longer-term effects of flooding on ant assemblages in a floodplain forest," *Oecologia*, vol. 152, no. 2, pp. 227–238, 2007.

[53] J. D. Majer and J. H. C. Delabie, "Comparison of the ant communities of annually inundated and terra firme forests at Trombetas in the Brazilian Amazon," *Insectes Sociaux*, vol. 41, no. 4, pp. 343–359, 1994.

[54] A. Dejean and M. Gibernau, "A rainforest ant mosaic: the edge effect (Hymenoptera: Formicidae)," *Sociobiology*, vol. 35, no. 3, pp. 385–402, 2000.

[55] J. H. Ness, "Forest edges and fire ants alter the seed shadow of an ant-dispersed plant," *Oecologia*, vol. 138, no. 3, pp. 448–454, 2004.

[56] J. P. Lessard and C. M. Buddle, "The effects of urbanization on ant assemblages (Hymenoptera: Formicidae) associated with the Molson Nature Reserve, Quebec," *Canadian Entomologist*, vol. 137, no. 2, pp. 215–225, 2005.

[57] L. Tennant, "The ecology of *Wasmanniaauropunctata* in primary tropical rainforest in Costa Rica and Panama," in *Exotic Ants: Biology Impact and Control of Introduced Species*, D. F. Williams, Ed., pp. 80–90, Westview Studies in Insect Biology, Boulder, Colo, USA, 1994.

[58] L. E. Alonso, "Spatial and temporal variation in the ant occupants of a facultative ant-plant," *Biotropica*, vol. 30, no. 2, pp. 201–213, 1998.

[59] C. R. F. Brandão and R. R. Silva, "Synecology of *Wasmanniaauropunctata*, an invasive ant species (Hymenoptera: Formicidae), in continuous and fragmented areas in the Brazilian Atlantic forest," in *Invasive Forest Insects, Introduced Forest Trees and Altered Ecosystems*, T. D. Paine, Ed., pp. 141–151, Springer, Dordrecht, The Netherlands, 2006.

[60] J. K. Wetterer and S. D. Porter, "The little fire ant, *Wasmanniaauropunctata*: distribution, impact, and control," *Sociobiology*, vol. 42, no. 3, pp. 1–41, 2003.

[61] J. Le Breton, H. Jourdan, J. Chazeau, J. Orivel, and A. Dejean, "Niche opportunity and ant invasion: the case of *Wasmanniaauropunctata* in a New Caledonian rain forest," *Journal of Tropical Ecology*, vol. 21, no. 1, pp. 93–98, 2005.

[62] I. Armbrecht and I. Perfecto, "Litter-twig dwelling ant species richness and predation potential within a forest fragment and neighboring coffee plantations of contrasting habitat quality in Mexico," *Agriculture, Ecosystems and Environment*, vol. 97, no. 1–3, pp. 107–115, 2003.

[63] J. D. Majer, J. H. C. Delabie, and N. L. McKenzie, "Ant litter fauna of forest, forest edges and adjacent grassland in the Atlantic rain forest region of Bahia, Brazil," *Insectes Sociaux*, vol. 44, no. 3, pp. 255–266, 1997.

[64] I. Perfecto, I. Armbrecht, S. M. Philpott, L. Soto-Pinto, and T. V. Dietsch, "Shaded coffee and the stability of rainforest margins in Latin America," in *The Stability of Tropical Rainforest Margins: Linking Ecological, Economic and Social Constraints of Land Use and Conservation*, T. Tscharntke, C. Leuschner, M. Zelle, E. Guhadja, and A. Bidin, Eds., pp. 227–263, Springer, Berlin, Germany, 2007.

[65] B. T. Bestelmeyer and J. A. Wiens, "The effects of land use on the structure of ground-foraging ant communities in the Argentine Chaco," *Ecological Applications*, vol. 6, no. 4, pp. 1225–1240, 1996.

[66] M. Ramírez, I. Armbrecht, and M. L. Enríquez, "Importancia del manejo agrícola para la biodiversidad: caso de las hormigas en caña de azúca," *Revista Colombiana de Entomología*, vol. 30, no. 1, pp. 115–123, 2004.

[67] R. Savolainen and K. Vepsalainen, "A competition hierarchy among boreal ants: impact on resource partitioning and community structure," *Oikos*, vol. 51, no. 2, pp. 135–155, 1988.

[68] M. Kaspari, "Litter ant patchiness at the 1-m^2 scale: disturbance dynamics in three neotropical forests," *Oecologia*, vol. 107, no. 2, pp. 265–273, 1996.

[69] I. Armbrecht, I. Perfecto, and J. Vandermeer, "Enigmatic biodiversity correlations: ant diversity responds to diverse resources," *Science*, vol. 304, no. 5668, pp. 284–286, 2004.

[70] D. Nestel and F. Dickschen, "The foraging kinetics of ground ant communities in different mexican coffee agroecosystems," *Oecologia*, vol. 84, no. 1, pp. 58–63, 1990.

[71] L. E. Alonso, "Ants as indicators of diversity," in *Ants: Standard Methods for Measuring and Monitoring Biodiversity*, D. Agosti, J. Majer, L. Alonso, and T. Schultz, Eds., pp. 80–88, Smithsonian Institution Press, Washington, DC, USA, 2000.

[72] A. N. Andersen and J. D. Majer, "Ants show the way down under: invertebrates as bioindicators in land management," *Frontiers in Ecology and the Environment*, vol. 2, no. 6, pp. 291–298, 2004.

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 349896, 8 pages
doi:10.1155/2012/349896

Research Article

Behavioral Differentiation and Ovarian Development of Unmated Gynes, Queens, and Workers of *Ectatomma vizottoi* Almeida 1987 (Formicidae, Ectatomminae)

Alexsandro Santana Vieira,[1] Wedson Desidério Fernandes,[2] and William Fernando Antonialli-Junior[3]

[1] *Programa de Pós-graduação em Entomologia e Conservação da Natureza, Universidade Federal da Grande Dourados. 241, 79804-970 Dourados, MS, Brazil*
[2] *Faculdade de Ciências Biológicas e Ambientais, Universidade Federal da Grande Dourados. 241, 79804-970 Dourados, MS, Brazil*
[3] *Laboratório de Ecologia do Centro de Análise Integrado e Monitoramento Ambiental, Universidade Estadual de Mato Grosso do Sul, 351 79804-907 Dourados, MS, Brazil*

Correspondence should be addressed to Alexsandro Santana Vieira, alexsvieira@yahoo.com.br

Received 30 June 2011; Revised 14 July 2011; Accepted 22 July 2011

Academic Editor: Jacques H. C. Delabie

Behavioral differentiation and ovarian development of unmated gynes, queens, and workers of *Ectatomma vizottoi* were investigated in laboratory conditions. Forty-one behavioral acts were identified and quantified for workers, 19 for queens and 24 for unmated gynes, for an overall species repertoire of 42 different behavioral acts. Ovipositing reproductive eggs was an exclusive task of the queen, whereas workers showed 15 caste-specific behaviors. The most important (frequent) behaviors for the queens were brood care, immobility, and reproduction, and for workers were immobility, grooming/interaction, brood care, and foraging. Unmated gynes (not winged) primarily showed immobility, brood care, grooming/interaction, and foraging. Analysis of ovarian development showed that unmated gynes had little-developed ovarioles, in contrast to queens. Queens and unmated gynes showed a clear behavioral differentiation, in which queens played the role of reproducers and unmated gynes performed activities belonging to the worker repertoire. Despite the presence of several breeding queens in the colony, functional monogyny was the rule.

1. Introduction

The basic characteristic responsible for the reproductive success of the social insects is the division of labor among the individuals of the colony [1, 2]. This is an important topic for understanding the evolution of social behavior [3, 4]. The behavior of different individuals in a colony of ants is controlled by a sophisticated system of transfer of information, which allows the entire colony to work as a single superorganism [1].

As discussed by Bolton [5] the group of poneromorph ants is very diverse, and the individuals show a mixture of basal and derived morphological and social characters. For example, morphologically and behaviorally, *Amblyopone* Erichson shows basal characteristics, while other genus of the Amblyoponinae subfamily show derived characteristics, for example *Prionopelta amabilis* Borgmeier [6–8]. There is wide variation of behavior among the species of the poneromorph group, ranging from generalist predators that make use of a well-developed sting to dominate their prey, such as the Ponerinae *Pachycondyla harpax* Fabricius and Ectatomminae *Ectatomma ruidum* Roger, to others that are more limited in their feeding habits, such as *Proceratium* Roger, Proceratinae subfamily, which feeds on arthropod eggs, or *Leptogenys* Roger, Ponerinae subfamily, which feeds on isopods. Others, such as *Ectatomma tuberculatum* Olivier, add to their diet sweet substances secreted by hemipterans, secretions from the extrafloral nectary, or fallen fruit pulps [9, 10]. The foraging pattern in this group is termed “social facilitation” [1] and is typical of species of small ant colonies such as *E. ruidum*, where the workers forage individually (each forager in its own hunting area) [9, 10].

There are two reproductive systems in ants, monogyny and polygyny. Hölldobler and Wilson [6] defined monogyny as the situation in which several queens are present in the colony, but only one is inseminated and able to produce fertile eggs. Polygyny refers to the occurrence of several queens in the same colony, all able to produce fertile eggs. This characteristic is present in many species of ants, and the number of queens can vary among and within the species [4]. As discussed by Brandão [11] there is a clear division of labor between queen and workers in monogynic colonies, in which the workers are responsible for most of the tasks; some examples are *Ectatomma permagnum* Forel [12] and *Ectatomma planidens* Borgmeier [13] (erroneously identified as *Ectatomma edentatum* Roger [14]). The subfamily Ectatomminae also includes several polygynous species, such as *E. ruidum* [15], *Gnamptogenys striatula* Mayr [16], and *E. tuberculatum* [17]. Also, social organization has been studied in some species of *Ectatomma* Smith, including *E. tuberculatum* [18], *E. permagnum* [12], *Ectatomma brunneum* (=*quadridens*) Smith [19], *E. ruidum* [20, 21], *E. planidens* [13], and *Ectatomma opaciventre* (Roger) [22, 23].

The nest of *Ectatomma vizottoi* has ellipsoid entrance and exit openings that lead to a wide tunnel, similar to a hall, which is connected to other chambers deeper in the nest. The nests are up to 360 cm deep and contain three to ten chambers. This species builds more elaborate nests than other species of Ectatomminae, and its colonies can have up to 10 queens [24]. This study investigated whether colonies of this species can also show behavioral and ovarian development that differentiates it from other members of the genus *Ectatomma*.

2. Methods

Three colonies of *E. vizottoi* were collected according to the methodology described by Antonialli-Junior and Giannotti [26], on the campus of UEMS—Universidade Estadual de Mato Grosso do Sul (22 12 S 54 48 W), in August 2006. Behavioral observations were conducted, and the ovarian development of unmated gynes, queens, and workers was also evaluated. The behavioral observations continued from December 2006 until July 2007. The population composition of the colonies is described in Table 1.

Table 1: Number of adult and immature individuals from three colonies of *Ectatomma vizottoi* collected on the campus of Mato Grosso do Sul State University, in August 2006.

Colonies	Queen	Unmated gyne	Workers	Males	Immature (larvae and pupae)
colony 1	1	1	92	—	7
colony 2	1	2	82	—	55
colony 3	1	4	123	11	222

2.1. Division of Labor. Ethograms of different species of ants have contributed to the quantification and qualification of the ways in which the tasks are divided among individuals [27, 28]. Drogoul et al. [29] introduced the concept of the Structural Ethomodel (EMF), defining a method to model complex organizations such as social insect societies.

The reproductive and sterile castes were marked individually on the thorax with model-airplane paint, similarly to the method used by Nakata [30]. The colonies were kept in laboratory conditions at a temperature of 26 ± 2 C, relative humidity 55–81%, and a natural light cycle, in artificial nests (28 × 18 cm), made of molded plaster with three chambers and tunnels connecting them in the horizontal plane [13]. Each nest was maintained in a glass box (68 × 38 × 30 cm), which functioned as a foraging arena, and the ants were offered larvae of *Tenebrio molitor* L. (Coleoptera: Tenebrionidae) and a 1 : 1 honey-water solution as food, in addition to water.

We carried out 20 hours of qualitative observation, with the help of a hand lens, in sessions of 60 minutes each. We used the method of all occurrences ("*ad libitum*" *sensu* [31]) to define the main categories and behavioral acts of all unmated gynes, queens, and workers in the three colonies.

After this step, we carried out 121 hours of quantitative observation, in 60-minute sessions with intervals of 2 minutes after every 5 minutes, using the scanning sample method [31], totaling 43,270 reports. After the quantification of the behavioral acts, the sample coverage value was calculated, estimated according to Fagen and Goldman [32], calculated by the expression: $\theta = 1 - (N_1/i)$, with "N_1" the number of behavioral acts observed only once and "i" the total number of behavioral acts. The closer θ is to 1.0, the better is the sample coverage. The study can be considered complete when θ ranges between 0.90 and 0.99. The behavioral repertoires of queens, workers, and unmated gynes were compared through Morisita-Horn cluster analysis (multivariate analysis), which is most appropriate for percentage data [33]. The daily 24-hour cycle was divided into three periods (06:00–12:00 h, 12:00–18:00 h, and 18:00–06:00 h) to determine the peak foraging period.

All behavioral acts shown by *E. vizottoi* also occur similarly in other species. These acts have been described in detail for other species, for example *E. planidens* [13] and are therefore not described here.

2.2. Ovarian Development. For the comparative analysis of the ovarian development, 12 workers and 10 queens from the 3 colonies were anesthetized by thermal shock (3 to 5 min. at 4 C) and dissected in a Petri dish in a saline solution for insects, with the aid of a stereomicroscope. The ovaries were removed, and morphological data were obtained, as well as the number of ovarioles in each case, and then schematized.

3. Results

3.1. Ethogram. The sample cover value of the behavioral repertoire was $\theta = 0.98$, showing 42 behavioral acts of which 41 were performed by workers, 19 by queens, and 24 by unmated gynes. The "ovipositing reproductive eggs"

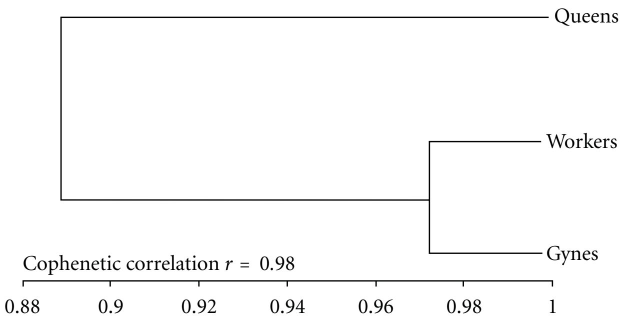


FIGURE 1: Dendrogram of similarity (Morisita-Horn) of the behavioral repertoires among the queens, workers, and unmated gynes of *Ectatomma vizottoi*.

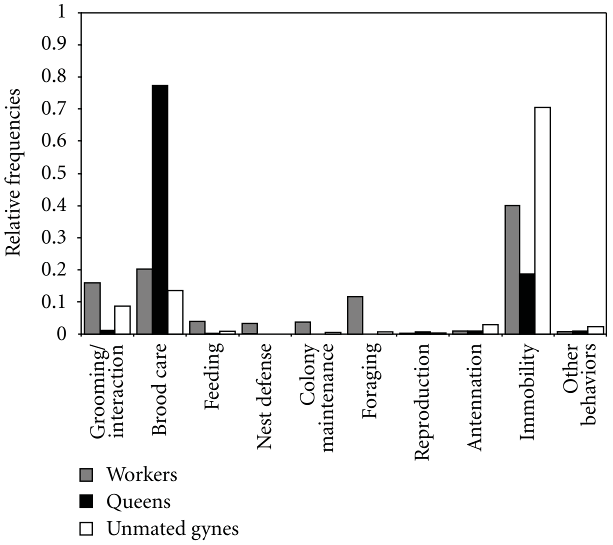


FIGURE 2: Relative frequency with which workers, queens, and gynes performed ten behavioral categories, in colonies of *Ectatomma vizottoi* under laboratory conditions.

was exclusive to only one queen in each colony, while the workers showed 15 exclusive behaviors (Table 2). Cluster analysis revealed that the unmated gynes showed a behavioral repertoire similar to the workers (Figure 1).

The behavioral tasks were grouped to 10 distinct categories. The queens were more effectively involved with the categories “brood care”, “immobility”, and “reproduction” (Table 2, Figures 1 and 2). Unmated gynes performed mainly tasks in the categories “immobility”, “brood care”, “grooming/interaction”, and “foraging” (Table 2, Figures 1 and 2), while the repertoire of the workers was distributed in all the categories, mainly “immobility”, “grooming/interaction”, “brood care”, and “foraging” (Table 2, Figures 1 and 2).

(A) Grooming/Interaction. In this behavioral category, eight behaviors were observed, of which the most significant were: “self-grooming of the 1st, 2nd, and 3rd pairs of legs”, “self-grooming of the gaster extremity”, and “*allogrooming* in workers”, most frequently performed by the workers; while the task “touch workers with antennas” was performed more frequently by unmated gynes (Table 2, Figure 2).

(B) Brood Care. Fourteen behavioral acts were observed in this category, which includes the tasks that are mostly performed by the queens, in comparison to unmated gynes and workers (Figure 2, Table 2), for example, “standing on or beside the pile of eggs”, “standing on or beside the pile of larvae”, and “standing on or beside the pile of pupae”. On the other hand, the tasks “inspecting larvae”, “licking larvae”, and “inspecting pupae” were performed more frequently by the workers (Table 2).

(C) Feeding. Seven behavioral acts were included in this category, most of them were performed more frequently by workers and unmated gynes (Figure 2, Table 2). The tasks of “feeding larva with solid food” (pieces of prey), “feeding on solid food”, and “worker-larva transfer of food” were notable. “Ovipositing trophic eggs” was performed only by workers and unmated gynes, and these eggs were whitish.

(D) Nest Defense. This category includes only the task of “guarding the entrance of the nest”, which was performed by workers and unmated gynes (Figure 1, Table 2).

(E) Colony Maintenance. Four behavioral acts are included in this category, and they were performed only by workers and unmated gynes (Table 2, Figure 1). The queen performed only the task “inspecting the nest” (Table 2).

(F) Foraging. “Foraging” (Table 2, Figure 2) was defined as any activity outside the nest, including the search for any resource or transportation of detritus from the nest to the foraging arena. No forms of recruitment were observed for workers and unmated gynes in this activity. The peak of the “foraging” activity was during the morning, between 06:00 and 12:00. During the other periods the activity was continuous, decreasing gradually.

(G) Reproduction. Only the queens performed the task “ovipositing reproductive eggs” (Table 2, Figure 2).

(H) Antennation. This category involved the acts of antennating and being antennated by workers and queen and unmated gynes from the colony (Table 2, Figure 2).

(I) Immobility. Remaining immobile without performing any other task was the most frequent act among the unmated gynes, followed by workers and queens (Figure 2, Table 2).

(J) Other Behaviors. In this category the acts of “moving inside the nest”, carrying workers and queens were observed, and the last three acts were performed only by the workers (Figure 2, Table 2).

3.2. Ovarian Development. The workers possess 1 or 2 ovarioles per ovary (Figure 3, IA–C). Three degrees of

Table 2: Relative frequency of behavioral acts from the behavioral repertoire of workers, queens, and unmated gynes of *Ectatomma vizottoi*.

Categories and behavioral acts	Workers	Queens	Unmated gynes
(A) Grooming/Interation			
(1) Self-grooming; 1st pair of legs	0.05014	0.00672	0.04898
(2) Self-grooming; 2nd pair of legs	0.01732	0.00134	0.01503
(3) Self-grooming; 3rd pair of legs	0.01727	0.00134	0.01503
(4) Self-c grooming; extremity of the gaster	0.00818	0.00134	0.00436
(5) Self-grooming of mandibles	0.00010	—	—
(6) *Allogrooming* in workers	0.04616	—	0.00436
(7) *Allogrooming* in queens	0.01685	—	—
(8) *Allogrooming* in males	0.00297	—	—
(B) Brood Care			
(9) Standing on or beside the pile of eggs	0.01957	0.31720	0.00048
(10) Inspecting eggs	0.00497	0.01613	—
(11) Carrying eggs	0.00049	0.00403	—
(12) Licking eggs	0.00163	0.00269	0.00048
(13) Standing on or beside the pile of larvae	0.04540	0.38575	0.03055
(14) Inspecting larvae	0.01819	0.00538	0.00194
(15) Carrying larvae	0.00121	—	—
(16) Licking larvae	0.03057	0.00134	0.00194
(17) Helping larvae to pupate	0.00816	—	—
(18) Standing on or beside the pile of pupae	0.04537	0.04032	0.08972
(19) Inspecting pupa	0.01792	0.00269	0.00970
(20) Carrying pupa	0.00304	—	—
(21) Licking pupa	0.00529	—	—
(22) Helping individual to emerge	0.00007	—	—
(C) Feeding			
(23) Feeding larvae with solid food	0.01221	—	0.00048
(24) Worker-larva food of transfer	0.00094	—	0.00048
(25) Feeding with solid	0.02054	—	0.00533
(26) Cannibalism of immature	0.00289	0.00134	0.00097
(27) Feeding of detritus	0.00049	—	—
(28) Ovipositing trophic eggs	0.00079	—	0.00048
(D) Nest Defense			
(29) Guarding the entrance to the nest	0.03349	—	—
(E) Colony Maintenance			
(30) Carrying material in the nest	0.00175	—	—
(31) Carrying detritus	0.00796	—	—
(32) Licking walls of the chambers	0.00042	—	0.00048
(33) Inspecting the nest	0.02568	0.00134	0.00630
(F) Foraging			
(34) Foraging	0.11702	—	0.00533
(G) Reproduction			
(35) Ovipositing reproductive eggs	—	0.00672	—
(H) Antennation			
(36) Touch workers with antennas	0.00786	0.00941	0.02861
(37) Touch queen with antennas	0.00079	—	0.00048

Table 2: Continued.

Categories and behavioral acts		Workers	Queens	Unmated gynes
(I)	**Immobility**			
(38)	Immobility	0.39858	0.18817	0.70514
(J)	**Other Behaviors**			
(39)	Moving inside the nest	0.00472	0.00806	0.02328
(40)	Carrying workers	0.00133	—	—
(41)	Carrying males	0.00010	—	—
(42)	Carrying queens	0.00002	—	—

Table 3: Number of acts from behavioral repertoires in different species of poneromorph ants (W = worker; Q = queen; G = gyne).

Species	Subfamily	Number of behavioral acts	References
Ectatomma brunneum	Ectatomminae	?	Overal [19]
Ectatomma tuberculatum	Ectatomminae	?	Lachaud and Fresneau [18]
Ectatomma permagnun	Ectatomminae	40?	Paiva and Brandão [12]
Ectatomma ruidum	Ectatomminae	?	Corbara et al. [20]
Ectatomma opaciventre	Ectatomminae	27 W; 7 Q	Pie [22]
Ectatomma planidens	Ectatomminae	42 W; 28 Q	Antonialli-Junior et al. [13]
Ectatomma opaciventre	Ectatomminae	47 W; 12 Q	Miguel and Del-Claro [23]
Ectatomma vizottoi	Ectatomminae	42 W; 19 Q; 24 G	This work
Gnamptogenys horni	Ectatomminae	31?	Pratt [25]

ovarian development were found (Figure 3, IA–C): 67% of the analyzed workers had two filamentous ovarioles, without oocytes (Figure 3, IA); 25% had more defined ovaries, with oocytes in the initial stage (Figure 3, IB); 8% had two ovarioles, with more developed oocytes in comparison to the previous case (Figure 3, IC).

The results showed that only one queen of each colony was inseminated (Figure 3, IIA), and therefore the other queens were confirmed as unmated gynes. All queens and unmated gynes possess 7 and 5 ovarioles in the left and right ovaries, respectively, totaling 12 ovarioles (Figure 3, IIA–D). The queens of all colonies had developed ovaries, with mature oocytes, a corpus luteum and spermatheca filled with sperm (Figure 3, IIA).

For unmated gynes, three different degrees of ovarian development were found. In the first type, most of the ovarioles were little developed, each with one large and several smaller oocytes, with the presence of a corpus luteum and empty spermatheca (not sperm) (Figure 3, IIB). In the second type, there are two developed ovarioles, each with one large and another smaller oocyte, with a corpus luteum and empty spermatheca (Figure 3, IIC). In the third type, all 12 ovarioles were filamentous, with a few small oocytes and empty spermatheca (Figure 3, IID).

4. Discussion

The sample coverage value shows that the behavioral repertoire can be considered complete, according to Fagen and Goldman [32]. The number of behavioral tasks was very close to those described for other species of Ectatomminae ants (Table 3).

The tasks related to "grooming/interaction" (Table 2) were also described for *E. planidens* [13], *E. permagnum* [12], and *E. opaciventre* [22, 23]. *Allogrooming* is defined by Hölldobler and Wilson [6] as the act of grooming the body of another individual. One of the functions of grooming the body is to impregnate the cuticle of the nestmate with the odor of the colony, which is related to the content of cuticular hydrocarbons or surface pheromones present in the exoskeleton [6]. Studies performed in *E. vizottoi* have shown that the cuticular hydrocarbons can be involved in the process of recognizing nestmates and distinguishing the castes within the colony [34]. Also, the grooming of the body is a way to inhibit the proliferation of microorganisms; studies such as that by Vieira et al. [35] have revealed that derived ants (*Atta laevigata*) produce antibiotic secretion by metapleural glands.

Queens of *E. vizottoi* remain most of the time standing near the pile of immatures, while unmated gynes and workers spend most of the time performing other tasks. In fact, activities involving "brood care" were significant in the repertoire of the queens (Table 2) as previously described for *E. planidens* [13] and *E. opaciventre* [23]. Still, unmated gynes in *E. vizottoi* performed this activity least often.

According to Hora et al. [36] queens of *E. tuberculatum* spend more time protecting the eggs, because they invest a large amount of energy in their production. However, in other members of Ectatomminae, such as *E. permagnum* [12], only workers were seen protecting the eggs. In colonies of *E. permagnum* [12] and *Gnamptogenys horni* Santschi [25] workers were never seen protecting pupae. In addition, in *E. planidens* [13] and *E. opaciventre* [23] workers were seen cannibalizing immatures.

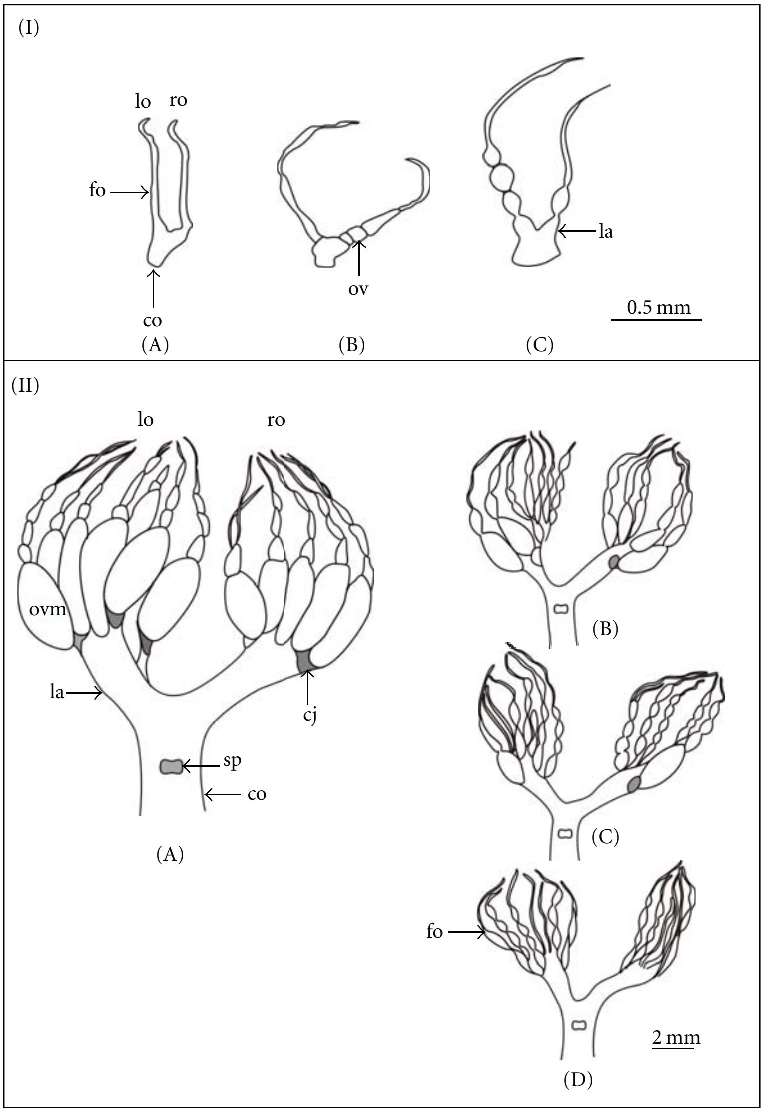


Figure 3: Morphological condition of the different degrees of ovarian development in workers, queens, and unmated gynes of *Ectatomma vizottoi*. (I) three types of ovarian development in workers (A–C), lo: left ovariole, la: lateral ovariole, co: common oviduct, ro: right ovariole, fo: filamentous ovariole, ov: oocyte. (II) A: ovaries of queens. (B–D): three degrees of ovarian development of unmated gynes. Ovm: mature oocyte, cj: corpus luteum, sp: spermatheca.

The task "worker-larva food transfer" was performed by both unmated gynes and workers (Table 2). However, in colonies of *E. opaciventre* [22, 23], *E. tuberculatum* [36] only workers fed the larvae. According to Wilson [1], ants from the subfamilies Myrmicinae, Aneuretinae, Dolichoderinae, and Formicinae exchange regurgitated food, and their intestine is modified to store and distribute food for nestmates, a process called trophallaxis. In poneromorph ants such as *E. tuberculatum* [37] this behavior is defined as pseudo-regurgitation, in which an individual transfers previously collected liquid food to the open jaw of a nestmate. Feeding larvae with solid items without trophallaxis is a "primitive" characteristic [38, 39], as is pseudo-trophallaxis, which is present in the poneromorph group [36].

Both workers and unmated gynes were involved in the activity "foraging", differently from *E. planidens* [13] and *E. opaciventre* [22, 23], in which only the workers performed this task. However, Hora et al. [17] also observed unmated gynes of *E. tuberculatum* foraging.

During the foraging activity by the workers of this species, no recruitment of nestmates was observed, in contrast to *E. brunneum* [19] and *G. horni* [25]. The peak of foraging occurred during the morning. However, in *E. planidens* [13] and *E. tuberculatum* [40] this activity is more intense during the night.

Workers, unmated gynes, and queens of *E. vizottoi* performed the activity "inspecting the nest" (Table 2). In the colonies of *E. planidens* [13] and *E. opaciventre* [22, 23], this activity is performed only by workers.

Although there was more than one individual with reproductive potential present, "ovipositing reproductive eggs" was performed by only one inseminated queen. The appearance of these eggs was similar to those described by Hora et al. [36] for *E. tuberculatum*, in which they change color from white to dark some hours after oviposition. Eggs of *E. planidens* [13] and *E. opaciventre* [22, 23] show a yellowish color. On the other hand, the trophic eggs, such as those of *E. planidens* [13], *E. opaciventre* [22, 23], and *E. tuberculatum* [36] are whitish. In ants, there is an inverse relationship between the existence of either trophallaxis or trophic eggs as a means of food exchange within the society [1]. Trophic eggs are efficient to furnish proteins that are necessary for vitellogenesis for reproductive eggs, and they also enable colony members to store and distribute nutrients and to survive seasonal food shortages [41, 42]. Trophic eggs produced by workers are common in many ants [6]. Although trophallaxis is absent in the poneromorphs, trophic eggs are known in five queens of the poneromorph group [8, 43].

The most frequent activity among the workers, queens, and unmated gynes (Table 2) was "immobility" as described for *E. planidens* [13]. According to Hölldobler and Wilson [6], all poecilotherms spend most of the time doing nothing in particular, except for carrying out physiological functions.

The same number of ovarioles (1-2) in the workers of *E. vizottoi* also occurs in the ovaries of workers of *E. brunneum* [44] and *E. planidens* [13]. The three degrees of ovarian development and the presence of developed oocytes (Figure 3, IA, B, and C) in *E. vizottoi* also occur in workers of *E. brunneum* [44]. However, in workers of *E. planidens* [13] only filamentous ovarioles were found, with no trace of developed oocytes. Probably the workers with a greater degree of ovarian development are those that show trophic oviposition, as observed in workers of *E. brunneum* [44]. The presence of oocytes in the reabsorption stage may indicate previous production of reproductive or trophic eggs by workers [45]. However, workers of *E. vizottoi* possess atrophied spermatheca (Figure 3), similarly to *E. brunneum* [44] and *E. planidens* [13]. Therefore, in *Gnamptogenys menadensis* Mayr [46] virgin workers may lay trophic eggs, and only mated workers produce reproductive eggs.

Queens and unmated gynes of *E. vizottoi* contained 12 ovarioles (Figure 3 IIA, B, C, and D), while queens of *E. planidens* [13] contained 4 and queens of *E. brunneum* [44] 7 to 8 ovarioles. The ovaries of the queens contain mature oocytes and sperm-filled spermatheca, in contrast to unmated gynes which do not contain sperm and also have little-developed ovarioles. This corroborates the behavioral observations, in which it was possible to identify only one queen laying reproductive eggs. Unmated gynes have never been observed laying fertilized eggs and performing activities related to "colony maintenance", and therefore show a repertoire which is more similar to the workers' than to the queen's. However, even if there are several reproductive castes in a colony, a functional monogyny occurs, in which only one queen lays fertilized eggs [17].

The presence of several queens may be the result of adoption, as described for *E. permagnum* [12], *E. ruidum* [15], and *E. tuberculatum*, which, in this case, show facultative polygyny [17]. However, queens and unmated gynes showed a clear behavioral differentiation, in which queens played the role of reproducers and unmated gynes performed activities belonging to the worker repertoire. Analysis of ovarian development showed that unmated gynes had little-developed ovarioles, in contrast to queens. Despite the presence of several breeding queens in the colony, functional monogyny was the rule.

Acknowledgments

The authors thank Dr. Jacques Hubert Charles Delabie from the Myrmecology Laboratory of the Cocoa Research Center (Ceplac-Ilhéus, BA) for the identification of the specimens, and voucher specimens were deposited under no. 2196; Dr. Riviane R. Hora for her help in the ovarian development study; Thiago dos Santos Montagna (PPGECB) for help in the maintenance of the colonies; Janet W. Reid for the linguistic revision. They are grateful to Capes for a grant awarded to the first author, Fundect (Fundação de Apoio à Pesquisa de Mato Grosso do Sul) for financial support (Grant no. 23/200.085/2007) and CNPQ for a productivity grant to W. F. Antonialli-Junior.

References

[1] E. O. Wilson, *The Insect Societies*, Harvard University Press, Cambridge, Mass, USA, 1971.

[2] W. Gronenberg, "Neuroethology of ants," *Naturwissenschaften*, vol. 83, no. 1, pp. 15–27, 1996.

[3] G. Oster and E. O. Wilson, *Caste and Ecology in the Social Insects*, vol. 12, Princeton University Press, Princeton, NJ, USA, 1978.

[4] A. F. G. Bourke and N. R. Franks, *Social Evolution in Ants*, Princeton University Press, Princeton, NJ, USA, 1995.

[5] B. Bolton, *Synopsis and Classification of Formicidae*, Memoirs of the American Entomological Institute, Gainesville, Fla, USA, 2003.

[6] B. Hölldobler and E. O. Wilson, *The Ants*, Spring, Berlin, Germany, 1990.

[7] C. P. Peeters, "Monogyny and polygyny in ponerine ants with and without queens," in *Queen Number and Sociality in Insects*, L. Keller, Ed., pp. 234–261, Oxford University Press, New York, NY, USA, 1993.

[8] C. P. Peeters, "Morphologically "primitive" ants: comparative review of social characters, and the importance of queen-worker dimorphism," in *The Evolution of Social Behavior in Insects and Arachnids*, J. C. Choe and B. J. Crespi, Eds., pp. 372–391, Cambridge University Press, 1997.

[9] K. C. Jaffé, *El Mundo de las Hormigas*, Equinoccio, Baruta, Venezuela, 1993.

[10] F. H. Caetano, K. Jaffé, and F. J. Zara, *Formigas: Biologia e Anatomia*, F. H. C., 2002.

[11] C. R. F. Brandão, "Sequential ethograms along colony development of *Odontomachus affinis* Guérin (Hymenoptera, Formicidae, Ponerinae)," *Insectes Sociaux*, vol. 30, no. 2, pp. 193–203, 1983.

[12] R. V. S. Paiva and C. R. F. Brandão, "Estudos sobre a organização social de *Ectatomma permagnum* Forel, 1908 (Hymenoptera: Formicidae)," *Revista Brasileira de Biologia*, vol. 49, no. 3, pp. 783–792, 1989.

[13] W. F. Antonialli-Junior, V. C. Tofolo, and E. Giannotti, "Population dynamics of *Ectatomma planidens* (Hymenoptera: Formicidae) under laboratory conditions," *Sociobiology*, vol. 50, no. 3, pp. 1005–1013, 2007.

[14] W. F. Antonialli-Junior and E. Giannotti, "Division of labor in *Ectatomma edentatum*," *Sociobiology*, vol. 39, no. 1, pp. 37–63, 2002.

[15] J. P. Lachaud, A. Cadena, B. Schatz, G. Pérez-Lachaud, and G. Ibarra-Núñez, "Queen dimorphism and reproductive capacity in the ponerine ant, *Ectatomma ruidum* Roger," *Oecologia*, vol. 120, no. 4, pp. 515–523, 1999.

[16] R. Blatrix and P. Jaisson, "Reproductive strategy of the ponerinae ant *Gnamptogenys striatula* Mayer (Hymenoptera: Formicidae)," *Sociobiology*, vol. 37, pp. 147–161, 2001.

[17] R. R. Hora, E. Vilela, R. Fénéron, A. Pezon, D. Fresneau, and J. Delabie, "Facultative polygyny in ‚*Ectatomma tuberculatum* (Formicidae, Ectatomminae)," *Insectes Sociaux*, vol. 52, no. 2, pp. 194–200, 2005.

[18] J.-P. Lachaud and D. Fresneau, "Social regulation in ponerine ants," in *From Individual to Collective Behavior in Social Insects*, J. M. Pasteels and J.-P. Deneubourg, Eds., vol. 54 of *Basel Experientia Supplementum*, pp. 197–217, Birkähuser, 1987.

[19] W. L. Overal, "Recrutamento e divisão de trabalho em colônias naturais da formiga *Ectatomma quadridens* (Fabr.) (Hymenoptera: Formicidae: Ponerinae)," *Boletim do Museu do Para. Emilio Goeldi, Zoologia*, vol. 2, no. 2, pp. 113–135, 1986.

[20] B. Corbara, J. P. Lachaud, and D. Fresneau, "Individual variability, social structure and division of labour in the ponerine and *Ectatomma ruidum* Roger (Hymenoptera: Formicidae)," *Ethology*, vol. 82, pp. 89–100, 1989.

[21] S. C. Pratt, "Recruitment and other communication behavior in the ponerine ant *Ectatomma ruidum*," *Ethology*, vol. 81, pp. 313–331, 1989.

[22] M. R. Pie, "Behavioral repertoire, age polyethism and adult transport in *Ectatomma opaciventre* (Formicidae: Ponerinae)," *Journal of Insect Behavior*, vol. 15, no. 1, pp. 25–35, 2002.

[23] T. B. Miguel and K. Del-Claro, "Polietismo etário e repertório comportamental de *Ectatomma opaciventre* Roger, 1861 (Formicidae, Ponerinae)," *Revista Brasileira de Zoociencias*, vol. 7, no. 2, pp. 297–310, 2005.

[24] A. S. Vieira, W. F. Antonialli, and W. D. Fernandes, "Modelo arquitetônico de ninhos da formiga *Ectatomma vizottoi* Almeida (Hymenoptera, Formicidae)," *Revista Brasileira de Entomologia*, vol. 51, no. 4, pp. 313–317, 2007.

[25] S. C. Pratt, "Ecology and behavior of *Gnamptogenys horni* (Formicidae: Ponerinae)," *Insectes Sociaux*, vol. 41, no. 3, pp. 255–262, 1994.

[26] W. F. Antonialli and E. Giannotti, "Nest architecture and population dynamics of the ponerine ant *Ectatomma edentatum* (Hymenoptera, Formicidae)," *Sociobiology*, vol. 38, no. 3, pp. 475–486, 2001.

[27] E. O. Wilson, "Leptothorax duloticus and the beginnings of slavery in ants," *Evolution*, vol. 29, pp. 108–119, 1975.

[28] C. R. F. Brandão, "Division for labor within the worker caste of *Formica perpilosa* Wheeler (Hymenoptera: Formicidae)," *Psyche*, vol. 85, no. 2-3, pp. 229–237, 1978.

[29] A. Drogoul, B. Corbara, and D. Fresneau, "Applying ethomodelling to social organization in ants," in *Biology and Evolution of Social Insects*, pp. 375–383, Leuven University Press, Leuven, Belgium, 1992.

[30] K. Nakata, "The difference in behavioral flexibility among task behaviors in a ponerine ant, *Diacamma* sp," *Sociobiology*, vol. 27, no. 2, pp. 119–128, 1996.

[31] J. Altmann, "Observational study of behavior: sampling methods," *Behaviour*, vol. 49, no. 3-4, pp. 227–267, 1974.

[32] R. M. Fagen and R. N. Goldman, "Behavioural catalogue analysis methods," *Animal Behaviour*, vol. 25, no. 2, pp. 261–274, 1977.

[33] H. Wolda, "Similarity indices, sample size and diversity," *Oecologia*, vol. 50, no. 3, pp. 296–302, 1981.

[34] W. F. Antonialli, S. M. Lima, L. H. C. Andrade, and Y. R. Súarez, "Comparative study of the cuticular hydrocarbon in queens, workers and males of *Ectatomma vizottoi* (Hymenoptera, Formicidae) by Fourier transform-infrared photoacoustic spectroscopy," *Genetics and Molecular Research*, vol. 6, no. 3, pp. 492–499, 2007.

[35] A. S. Vieira, O. C. Bueno, and M. I. Camargo-Mathias, "The functional morphology of the metapleural gland of the leaf-cutting ant *Atta laevigata* (Formicidae: Attini)," *Micron*, vol. 41, no. 2, pp. 149–157, 2010.

[36] R. R. Hora, C. Poteaux, C. Doums, D. Fresneau, and R. Fénéron, "Egg cannibalism in a facultative polygynous ant: conflict for reproduction or strategy to survive?" *Ethology*, vol. 113, no. 9, pp. 909–916, 2007.

[37] F. J. Richard, A. Dejean, and J. P. Lachaud, "Sugary food robbing in ants: a case of temporal cleptobiosis," *Comptes Rendus—Biologies*, vol. 327, no. 5, pp. 509–517, 2004.

[38] B. Hölldobler and E. O. Wilson, "Ecology and Behavior of the primitive cryptobiotic ant *Prionopelta amabilis* (Hymenoptera: Formicidae)," *Insectes Sociaux*, vol. 33, no. 1, pp. 45–58, 1986.

[39] J. F. A. Traniello and A. K. Jayasuriya, "The biology of the primitive ant *Aneuretus simoni* (Emery) (Formicidae: Aneuretinae) II. The social ethogram and division of labor," *Insectes Sociaux*, vol. 32, no. 4, pp. 375–388, 1985.

[40] N. A. Weber, "Two commom ponerine ants of possible economic significance, *Ectatomma tuberculatum* (Oliver) and *E. ruidum* Roger," *Proceedings of the Entomological Society of Washington*, vol. 48, no. 1, pp. 1–16, 1946.

[41] S. H. Voss, J. F. Mcdonald, and C. H. Keith, "Production and abortive development of fire ant trophic eggs," in *Advances in Myrmecology*, J. C. Trager, Ed., pp. 517–534, 1998.

[42] B. J. Crespi, "Cannibalism and trophic eggs in subsocial and eusocial insects," in *Cannibalism: Ecology and Evolution among Diverse Taxa*, M. A. Elgar and B. J. Crespi, Eds., pp. 176–213, Oxford University Press, Oxfordm, UK, 1992.

[43] B. Gobin, C. Peeters, and J. Billen, "Production of trophic eggs by virgin workers in the ponerine ant *Gnamptogenys menadensis*," *Physiological Entomology*, vol. 23, no. 4, pp. 329–336, 1998.

[44] L. V. Toledo-Mello and F. H. Caetano, "Padrões morfológicos do ovário de formigas *Ectatomma quadridens* (Hymenoptera: Ponerinae) e suas implicações funcionais," Rio Claro, 16p, (Trabalho de formatura—UNESP, Rio Claro, SP), 1980.

[45] M. W. J. Crossland, R. H. Crozier, and E. Jefferson, "Aspects of the biology of the primitive ant genus *Myrmecia F.* (Hymenoptera: Formicidae)," *Journal of the Australian Entomological Society*, vol. 27, no. 4, pp. 305–309, 1988.

[46] B. Gobin, C. Peeters, and J. Billen, "Colony reproduction and arboreal life in the ponerine ant *Gnamptogenys menadensis* (Hymenoptera: Formicidae)," *Netherlands Journal of Zoology*, vol. 48, no. 1, pp. 53–63, 1998.

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 951029, 8 pages
doi:10.1155/2012/951029

Research Article

Removal of Nonmyrmecochorous Seeds by Ants: Role of Ants in Cattle Grasslands

Selene Escobar-Ramírez, Sebastián Duque, Natalia Henao,
Alejandra Hurtado-Giraldo, and Inge Armbrecht

Department of Biology, University of Valle, A.A., 25360 Cali, Colombia

Correspondence should be addressed to Selene Escobar-Ramírez, escobar.selene@gmail.com

Received 2 June 2011; Accepted 27 July 2011

Academic Editor: Jacques H. C. Delabie

Livestock production models prevailing in Colombian Andes are simplified treeless pastures for extensive ranching, with the consequent reduction of environmental services, such as seed dispersal, due to lack of primary dispersers, scarcity of adequate sites for seedling establishment and competition with grasses. This study evaluated if, in these harsh environments, ants can promote the colonization of arboreal species through directed dispersion of seeds towards the nests. Ten seeds of each species were offered to ants in six grazing pastures. Ants removed 25% of the seeds (1827) in 48 hours. Preference for arillated and small-to-medium sized seeds, such as *Pithecellobium dulce*, and *Guazuma ulmifolia*, was observed. *Cyphomyrmex major, Ectatomma ruidum, Solenopsis geminata* and *Atta cephalotes* were the key ant species in seed removal. It was concluded that functional ant groups present in the pastures could contribute to secondary dispersion of seeds with potential for restoration.

1. Introduction

In Latin America, cattle raising is perhaps the productive activity that most contributes to simplification of the landscape. For instance, in Colombia, cattle raising is predominant in more than 80% of the Andean Region, an area inhabited by 70% of the population [1]. The concept of functional diversity relates ecosystemic processes to species diversity through patterns of resource use [2, 3]. Thus, reduction in plant heterogeneity caused by traditional production systems of cattle raising leads to a reduction of both ecosystemic processes and the environmental services they provide [1].

Vegetal regeneration is limited in cattle pastures due to the absence of dispersers, little availability of viable propagules and of adequate sites for germination, and establishment of seedlings [4, 5]. Also, competition for the few nutrients with introduced grasses under rude environmental conditions reduces establishment options for arboreal species.

Ants could play a role in the recovery of disturbed systems potentiating recolonization of plant species in agro ecosystems by removing seeds towards their nests [6, 7]. This interaction could affect the local abundance and distribution of myrmecochorus and nonmyrmecochorous species [8–10]. In spite of the growing information on the interaction between ants and seeds in neotropical forests [11–14], few studies document the process in neotropical agroecosystems (but see [15–17]). Thus, the role of ants as dispersers of nonmyrmecochorus seeds in pastures is unknown.

The use of diaspores by opportunistic ground dwelling ants can affect the biology of seeds and seedlings of plant species dispersed mainly by vertebrates [18]. The ants can rearrange the rain of seeds produced by primary disperser, facilitate their germination [19, 20], and promote the establishment of their seedlings [21, 22]. The seeds introduced into the nests are not found by predators and remain protected from adverse environmental events, such as burning in ecosystems that experience regular fires [8]. Although nonmyrmecochorous plants produce seeds without specialized adaptations for dispersal by ants, the presence of arils or nutritious tissues is not indispensable for transport to occur [16, 23].

Events of seed removal by ants are influenced by both morphological factors of the seeds and morphological and behavioral traits of the ants. The presence of a nutritious tissue or aril attracts the attention of ants thereby increasing probability of an encounter [24]. Once the ant locates the seed, removal will depend on its weight and the carrying capacity of the ant [25, 26]. In general, large ants possess a greater carrying capacity in their jaws and can remove seeds greater distances [27, 28]. Nevertheless, small ants usually massively recruit workers towards the seeds and then displace them towards the nests [17, 29].

Characterization of ant-seed interaction under pasture conditions is a first step towards understanding the potential of ants as functional agents in the ecological recovery of cattle pasture by the dispersal of seeds of plants useful for ecological restoration and seeds of interest to peasant farmers (i.e., forage). This study predicted that ants associated with grasslands act as functional agents by removing nonmyrmecochorous seeds from trees that are useful for ecological rehabilitation. Specifically, the following questions were addressed. Do ants in open pastures actively remove seeds of nonmyrmecochorous plant species with a potential for the ecological recovery of pastures? Do these ants exhibit a preference for a certain kind of seed? Which ant species are most frequently involved in removal events? In addition, the implications of the observed interactions were discussed.

2. Materials and Methods

2.1. Study Site. Fieldwork was carried out between September and October 2009 in six cattle pastures located in the flat inter-Andean Cauca River Valley area in the Departments of Valle and Cauca (Southwestern Colombia) covering an area of approximately 627 km^2. The farms and geographic locations are as follows: I. Department of Cauca, (1) Limonar (03 08 10.1 N; 76 27 42.2 W), (2) La Josefina (3 5 17.3 N; 76 28 18.5 W), (3) Cachimbalito 3 9 1.00 N; 76 27 46.00 W); II. Department of Valle del Cauca, (4) Sachamate (3 16 27.49 N; 76 33 28.00 W), (5) Lituania (3 20 48.5 N; 76 30 30.6 W), (6) Marañón (3 20 48.30 N; 76 31 23.91 W). Over a century ago, dry tropical forest dominated the region [30], but at present only 2.7% of the original forest remains, the remainder having been replaced with great expanses of sugarcane fields and cattle farms [31]. Average annual temperature is 24 C, and average annual precipitation fluctuates between 1000–15000 mm [30] with peaks in March-May and October-December [32]. During the sampling, the pastures averaged temperatures of 29.4 ± 3.7 C and an average relative humidity of 63.4 ± 11%. Each pasture was open, with an average extension of at least two hectares and an arboreal density inferior to 4%. Dominant vegetation consisted of *Cynodon plectostachyus*, an introduced grass, as well as other African grasses like *Brachiaria decumbens*, accompanied by weeds from Malvaceae and Asteraceae families. Inside the pasture, some isolated trees of *Guazuma ulmifolia*, *Pithecellobium dulce,* and *Albizia saman* are allowed by the farmers to provide shade to the cattle and supplement its feed. During the experiments, the cattle were removed from the lot.

Orthodox seeds from five arboreal species commonly found in pastures were used: (1) *Guazuma ulmifolia* Lam. (Sterculiaceae), seeds with hydrophilic mucilage; (2) *Pithecellobium dulce* (Roxb.) Benth. (Leguminosae-Mimosoideae), arillated seeds; (3) *Senna spectabilis* (DC.) H. S. Irwin & Barneby (Leguminosae-Caesalpinioideae), nonarillated seeds; (4) *Leucaena leucocephala* (Lam.) de Wit. (Leguminosae-Mimosoideae), seeds without arils, and (5) *Albizia saman* (Jacq.) Merr. (Leguminosae-Mimosoideae) which seeds are usually impregnated with a sweet, oily substance (seeds of *A. saman* used here lack of this substances as they become from a certified seed company provider). Seeds used have a potential for the restoration of livestock systems and with exception of *L. leucocephala* represent part of the native vegetation of open areas. These trees also serve as forage for cattle as they consume the foliage and/or fruit, provide shade for the cattle, protect the ground from erosion, and offer new habitats for other animals. Seeds of *Passiflora ligularis* Juss. (Passifloraceae) was employed as a positive control. Its seeds are intermediate in size, and they are neither orthodox nor recalcitrant [33]. Their removal by ants was verified in previous studies in disturbed habitats such as pastures [16, 34] and mining areas undergoing rehabilitation [17].

In order to sample the ant community, a lineal transect of 190 m with 10 sampling units (SUs), separated 20 m from one another, was established. Each SU consisted of a circle of white paper 12 cm in diameter with 5 g of tuna in oil and approximately 0.5 mL of honey. These were left on the ground for a period of 2 hours. The ants attracted to baits were collected in alcohol (96%), identified to morphospecies, and conserved in a reference collection deposited in the Entomology Museum of the Universidad del Valle (Cali, Colombia). The functional guilds (*sensu* Silvestre et al. [35]) to which the collected ants belonged were identified. Hill N1 and N2 Number Series were calculated [36] for establishing the number of abundant and very abundant species, respectively.

Three transects were simultaneously established in each pasture: a transect that allows ants access to the seeds ("Ant Transect"), a transect that excluded the ants ("Exclusion transect"), and a transect with seeds of *P. ligularis* to which the ants had access (*P. ligularis* Transect). Each transect consisted of 20 seed depots located 10 meters apart. A depot consisted of a disk of white paper 12 cm in diameter containing 10 seeds of each of the five species used in the study and covered by netting to exclude vertebrate activity. In the excluded transect, each depot was isolated by encircling it within a PVC arum, 12 cm in diameter and 6 cm high, the upper edge impregnated with an adhesive substance (tangle foot). In order to guarantee independence, transects were 5 to 10 m apart. Seeds were served at 0700 hours, and the number of seeds of each species removed at 2, 4, 8, 24, and 48 hours after serving the depots was registered. A seed removed out of the depot was considered a removal event. The species of ants observed removing seeds were identified. A total of 2400 seeds of each species in the study and 1200 *P. ligularis* seeds were offered, for a total of 13200 seeds offered during the entire experiment. The response variable was the proportion of seeds removed per depot (P_i). For purposes of analysis, the response variable was transformed by the function *arcsine* P_i. To evaluate ant preference for seeds, a two-factor analysis of variance under a mixed effect model [37] of the following type was carried out:

$$P_{ij}(\text{Removal proportion}) = \mu + \alpha_i(\text{plant species}) + \beta_j(\text{cattle pasture}) + E_{ij}(\text{error}), \quad (1)$$

where types of seeds represent fixed effects and the pastures the random effects. To establish whether the removal events were associated with removal by ants and not other factors, the proportion of seeds removed in Ant Transect and Exclusion Transect were compared. Removal dynamics over time was described for all species. For the two most preferred species, 0, 25, 50, 75, and 100% percentiles were calculated to estimate removal percentages at 2, 4, 8, 24, and 48 hours after offer, respectively.

3. Results

A total of 21 morphospecies distributed in 13 genera and 5 subfamilies for a total of 3471 individuals were collected (Table 1). The most representative genera were *Pheidole* (6 morphospecies and 176 individuals) and *Solenopsis* (four morphospecies and 1315 individuals) (both Myrmicinae). *Crematogaster abstinens* (Myrmicinae), present in six pastures, was the most abundant species with 1774 individuals. The number of ant species found in baits in each pasture fluctuated between 6 and 11. Diversity (H' index between 0.52 and 1.75) and equitability (J' index between 0.29 and 0.51) were also consistently low in all the lots, there being from two to three very abundant species in each pasture (averages values of N1 and N2 estimated as 3 and 2 species, respectively).

The composition of ants attracted to tuna baits was characterized by a predominance of generalist species native to open and degraded habitats. In spite of low richness and equitability, the genera collected represent 8 of the 15 functional guilds described by Silvestre et al. [35] for the Cerrado, Brazil.

Based on ant species composition, the lots do not form agglomerations corresponding to their spatial proximity. In spite of the spacial scale, important variations in ant composition were found (Table 1). But, on a functional level, the pastures contained the same functional guilds.

Ants removed 25% of the seeds, for a total of 1827 seeds removed in 48 hours period. In general, ant preference for seeds with attractive external tissues was found ($F = 17.6$; $P < 0.01$; $gl = 5$). Of the five species of interest to the cattleman, the most preferred was *G. ulmifolia* with 56% removal, followed by *P. dulce* with 25% removal while removal did not surpass 10% for the other species (Table 2).

The presence of ants notably favored the removal of *G ulmifolia* and *P. dulce.* In the absence of ants (Exclusion Transect), the removal of these species was drastically reduced. Actually, in the case of *P. dulce*, removal was null when the ants were excluded. On the other hand, access of ants to the depots (Ant Transect) did not significantly favor the removal of *S. spectabilis* ($F_{1.5} = 4.35$; $P = 0.09$), *L. leucocephala* ($F_{1.5} = 5.17$; $P = 0.07$), and *A. saman* ($F_{1.5} = 4.37$; $P = 0.09$) (Figure 1). The seeds preferred by the ants were separated into three main groups in the following order of preference: Group A with small *G. ulmifolia* seeds with mucilage, which were preferred as much as the arillated *P. ligularis* seeds in the positive control (*P. ligularis* Transect) ($t = 0.28$; $P = 0.78$). Group B consisted of arillated but heavier *P. dulce* seeds. Group C was made up of smooth covered, nonarillated *S. spectabilis, L. leucocephala,* and *A. saman* seeds (Figure 1).

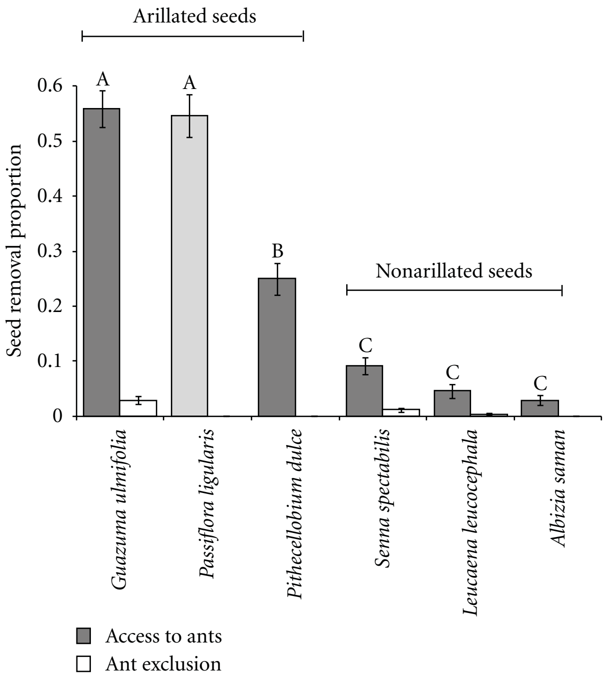


Figure 1: Mean (± SE) removal of nonmyrmecochorous seeds by ants in cattle grasslands. Letters above columns show different seed preference groups by ants after a Newman-Kewls test ($\alpha = 0{,}05$).

In general, a greater seed removal rate was observed from 8 to 24 hours after initiating the offer (Figure 2), a pattern maintained in each of the cattle pastures sampled. The removal dynamic overtime of the two most preferred seeds suggests an increase in transporting *G. ulmifolia* and *P. dulce* seeds during the night (Table 3).

Very low percentages of removed seeds of *G. ulmifolia* and *P. dulce* seeds were re-located: only 2% and 24%, respectively. The majority of the *G. ulmifolia* and *P. dulce* seeds were removed an average of 20 cm from the depot, and an important part of the seeds were removed a distance of at least 10 cm. However, the final distance of these seeds could not be established. A *Cyphomyrmex major* worker transported a *G. ulmifolia* seed 1.20 m before entering the nest in the ground while an *Ectatomma ruidum* worker transported a *P. ligularis* seed 4.6 m from the depot.

The ant species that most frequently, and in greatest number, approached the tuna baits were, also, those most frequently involved in seed removal events. The ants observed transporting seeds in grasslands belong to three functional groups: (1) a dominant group of small-sized myrmicines

Table 1: Composition and total abundance of ant species attracted to tuna and honey baits in each locality. (Sa: Sachamate, LJ: La Josefina, Ca: Cachimbalito, Lit: Lituania, Ma: Marañón, Li: Limonar).

Morphospecies	Sa	LJ	Ca	Lit	Ma	Lim	Total abund.
Myrmicinae							
Atta cephalotes						1	1
Cardiocondyla gr. *minutior*	7						7
Crematogaster abstinens	73	644	75	56	822	104	1774
Cyphomyrmex major		4	5			3	12
Pheidole ebenina		22					22
Pheidole susannae		26	85	7	8	4	130
Pheidole sp1	1		1				2
Pheidole sp2				5			5
Pheidole sp3			3			2	5
Pheidole sp5						12	12
Solenopsis geminata	213	206	298	72	160	321	1270
Solenopsis sp1	4			35		1	40
Solenopsis sp2	4						4
Solenopsis sp3	1						1
Wasmannia auropunctata	27	43		10		41	121
Formicinae							
Brachymyrmex sp1	6						6
Camponotus sp1				4			4
Nylanderia sp1				8	3		11
Ectatomminae							
Ectatomma ruidum		11	6	11	1	9	38
Ponerinae							
Hypoponera sp1		1					1
Pseudomyrmecinae							
Pseudomyrmex sp1			2	1	1	1	5

Table 2: Mean seed removal of nonmyrmecochorous seeds by ants in cattle grasslands. Standard errors are shown for seed weights.

Type of seed	Species	Seed weight (g)	*Ant access*		*Ant exclusion*	
			Seeds removed	Removal percentage	Seeds removed	Removal percentage
Arillated	*G. ulmifolia*	0.005 ± 0.00	672	56.0%	35	2.9
	P. dulce	0.307 ± 0.10	300	25.0%	0	0.0
	P. ligularis	0.16 ± 0.02	656	54.7%	N/A	N/A
Nonarillated	*S. spectabilis*	0.026 ± 0.00	109	9.1%	14	1.2
	L. leucocephala	0.062 ± 0.01	55	4.6%	4	0.3
	A. saman	0.233 ± 0.03	35	2.9%	0	0.0
	Total		1827	25.4%	53	4.4%

N/A: Not Applicable. Ant exclosures were not performed in *P. ligularis* transect.

Table 3: Percentiles for the total removal percentage of *Pithecellobium dulce* and *Guazuma ulmifolia* nonmyrmecochorous seeds in six cattle pastures in Cauca and Valle.

Percentile	Observation period	Hour of the day	Percentage of seeds removed	
			P. dulce	*G. ulmifolia*
0%	2 hours	0800 hours	2.17	1.08
25%	4 hours	1200 hours	2.92	1.33
50%	8 hours	1600 hours	16.6	1.92
75%	24 hours	0800 hours	44.8	15.7
100%	48 hours	0800 hours	56.3	25.0

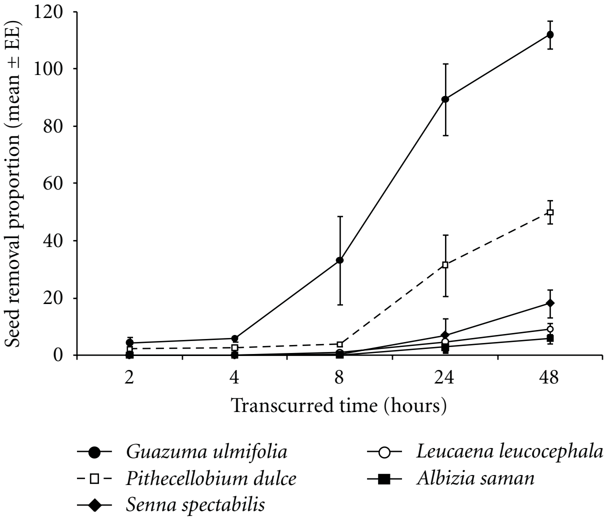


Figure 2: Removal of seeds by ants overtime. Average number of seeds removed from depots 2, 4, 8, 24, and 48 hours, after initiating offer, are showed ($n = 6$).

with generalist habits (*Pheidole* spp., *Solenopsis geminata,* and *C. abstinens*); (2) two species of attine, a leaf-cutter (*Atta cephalotes*), and a cryptic fungus grower (*Cyphomyrmex major*) which were the main seed transporters of *P. dulce* and *G. ulmifolia*, respectively; (3) a large epigeal ponerinae (*E. ruidum*), very common and abundant in disturbed lowland habitats (0 to 1500 m.a.s.l.) (Table 4).

Removal activity seems to be occurring throughout the day, with great activity of generalist species during the morning hours such as *E. ruidum* and other small myrmicine, and great activity of attines after 17:00 hours, the activity of *C. major* and *A. cephalotes* increased.

4. Discussion

The ant community associated to cattle pastures in the study area is not very diverse and has a great predominance of only a few species and a relatively predictable composition. The simplification of plant structure in pastures and the surrounding matrix could explain the limited ant diversity [38]. The pattern of diversity found is that expected for the highly fragmented landscape of the biogeographical valley of the Cauca River where pastures and sugar cane fields dominate, and there is only 2% forest cover immersed in a low-quality matrix [39, 40]. The results of this study are consistent with Armbrecht and Ulloa-Chacón [41] who, one decade earlier, found that ant diversity reduced drastically in the pasturelands with respect to forest fragments. In the same area of this study, they found only 21 species in the productive systems, using six capture methods. In spite of limited diversity, generalist ants in pastures rapidly located and displaced the seeds offered in the depots. Twenty-four percent of the seeds were removed for a total of 1827 removal events during a 48-hour period in treeless pastures with cattle activity and compact, ecologically degraded soil. These removal values are similar to those found by Escobar et al. [16] who reported a 26% total removal in open grasslands and silvopastoral systems in Valle del Cauca and Quindío, while Zelikova and Breed [15] reported 38.3.% removal in open pastureland in Costa Rica. Although total seed removal did not exceed 40%, each removal event as such is of biological importance because it potentiates a possibly effective dispersion event. This is particularly critical in highly disturbed habitats rarely visited by primary dispersers.

Results in the Excluded Transect and direct observation indicate that ants are important seed dispersers of trees useful in ecological recovery of degraded ecosystems. Ants have morphological adaptations which allow them to carrying seeds. Also, their social behavior promotes seed transport from the foraging point to their nests, where conditions may be more favorable for the germination and growth of seedlings. Tendency towards territoriality and the stability of their colonies in the tropics makes removal by ants a permanent ecological service throughout the year. These aspects allow to consider ants as key functional agents, facilitating the distribution of seeds of interest in pasturelands.

Ant preference for seeds with an attractive, nutritious tissue in *G. ulmifolia, P. dulce,* and *P. ligularis* was found. This result coincides with the pattern identified for myrmecochorus and nonmyrmecochorous seeds in multiple habitats worldwide [14, 18]. The *G. ulmifolia* species was preferred as much, or more than the *P. ligularis* (positive control) seeds. However, while in the present study, the ants removed 56% of the *G. ulmifolia* seeds, this species was the less preferred in mining areas undergoing rehabilitation [17] in a subxerophytic area where the ants removed only 5% of its seeds. Instead, in the same experiment, ants preferred larger arillated seeds such as *Capparis* sp. (5 mm in diameter) and *Seguieira* sp. (4 mm in diameter). In this experiment, the second most preferred seeds (*P. dulce*) are 60 times heavier than *G. ulmifolia* seeds, the lightest in this study. This suggests that the context is an important factor in modeling the way ant-seed interactions occur: the presence of other arillated species that compete for the "transporting energy" of foraging ants as well as the presence of key ant species.

Removal occurred with a great degree of activity of key species such as *E. ruidum, S. geminata, C. abstinens,* and *Pheidole* spp. during the day while, after 17:00, removal was continued by *C. major* and *A. cephalotes*. The genera observed transporting seeds in the pasturelands (Table 5) coincide with the functional ant guilds exploiting diaspores in flat, sandy forests, and humid tropical forests in the Brazilian lowlands [14, 42]. In these habitats, small myrmicines as well as attine actively interacted with diaspores. Dominguez-Haydar & Armbrecht [17] identified species of these same functional groups removing seeds. *E. ruidum, S. geminate,* and *Acromyrmex octospinosus* were the species that removed the greatest number of seeds from mining lands in early rehabilitation, suggesting that they are key species in the recovery of the ecological function of disturbed areas.

Morphological seed traits, like weight and presence of arils, and foraging strategies in the different ant functional groups are ecologically relevant because they determine how the transport process occur [28]. For example, the foraging of the small-sized myrmicines with generalist habits

Table 4: Description of ant species carrying seeds. Body length of workers and its incidence in baits and seed depots (SDs) were recorded, as the seed species they removed. The body length of workers was measured from the posterior margin of clypeus to the posterior end of the last petiole.

Ant species	Workers body length (mm)	Presence		Seed species removed		
		In baits %	In SD %	*P. dulce*	*G. ulmifolia*	*P. ligularis*
Atta cephalotes	12.36 ± 10.9	1.7	1.7	X		
Ectatomma ruidum	5.52 ± 0.12	36.7	35.0		X	X
Solenopsis geminata	2.12 ± 0.01	41.7	16.7		X	
Cyphomyrmex major	1.85 ± 0.11	6.7	36.7		X	
Pheidole susannae	1.67 ± 0.01	20.0	10.0		X	X
Crematogaster abstinens	1.58 ± 0.21	41.7	40.8	X		X

Table 5: Ant genus classification of ants attracted to baits into the functional groups established by Silvestre et al. [35].

Item	Functional guild (*sensu* Silvestre et al. [35])	Genus attracted to baits
(1)	Omnivorous soil dominants	*Crematogaster, Pheidole, Solenopsis*
(2)	Large epigean predators	*Ectatomma*
(3)	Cryptic fungus growers attines	*Cyphomyrmex*
(4)	Leaf-cutter attines	*Atta*
(5)	Agile pseudomyrmecinae	*Pseudomyrmex*
(6)	Soil and vegetation opportunistics	*Nylanderia*
(7)	Small arboreal ants with massive recruitment	*Wasmannia*
(8)	Cryptic ponerinae, specialized predators	*Hypoponera*

is characterized by mass recruiting of workers towards the food resource [35]. The carrying capacity of these ants is limited by their small size, and those seeds that surpass their carrying capacity are foraged on the ground without being displaced [43]. This was observed in the field with species of the *Pheidole*, *Solenopsis*, and *Wasmannia* genera (body length less than 3 mm) that foraged the aril of *P. ligularis* and *P. dulce* seeds without removing them. Nevertheless, small myrmicines also team up to transport heavy seeds. In this study, dozens of *C. abstinens* workers succeeded in moving heavy *P. dulce* seeds from the depots, suggesting that this species is an important functional agent for seed dispersal too.

This study also emphasizes on species of generalist ants considered pests such as *S. geminata, E. ruidum,* and attines. The tropical fire ant (*S. geminata*) could be playing a dual role as both predator and seed disperser because, although it is a regular grain collector and eater [44, 45], some seeds could survive and germinate in garbage dumps or soils near the nests [29]. On the other hand, *E. ruidum* has already been identified in Colombia as one of the main seed transporter species in pastures and mining areas under rehabilitation [16, 17, 34]. In Costa Rican agroecosystems, *E. ruidum*, together with *Pheidole fallax*, were responsible for 92% of all observed removal events, *E. ruidum* being the species that removed most seeds in pastures [15]. The greater size of this ant allows a single worker to carry seeds of different sizes thus increasing the range of seeds that can be dispersed by this species.

Finally, attines such as *C. major* and *A. cephalotes* were key transporters of arillated *G. ulmifolia* and *P. dulce* seeds, respectively. They also acted during evening and nocturnal hours (obs. pers.) thus relaxing competition with other generalist species. These results coincide with the pattern of seed attention described by Rico-Gray & Oliveira [18] and Bas et al. [46] where attines are usually attracted by nonmyrmecochorous diaspores with large arils and low lipid content (<8%). According to the authors, if these diasporas are also light in weight (<0.1 g), they can be transported greater distances (to 10 m), something that could be significant for the lighter *G. ulmifolia* seeds. The hypothesis of directed dispersion [47–49] can be reinforced when seed removal involves species of attines because the seeds are directed towards the nest where appropriate conditions for germination can be provided. Under conditions of dehydration, aridness, and high temperatures, *A. cephalotes* can concentrate foraging activity at night, and its workers can obtain foraging distances of up to 235 m. Genera of cryptic attine, such as *Cyphomyrmex,* usually collect seeds during the dry months, and it is when greater foraging distances are reached by its workers [50].

Despite the low removal distances reported for some functional groups, ants can act as complementary dispersing agents [51] bringing up to their nests seeds that have been dispersed long distances (meters, even kilometers) by primary seed dispersers such as cattle, birds, bats, and rodents [52].

In summary, this study presents evidence supporting the idea of ants as functional agents for the ecological recovery of degraded pastures. The preference pattern of the ants for small-sized seeds with attractive structures was confirmed. In spite of the limited diversity of persistent ants in the pastures, key species were identified that could provide dispersion service for nonmyrmecochorous species in pastures where barriers to the advance of plant succession exist. The interaction of the different foraging strategies of the participating ants can contribute to the dispersion of seeds through different mechanisms; leaf cutters offer the greatest carrying capacity (quantity and size), and the great majority of seeds will be taken to nests thereby contributing to the reduction of s competence and depredation by aggregation. Large hunters such as *E. ruidum* removed seed greater distances and feed on the aril instead of the seed. Ant-seed interaction was facultative and generalist instead of an obligatory mutualism specific to one species in particular. Far from being an inconvenience, this generalism opens the way to the use of grassland ants as dispersers of plant species ecologically important. This would also be of interest to producers if seed hauling of economically valuable seeds by ants could be induced, for example, through the simulation of artificial arils in those seeds (Henao-Gallego et al. [53]). Ant-seed interaction in grasslands can be taken into account for ecological rehabilitation plans by directing this functional diversity. For the rehabilitation of degraded habitats, these facts could mean that, with an abundant although not very diverse ant biota, rehabilitation actions can be initiated, and the plant species chosen will depend on ant preferences and the ecological context of the pasture to be rehabilitated.

Acknowledgments

Thanks are due to, Alba Marina Torres, James Montoya, and Zoraida Calle for advice, to Nili Betancur for assisting field work, and to the Ants and GEAHNA Research groups at the Universidad del Valle. To Carlos Moreno for statistical analysis support. Two anonymous reviewers made invaluable suggestions that improved the final version of the manuscript. Thanks are also due to the owners and managers of the farms where the studies were carried out, to the CIPAV Foundation for its institutional support, and to Marcia Dittmann for the English translation. This study was financed by Colciencias through The Project "*Las Hormigas como agentes funcionales para la recuperación ecológica de sistemas ganaderos*" (Code 110645221048), Basic Sciences Program, and the *Universidad del Valle.*

References

[1] E. Murgueitio, C. Cuartas, and J. Naranjo, *Ganadería del Futuro: Investigación Para el Desarrollo*, Fundación CIPAV, Cali, Colombia, 2008.

[2] P. Chesson, "Mechanisms of maintenance of species diversity," *Annual Review of Ecology and Systematics*, vol. 31, pp. 343–366, 2000.

[3] T. Tscharntke, C. H. Sekercioglu, T. V. Dietsch, N. S. Sodhi, P. Hoehn, and J. M. Tylianakis, "Landscape constraints on functional diversity of birds and insects in tropical agroecosystems," *Ecology*, vol. 89, no. 4, pp. 944–951, 2008.

[4] K. D. Holl, "Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil," *Biotropica*, vol. 31, no. 2, pp. 229–242, 1999.

[5] N. C. Nepstad, C. Uhl, C. A. Pereira, and J. M. C. Da Silva, "Comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia," *Oikos*, vol. 76, no. 1, pp. 25–39, 1996.

[6] P. S. Grimbacher and L. Hughes, "Response of ant communities and ant-seed interactions to bush regeneration," *Ecological Management and Restoration*, vol. 3, no. 3, pp. 188–197, 2002.

[7] P. J. Folgarait, "Ant biodiversity and its relationship to ecosystem functioning: a review," *Biodiversity and Conservation*, vol. 7, no. 9, pp. 1221–1244, 1998.

[8] S. N. Handel and A. J. Beattie, "Semillas dispersadas por hormigas," *Investigación y Ciencia*, vol. 263, pp. 76A–83A, 1990.

[9] M. A. Pizo and P. S. Oliveira, "Size and lipid content of nonmyrmecochorous diaspores: effects on the interaction with litter-foraging ants in the Atlantic rain forest of Brazil," *Plant Ecology*, vol. 157, no. 1, pp. 37–52, 2001.

[10] L. Passos and P. S. Oliveira, "Ants affect the distribution and performance of seedlings of *Clusia criuva*, a primarily bird-dispersed rain forest tree," *Journal of Ecology*, vol. 90, no. 3, pp. 517–528, 2002.

[11] C. C. Horvitz and A. J. Beattie, "Ant dispersal of *Calathea* (Marantaceae) seeds by carnivorous Ponerines (Formicidae) in a tropical rain-forest," *American Journal of Botany*, vol. 67, pp. 321–326, 1980.

[12] C. C. Horvitz and D. W. Schemske, "Seed dispersal of a neotropical myrmecochore: variation in removal rates and dispersal distance," *Biotropica*, vol. 18, pp. 319–323, 1986.

[13] J. W. Dalling and R. Wirth, "Dispersal of *Miconia argentea* seeds by the leaf-cutting ant *Atta Colombica*," *Journal of Tropical Ecology*, vol. 14, no. 5, pp. 705–710, 1998.

[14] M. A. Pizo and P. S. Oliveira, "The use of fruits and seeds by ants in the Atlantic forest of Southeast Brazil," *Biotropica*, vol. 32, no. 4b, pp. 851–861, 2000.

[15] T. J. Zelikova and M. D. Breed, "Effects of habitat disturbance on ant community composition and seed dispersal by ants in a tropical dry forest in Costa Rica," *Journal of Tropical Ecology*, vol. 24, no. 3, pp. 309–316, 2008.

[16] S. Escobar, I. Armbrecht, and Z. Calle, "Transporte de semillas por hormigas en bosques y agroecosistemas ganaderos de los Andes Colombianos," *Agroecología*, vol. 2, pp. 65–74, 2007.

[17] Y. Dominguez-Haydar and I. Armbrecht, "Response of ants and their seed removal in rehabilitation areas and forests at El Cerrejón Coal Mine in Colombia," *Restoration Ecology*, vol. 19, no. 201, pp. 178–184, 2011.

[18] V. Rico-Gray and P. S. Oliveira, *The Ecology and Evolution of Ant-Plant Interactions*, University of Chicago Press, Chicago, Ill, USA, 2007.

[19] M. A. Pizo and P. S. Oliveira, "Interaction between ants and seeds of a nonmyrmecochorous neotropical tree, *Cabralea canjerana* (Meliaceae), in the Atlantic forest of southeast Brazil," *American Journal of Botany*, vol. 85, no. 5, pp. 669–674, 1998.

[20] P. Dostál, M. Březnová, V. Kozlíčková, T. Herben, and P. Kovář, "Ant-induced soil modification and its effect on plant below-ground biomass," *Pedobiologia*, vol. 49, no. 2, pp. 127–137, 2005.

[21] A. G. Farji Brener and J. F. Silva, "Leaf-cutter ants' (*Atta laevigata*) aid to the establishment success of *Tapirira velutinifolia* (Anacardiaceae) seedlings in a parkland savanna," *Journal of Tropical Ecology*, vol. 12, no. 1, pp. 163–168, 1996.

[22] B. Lafleur, L. M. Hooper-Bùi, E. P. Mumma, and J. P. Geaghan, "Soil fertility and plant growth in soils from pine forests and plantations: effect of invasive red imported fire ants *Solenopsis*

invicta (Buren)," *Pedobiologia*, vol. 49, no. 5, pp. 415–423, 2005.

[23] J. Retana, F. X. Picó, and R. Anselm, "Dual role of harvesting ants as seed predators and dispersers of a non-myrmechorous Mediterranean perennial herb," *Oikos*, vol. 105, no. 2, pp. 377–385, 2004.

[24] C. Gómez and X. Espadaler, "Falling or movement of seeds and the presence of an elaiosome: its effect on ant reaction (Hymenoptera: Formicidae) in a myrmecochorous species, *Euphorbia characias* (Euphorbiaceae)," *Sociobiology*, vol. 30, no. 2, pp. 175–183, 1997.

[25] L. Hughes and M. Westoby, "Effect of diaspore characteristics on removal of seeds adapted for dispersal by ants," *Ecology*, vol. 73, no. 4, pp. 1300–1312, 1992.

[26] S. N. Gorb and E. V. Gorb, "Removal rates of seeds of five myrmecochorous plants by the ant *Formica polyctena* (Hymenoptera: Formicidae)," *Oikos*, vol. 73, no. 3, pp. 367–374, 1995.

[27] C. Gómez and X. Espadaler, "Myrmecochorous dispersal distances: a world survey," *Journal of Biogeography*, vol. 25, no. 3, pp. 573–580, 1998.

[28] J. H. Ness, J. L. Bronstein, A. N. Andersen, and J. N. Holland, "Ant body size predicts dispersal distance of ant-adapted seeds: implications of small-ant invasions," *Ecology*, vol. 85, no. 5, pp. 1244–1250, 2004.

[29] D. J. Levey and M. M. Byrne, "Complex ant-plant interactions: rain forest ants as secondary dispersers and post-dispersal seed predators," *Ecology*, vol. 74, no. 6, pp. 1802–1812, 1993.

[30] L. S. Espinal, *Zonas de vida de Colombia*, Universidad Nacional de Colombia, Facultad de Ciencias, Departamento de Ciencias de la Tierra, Medellín, Colombia, 1990.

[31] A. Perafán, "Transformaciones paisajísticas en la zona plana vallecaucana," *Historia y Espacio Revista del Departamento de Historia Universidad del Valle*, vol. 24, pp. 1–18, 2005.

[32] A. Jaramillo-Robledo and B. Chaves-Córdoba, "Distribución de la precipitación en Colombia analizada mediante conglomeración estadística," *Cenicafé*, vol. 51, no. 2, pp. 102–113, 2000.

[33] Royal Botanic Gardens Kew, "Seed information database (SID). Version 7.1," May 2008, http://data.kew.org/sid/ .

[34] C. Santamaría, I. Armbrecht, and J. P. Lachaud, "Nest distribution and food preferences of *Ectatomma ruidum* (Hymenoptera: Formicidae) in shaded and open cattle pastures of Colombia," *Sociobiology*, vol. 53, no. 2, pp. 517–541, 2009.

[35] R. Silvestre, C. R. F. Brandão, and R. Rosa da Silva, "Grupos funcionales de hormigas: el caso de los gremios del Cerrado," in *Introducción a Las Hormigas de La Región Neotropical*, F. Fernández, Ed., pp. 113–148, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia, 2003.

[36] J. A. Ludwig and J. F. Reynolds, *Statistical Ecology: A Primer of Methods and Computing*, John Wiley & Sons, New York, NY, USA, 1988.

[37] SAS Institute Inc., "SAS 9.1.3 Help and Documentation," Cary, NC: SAS Institute Inc., 2002-2004.

[38] M. Ramírez, I. Armbrecht, and M. L. Enríquez, "Importancia del manejo agrícola para la biodiversidad: caso de las hormigas en la caña de azúcar," *Revista Colombiana de Entomología*, vol. 30, no. 1, pp. 115–123, 2004.

[39] A. Arcila, *Afecta la fragmentación la colonización de especies oportunistas?*, Ph.D. thesis, Universidad del Valle, Biology Department, Cali, Colombia, 2007.

[40] R. Achury, P. Ulloa-Chacón, and A. M. Arcila, "Composición de hormigas e interacciones competitivas con *Wasmannia auropunctata* en fragmentos de bosque seco tropical," *Revista Colombiana de Entomología*, vol. 34, no. 2, pp. 209–216, 2008.

[41] I. Armbrecht and P. Ulloa-Chacón, "Rarity and diversity of ants in dry forest fragments and its matrices in Colombia," *Biotropica*, vol. 31, no. 4, pp. 646–653, 1999.

[42] L. Passos and P. S. Oliveira, "Interactions between ants, fruits and seeds in a restinga forest in south-eastern Brazil," *Journal of Tropical Ecology*, vol. 19, no. 3, pp. 261–270, 2003.

[43] C. R. Carroll and D. H. Janzen, "Ecology of foraging by ants," *Annual Review of Ecology and Systematics*, vol. 4, pp. 231–257, 1973.

[44] I. Perfecto, "Dynamics of *Solenopsis geminata* in a tropical fallow field after ploughing," *Oikos*, vol. 62, no. 2, pp. 139–144, 1991.

[45] C. R. Carroll and S. J. Risch, "The dynamics of seed harvesting in early successional communities by a tropical ant, *Solenopsis geminata*," *Oecologia*, vol. 61, no. 3, pp. 388–392, 1984.

[46] J. M. Bas, J. Oliveras, and C. Gómez, "Myrmecochory and short-term seed fate in *Rhamnus alaternus*: ant species and seed characteristics," *Acta Oecologica*, vol. 35, no. 3, pp. 380–384, 2009.

[47] F. Howe and J. Smallwood, "Ecology of seed dispersal," *Annual Review of Ecology and Systematics*, vol. 13, pp. 201–228, 1982.

[48] D. G. Wenny, "Advantages of seed dispersal: a re-evaluation of directed dispersal," *Evolutionary Ecology Research*, vol. 3, no. 1, pp. 51–74, 2001.

[49] I. Giladi, "Choosing benefits or partners: a review of the evidence for the evolution of myrmecochory," *Oikos*, vol. 112, no. 3, pp. 481–492, 2006.

[50] I. R. Leal and P. S. Oliveira, "Foraging ecology of attine ants in a Neotropical savanna: seasonal use of fungal substrate in the cerrado vegetation of Brazil," *Insectes Sociaux*, vol. 47, no. 4, pp. 376–382, 2000.

[51] S. B. Vander Wall and W. S. Longland, "Diplochory: are two seed dispersers better than one?" *Trends in Ecology and Evolution*, vol. 19, no. 3, pp. 155–161, 2004.

[52] A. V. Christianini and P. S. Oliveira, "Birds and ants provide complementary seed dispersal in a neotropical savanna," *Journal of Ecology*, vol. 98, no. 3, pp. 573–582, 2010.

[53] N. Henao-Gallego, S. Escobar-Ramírez, Z. Calle, J. Montoya-Lerma, and I. Armbrecht, "An artificial aril designed to induce seed hauling by ants for ecological rehabilitation purposes," *Restoration Ecology*. In press.

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 172739, 6 pages
doi:10.1155/2012/172739

Research Article

Tree-Dwelling Ants: Contrasting Two Brazilian Cerrado Plant Species without Extrafloral Nectaries

Jonas Maravalhas,[1] Jacques H. C. Delabie,[2] Rafael G. Macedo,[1] and Helena C. Morais[1]

[1] *Departamento de Ecologia, Instituto de Biologia, Universidade de Brasília, 70910-900 Brasília, DF, Brazil*
[2] *Laboratório de Mirmecologia, Convênio UESC/CEPLAC, Centro de Pesquisa do Cacau, CEPLAC, Cx. P. 07, 45600-000 Itabuna, BA, Brazil*

Correspondence should be addressed to Jonas Maravalhas, jmaravalhas@gmail.com

Received 31 May 2011; Revised 28 June 2011; Accepted 30 June 2011

Academic Editor: Fernando Fernández

Ants dominate vegetation stratum, exploiting resources like extrafloral nectaries (EFNs) and insect honeydew. These interactions are frequent in Brazilian cerrado and are well known, but few studies compare ant fauna and explored resources between plant species. We surveyed two cerrado plants without EFNs, *Roupala montana* (found on preserved environments of our study area) and *Solanum lycocarpum* (disturbed ones). Ants were collected and identified, and resources on each plant noted. Ant frequency and richness were higher on *R. montana* (67%; 35 spp) than *S. lycocarpum* (52%; 26), the occurrence of the common ant species varied between them, and similarity was low. Resources were explored mainly by *Camponotus crassus* and consisted of scale insects, aphids, and floral nectaries on *R. montana* and two treehopper species on *S. lycocarpum*. Ants have a high diversity on cerrado plants, exploring liquid and prey-based resources that vary in time and space and affect their presence on plants.

1. Introduction

Foliage-dwelling ants are an important component in tropical environments [1–3], affecting locally the composition and abundance of other insect communities [4–6] and directly or indirectly driving mutualistic and trophic interactions in plant-herbivore-predator/parasite interactions [7–11]. High abundance and richness of ants on this stratum are due to a highly energetic liquid diet, mainly extrafloral nectaries (EFNs) and hemipteran honeydew [12–14]. Ants use a variety of resources from plants and their herbivores and these associations are facultative and vary temporally and spatially [1].

In the cerrado, a savanna-like vegetation in central Brazil, there is a high proportion of plants bearing EFNs, representing up to 31% of the plant individuals surveyed [15, 16] and a rich fauna of ants exploiting them [2, 17–19]. A vast literature about direct and indirect associations of ants and plants in this biome is available [20], but there are few studies comparing ant faunas and their resources between plant species, especially those without EFNs. Results presented by Schoereder et al. [2] indicate that the presence of EFNs does not affect ant species richness within a given tree and there is no particular ant species composition typical of plants with EFNs.

To link the richness and seasonal variation of ants to attractive resources available on a particular plant species, we compared ant assemblages on two species that do not bear EFNs and are common of the cerrado region of central Brazil: *Roupala montana* Aubl. (Proteaceae) and *Solanum lycocarpum* St. Hill. (Solanaceae). In our sampling area, both plants have similar stature and structure, are consumed by myrmecophilous hemipterans [21, 22], and were found in different environments: *R. montana* occurring in native cerrado vegetation, where *S. lycocarpum* is rarely found, being common in altered areas at the borders of roads and agropastoral fields. The ability of *S. lycocarpum* to establish itself in a wider range of environments supposedly leads to bigger ant richness, in contrast to *R. montana*. On the other hand, impoverished areas, where *S. lycocarpum* occurs, can sustain weaker ant diversity, which can affect the ant fauna foraging on this species. We expect that differences on the area of occurrence and resource availability between these plant species may lead to important differences in the composition of ant species.

2. Material and Methods

2.1. Study Area. This study was conducted in the Fazenda Agua Limpa (15 57 S, 47 54 W), Federal District, Brazil. This 4,500 ha farm belongs to the University of Brasilia and includes mainly undisturbed cerrado vegetation and agro-silvo-pastoral experimental areas. The region has altitudes around 1,050 m a.s.l., average annual temperature of 22 C, and average annual rainfall of 1,417 mm (series from 1980 to 2004, data from RECOR Meteorological Station, http://www.recor.org.br/), and a marked seasonality, with a lengthy dry season ranging from May to September and a wet season from October to April.

2.2. Plant Species. Roupala montana is widely distributed in the Brazilian cerrado [23] and is abundant in cerrado remnants of the Federal District. It is an evergreen shrub that simultaneously sheds leaves and produces new ones, reaching up to three meters height, blooms for a long period during the year, and is pollinated by moths [24–26]. It hosts ant-tended hemipterans like scale insects (Coccoidea), aphids (Aphidoidea), and, especially a leafhopper species, *Rotundicerus* sp. (Cicadellidae and Idiocerinae), which forms large aggregates of nymphs feeding on new leaves at the beginning of the rainy season [21]. A rich fauna of caterpillars, including *Hallonympha paucipuncta* (Spitz, 1930) (Riodinidae) and at least 10 species of Lycaenidae, consumes its leaves and inflorescences [27–29].

Solanum lycocarpum is an evergreen shrub with maximum height of about two meters, being extremely common in disturbed environments [30, 31]. New leaves and flowers grow throughout the year, but flowers do not reward nectar to insects, and pollen is the floral resource collected by bumblebees through buzz pollination behavior [30]. Leaf surfaces are covered with simple glandular and nonglandular trichomes and stellate trichomes [32]. The treehopper *Enchenopa brasiliensis* Strümpel, 2007 (Membracidae) is a common species feeding on apical meristems and inflorescences [22]. In the study area, two species of Membracidae, one of Aetalionidae and an inderterminated number of species of scale insects were tended by ants on new leaves of this plant. One Cicadelidae species was very abundant too on the same plants, but it was not associated with ants. *Solanum lycocarpum* leaves are eaten by several microlepidoptera, especially *Symmetrischema chloroneura* (Meyrick, 1923) (Gelechiidae) [33], its stems are consumed by gall-forming weevil, *Collabismus clitellae* Boheman, 1837 (Curculionidae) [34] and its leaves and fruits are eaten by several species of mammals [31, 35–37]. Attini nests (Formicidae and Myrmicinae) favor the establishment of seedlings and enhance nutrient in the leaves of *S. lycocarpum* [38].

Table 1: Frequency of occurrence of ants and myrmecophilous hemipterans on *Roupala montana* (Proteaceae) and *Solanum lycocarpum* (Solanaceae), in Fazenda Agua Limpa, Federal District, Brazil. Comparisons made with contingency tables.

Caracteristics	Roupala	Solanum	χ^2	P
Examined plants	327	431		
Plants with ants	218	226	15.517	0.0001
Plants with myrmecophilous hemipterans	139	188	0.094	0.816
Co-occurrence of ants and hemipterans	115	143	0.328	0.620
Plants with hemipterans without ants	24	45	2.161	0.141
Plants with ants without hemipterans	103	83	15.046	0.0001

2.3. Samples and Data Analysis. Individuals of both plant species were carefully examined always in the morning period. Every ant observed on the plant was collected and the occurrence of myrmecophilous hemipterans registered. *Roupala montana* plants ($n = 327$) were examined between April and September (dry season) of 2007 in a typical cerrado vegetation area of 2 ha. Previous surveys in the same study area were made on this species during the wet season of 2006, when the focus was to collect the ants tending nymphs of *Rotundicerus* sp. ($n = 116$). *Solanum lycocarpum* plants ($n = 431$) were inspected between March 2007 and March 2008 along dirt roads that cross a mosaic of environments, including typical and "campo sujo" (a physiognomy dominated by herbaceous vegetation) native cerrado areas, pastures and cultures of coffee, sorghum, and pine. The sampling area of *S. lycocarpum* was more widely spread than that of *R. montana*.

The mean similarity of ant species composition between the two plant species was calculated by grouping the samples of each month from April and October ($n = 7$). The similarity indexes and rarefaction curves were generated using EstimateS [39]. The frequency tests were made using BioEstat 5.0 [40].

3. Results

Ants were more frequent on *R. montana* (67%) as compared to *S. lycocarpum* (52%) and this difference was due to higher occurrence of ants on *R. montana* plants without myrmecophilous hemipterans (Table 1). Along the study we collected a total of 45 ant species from 11 different genera. We recorded 35 species on *R. montana* and 26 on *S. lycocarpum*, with estimated richness (first order Jackknife ± standard deviation) of 40 (± 2.6) and 29 (± 2.3), respectively, (Figure 1; Table 2).

The frequency of occurrence of the most common ant species were different on the two plant species (Table 2) and the mean similarity (± sd) of the ant assemblages for the dry season was low (Sorensen Index = 0.419 ± 0.078), especially when the frequency of occurrence of ant species was considered (Morisita-Horn Index = 0.372 ± 0.167).

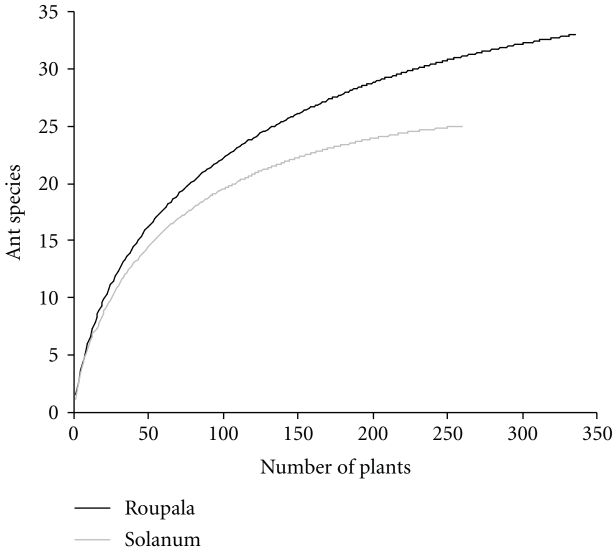


FIGURE 1: Rarefaction curves of ant species collected on *Roupala montana* (Proteaceae) and *Solanum lycocarpum* (Solanaceae), in Fazenda Agua Limpa, Federal District, Brazil.

Scale insects were an abundant resource in the leaves of *R. montana*, being found throughout the sampling period and 21% of ants in this plant were exploring this resource. We found 15 species of ants attending scale insects, and the most frequent were *Cephalotes pusillus* (Klug, 1824) (17 occurrences), *Camponotus crassus* (Mayr, 1862) (8), *Brachymyrmex* sp. (7), *Crematogaster evallans* (Forel, 1907) (6), and *Solenopsis* sp. (5). Some individuals of *R. montana* were flowering between April and July 2007 and developing inflorescences were explored by aphids, associated to four ant species, mainly *Cr. evallans* (4) and *Camponotus* (*Myrmaphaenus*) sp.2 (3). Seven species were recorded exploring mature floral nectaries, mostly *Ce. pusillus* (5) and *Camponotus* (*Myrmaphaenus*) sp.2 (4).

The frequency of occurrence of the commonest ant species was different on *R. montana* with and without *Rotundicerus* sp. A large proportion (67%) of the *R. montana* individuals examined during the dry season had ants, and 68% of the groups of *Rotundicerus* sp. on the same plant species and in the same area where tended by ants during the rainy season of 2006. Although the occurrence of the leafhopper did not enhance the frequency of visits of ants, it altered the composition of the ant fauna. The most notable cases were *Ca. crassus* and *Azteca instabilis* (Smith, 1862), which increased their frequency on the plants when *Rotundicerus* sp. was present, from 4 to 28% and 0 to 10%, respectively. *Cephalotes pusillus* and *Crematogaster stollii* Forel, 1885, on the other hand, decreased their frequency from 19% to 8% and from 7% to 0%, respectively.

Major resources explored by ants in *S. lycocarpum* were two species of Membracidae, each one present in 23% of the examined plants and *Ca. crassus* was the most frequent ant found in association with them. One species of Aetalionidae and scale insects were infrequent on this plant, being seen three and seven times, respectively. We lack nutritional information of glandular trichomes of *S. lycocarpum*, but small ants, like some species belonging to the genera *Brachymyrmex*, *Dorymyrmex*, *Pheidole,* and *Solenopsis*, possibly use this resource. *Pseudomyrmex* spp. were generally present (68%) on plants without myrmecophilous hemipterans.

4. Discussion

We found a high frequency of plants visited by ants, showing the prevalence of ants foraging on cerrado plants, even during the dry season, when *R. montana* plants were examined. The high availability of potential resources for ants [2, 13, 41], especially myrmecophilous hemipterans in the cerrado vegetation [21, 22, 42, 43], makes this stratum attractive to ants. Even with the predominance of liquid diet, it is important to stress that various species of ants forage for preys on plants, including myrmecophilous hemipterans [44]. In an urban area of Campinas (SP), for example, 70% of the diet of *Pseudomyrmex gracilis* (Fabricius, 1804) was based on arthropods, primarily a Psyllidae species (Hemiptera and Sternorryncha) [45]. This can explain the high frequency of *Pseudomyrmex* spp. in the samples, as well as the presence of *Pachycondyla* spp., a genus of predator ants [46]. Besides, some genera (e.g., *Cephalotes* and *Pseudomyrmex*) nest in dried plant branches, and this too can affect the ant assemblage that forage on an individual plant.

Richness of ants was high in both plant species, especially considering that the surveys were conducted only in the morning. Studies including day and night time observations, showed an average of 21 ant species visiting EFNs on six species of cerrado plants, with a minimum of nine on *Qualea multiflora* Mart. (Vochysiaceae) and a maximum of 34 on *Caryocar brasiliense* Camb. (Caryocaraceae) (Appendix 6.1 in [1]). Sequential samplings on *Schefflera vinosa* (Cham. & Schltdl.) Frondin and Fiasch (Araliacae) revealed that *Guayaquila xiphias* (Fabricius, 1803) treehoppers are attended day and night by 21 species of honeydew-gathering ants [42], whereas shrubs of *Solanum lycocarpum* hosting *Enchenopa brasiliensis* treehoppers are regularly visited by 10 ant species [22]. Campos et al. [19], using pitfall traps in a cerrado area of the state of Goias, found 16 species of ants on the shrub stratum (height between 0.5 and 1.5 m) and 28 on the arboreal stratum (dominated by taller, mature trees).

As expected, ant fauna between the two plants species investigated showed small similarity. The different habitats of occurrence of the plants undoubtedly had an effect on this result [47–50], but variation on resource availability might have an important influence on the composition of ant species [41]. So there must be a particular ant species composition typical of plants with these kinds of resources (e.g., big groups of myrmecophilous hemipterans and active EFNs) even though for a limited period of time. Probably the fidelity of dominant ants plays a key role in structuring assemblages of tending ants on this rich food resource. Hence, comparisons on the frequency of occurrence and composition of species of ants on plants with and without these resources need to be done when they are present

Table 2: Ant species and its occurrence on *Roupala montana* (Proteaceae) and *Solanum lycocarpum* (Solanaceae), in Fazenda Agua Limpa, Federal District, Brazil. The most frequent species are highlighted.

Formicidae	Roupala	Solanum
Myrmicinae		
Cephalotes adolphi Emery	2	0
Cephalotes atratus Linnaeus	0	2
Cephalotes betoi De Andrade	3	0
Cephalotes depressus (Klug)	5	10
Cephalotes grandinosus (Smith)	6	0
Cephalotes liepini de Andrade & Baroni Urbani	2	0
***Cephalotes pusillus* (Klug)**	**147**	**18**
Crematogaster distans Mayr	3	6
Crematogaster evallans Forel	11	3
Crematogaster stollii Forel	14	0
Crematogaster victima (Smith)	1	0
Crematogaster sp.	3	0
Nesomyrmex pleuriticus (Wheeler)	1	0
Nesomyrmex tristani Emery	1	0
Pheidole capillata Emery	10	7
Pheidole sp.1 grupo *fallax*	2	1
Solenopsis substituta (Santschi)	0	9
Solenopsis sp.	12	0
Formicinae		
Brachymyrmex sp.	14	9
Camponotus arboreus (Smith)	4	0
Camponotus atriceps (Smith)	2	0
Camponotus blandus (Smith)	1	2
***Camponotus crassus* Mayr**	**64**	**105**
Camponotus fastigatus Roger	0	2
Camponotus melanoticus Emery	1	5
Camponotus novogranadensis Mayr	3	0
***Camponotus rufipes* Fabricius**	**0**	**38**
Camponotus (*Myrmaphaenus*) sp.1	1	3
***Camponotus* (*Myrmaphaenus*) sp.2**	**34**	**2**
Camponotus (*Myrmaphaenus*) sp.3	0	1
Camponotus (*Myrmaphaenus*) sp.4	0	3
Camponotus (*Myrmobrachys*) sp.1	1	0
Camponotus (*Myrmobrachys*) sp.2	2	0
Camponotus (*Tanaemyrmex*) sp.	4	2
Dolichoderinae		
Azteca instabilis (Smith)	19	0
Azteca sp.	14	0
Dorymyrmex sp.1	0	6
Pseudomyrmecinae		
Pseudomyrmex gracilis (Fabricius)	0	14
Pseudomyrmex pupa (Forel)	0	2
Pseudomyrmex termitarius (Smith)	0	1
Pseudomyrmex tenuissimus (Emery)	7	2
Pseudomyrmex rufiventris (Forel)	1	4
Pseudomyrmex sp. gp. *Pallidus*	1	4
Ponerinae		
Pachycondyla inversa (Smith)	1	0
Pachycondyla villosa (Fabricius)	3	0

(e.g., active EFNs) and, preferentially, carefully choosing the species of plants, as phylogeny and genetic distance have a known influence in herbivore communities [51, 52].

Most studies about ant-hemipteran associations do not take into account records of ants on plants during periods of absence of these sap-sucking insects. Nevertheless they feed on young tissues of the host plant [9, 21, 22, 42, 43], so plant phenology has a direct effect on their occurrence and their potential association with ants. *Solanum lycocarpum* continuously produces leaves that are consumed by treehoppers practically throughout the year, while *R. montana* produces leaves roughly around September and November, period when its main sap-sucking insect, the myrmecophilous hemipteran, *Rotundicerus* sp., achieves its development and leaves the host plants. In any case, both plant species are patrolled by ants in the absence of their main hemipteran resources and other apparent ones. Plant phenology and seasonality have an effect on availability of resources exploited by tree-dwelling ants, producing a dynamics of niches occupied by a turnover of ant species. This yearly variation can reveal the strength of mutualistic associations between ants and myrmecophilous hemipterans and plants with or without EFNs, being important to understand the patterns of ant-plant-herbivore interactions.

Acknowledgments

The authors thank Ecology Graduate Program, technicians of the Tri Trophics Interaction laboratory, the University of Brasília—Fazenda Agua Limpa for the infrastructure, and Dr. Mundayatan Haridasan (Universidade de Brasília) who made suggestions and corrections in the manuscript. J. Maravalhas received Scientific Initiation scholarship from PIBIC/CNPq-UnB; J. H. C. Delabie acknowledges his research grant from CNPq.

References

[1] V. Rico-Gray and P. S. Oliveira, *The Ecology and Evolution of Ant-Plant Interactions*, Chicago Press, Chicago, Ill, USA.

[2] J. H. Schoereder, T. G. Sobrinho, M. S. Madureira, C. R. Ribas, and P. S. Oliveira, “The arboreal ant community visiting extrafloral nectaries in the Neotropical cerrado savanna,” *Terrestrial Arthropod Reviews*, vol. 3, pp. 3–27, 2010.

[3] P. Klimes, M. Janda, S. Ibalim, J. Kua, and V. Novotny, “Experimental suppression of ants foraging on rainforest vegetation in New Guinea: testing methods for a whole-forest manipulation of insect communities,” *Ecological Entomology*, vol. 36, no. 1, pp. 94–103, 2011.

[4] A. V. L. Freitas and P. S. Oliveira, “Ants as selective agents on herbivore biology: effects on the behaviour of a non-myrmecophilous butterfly,” *Journal of Animal Ecology*, vol. 65, no. 2, pp. 205–210, 1996.

[5] A. Floren, A. Biun, and K. Eduard Linsenmair, “Arboreal ants as key predators in tropical lowland rainforest trees,” *Oecologia*, vol. 131, no. 1, pp. 137–144, 2002.

[6] G. W. Fernandes, M. Fagundes, M. K. B. Greco, M. S. Barbeitos, and J. C. Santos, “Ants and their effects on an insect herbivore community associated with the inflorescences of *Byrsonima crassifolia* (Linnaeus) H.B.K. (Malpighiaceae),” *Revista Brasileira de Entomologia*, vol. 49, pp. 264–269, 2005.

[7] M. Heil and D. McKey, “Protective ant-plant interactions as model systems in ecological and evolutionary research,” *Annual Review of Ecology, Evolution, and Systematics*, vol. 34, pp. 425–453, 2003.

[8] J. A. Rudgers and S. Y. Strauss, “A selection mosaic in the facultative mutualism between ants and wild cotton,” *Proceedings of the Royal Society B*, vol. 271, no. 1556, pp. 2481–2488, 2004.

[9] D. McKey, L. Gaume, C. Brouat et al., “The trophic structure of tropical ant-plant-herbivore interactions: community consequences and coevolutionary dynamics,” in *Biotic Interactions in the Tropics: Their Role in the Maintenance of Species Diversity*, D. Burslem, M. Pinard, and S. Hartley, Eds., pp. 386–413, Cambridge University Press, Cambridge, UK, 2005.

[10] J. P. R. Guimarães, V. Rico-Gray, P. Oliveira, T. J. Izzo, S. F. dos Reis, and J. N. Thompson, “Interaction intimacy affects structure and coevolutionary dynamics in mutualistic networks,” *Current Biology*, vol. 17, no. 20, pp. 1–7, 2007.

[11] L. A. Kaminski, A. V. L. Freitas, and P. S. Oliveira, “Interaction between mutualisms: ant-tended butterflies exploit enemy-free space provided by ant-treehopper associations,” *American Naturalist*, vol. 176, no. 3, pp. 322–334, 2010.

[12] J. E. Tobin, “Ants as primary consumers: diet and abundance in the formicidae,” in *Nourishment and Evolution in Insect Societies*, J. H. Hunt and C. A. Napela, Eds., pp. 279–307, Westview Press, Boulder, Colo, USA, 1994.

[13] J. H. C. Delabie, “Trophobiosis between formicidae and hemiptera (sternorrhyncha and auchenorrhyncha): an overview,” *Neotropical Entomology*, vol. 30, no. 4, pp. 501–516, 2001.

[14] D. W. Davidson, S. C. Cook, R. R. Snelling, and T. H. Chua, “Explaining the abundance of ants in lowland tropical rainforest canopies,” *Science*, vol. 300, no. 5621, pp. 969–972, 2003.

[15] P. S. Oliveira and H. F. Leitão-Filho, “Extrafloral nectaries: their taxonomic distribution and abundance in the woody flora of Cerrado vegetation in Southeast Brazil,” *Biotropica*, vol. 19, pp. 140–148, 1987.

[16] P. S. Oliveira and A. T. Oliveira-Fliho, “Distribution of extrafloral nectaries in the woody flora of tropical communities in Western Brazil,” in *Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions*, P. W. Price, T. M. Lewinsohn, G. Fernandes, and W. W. Benson, Eds., pp. 163–175, John Wiley and Sons, New York, NY, USA, 1991.

[17] C. R. Ribas, J. H. Schoereder, M. Pic, and S. M. Soares, “Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness,” *Austral Ecology*, vol. 28, no. 3, pp. 305–314, 2003.

[18] G. D. V. Marques and K. Del-Claro, “The ant fauna in a cerrado area: the influence of vegetation structure and seasonality (Hymenoptera: Formicidae),” *Sociobiology*, vol. 47, no. 1, pp. 1–18, 2006.

[19] R. I. Campos, C. T. Lopes, W. C. S. Magalhães, and H. L. Vasconcelos, “Estratificação vertical de formigas em Cerrado strictu sensu no Parque Estadual da Serra de Caldas Novas, Goiás, Brasil,” *Iheringia*, vol. 98, no. 3, pp. 311–316, 2008.

[20] P. S. Oliveira and A. V. L. Freitas, “Ant-plant-herbivore interactions in the neotropical cerrado savanna,” *Naturwissenschaften*, vol. 91, no. 12, pp. 557–570, 2004.

[21] J. Maravalhas and H. C. Morais, “Association between ants and a leafhopper (Cicadellidae: Idiocerinae) in the central brazilian cerrado,” *Florida Entomologist*, vol. 92, no. 4, pp. 563–568, 2009.

[22] V. S. S. Moreira and K. Del-Claro, "The outcomes of an ant-treehopper association on *Solanum lycocarpum* St. Hill: increased membracid fecundity and reduced damage by chewing herbivores," *Neotropical Entomology*, vol. 34, no. 6, pp. 881–887, 2005.

[23] J. A. Ratter, S. Bridgewater, J. F. Ribeiro, T. A. Borges, and M. R. Silva, "Estudo preliminar da distribuição das espécies lenhosas da fitofisionomia cerrado sentido restrito nos estados compreendidos pelo bioma Cerrado," *Boletim do Herbário Ezechias Paulo Heringer*, vol. 5, pp. 5–43, 2000.

[24] A. C. Franco, M. Bustamante, L. S. Caldas et al., "Leaf functional traits of Neotropical savanna trees in relation to seasonal water deficit," *Trees*, vol. 19, no. 3, pp. 326–335, 2005.

[25] E. Lenza and C. A. Klink, "Comportamento fenológico de espécies lenhosas em um cerrado sentido restrito de Brasília, DF," *Revista Brasileira de Botanica*, vol. 29, no. 4, pp. 627–638, 2006.

[26] P. E. Oliveira, P. E. Gibbs, and A. A. Barbosa, "Moth pollination of woody species in the Cerrados of Central Brazil: a case of so much owed to so few?" *Plant Systematics and Evolution*, vol. 245, no. 1-2, pp. 41–54, 2004.

[27] A. Bendicho-López, H. C. Morais, J. D. Hay, and I. R. Diniz, "Lepidópteros folívoros em *Roupala montana* Aubl. (Proteaceae) no cerrado *sensu stricto*," *Neotropical Entomology*, vol. 35, no. 2, pp. 182–191, 2006.

[28] L. A. Kaminski, "Polyphagy and obligate myrmecophily in the butterfly *Hallonympha paucipuncta* (Lepidoptera: Riodinidae) in the neotropical cerrado savanna," *Biotropica*, vol. 40, no. 3, pp. 390–394, 2008.

[29] N. A. P. Silva, *Biologia de lagartas de lycaenidae em inflorescências de plantas no cerrado do Brazil Central*, M.S. thesis, Universidade de Brasília, Brasília, Brazil, 2011.

[30] A. T. Oliveira-Filho and L. C. A. Oliveira, "Biologia floral de Solanum lycocarpum St. Hil. (Solanaceae) em Larvras, MG," *Revista Brasileira de Botânica*, vol. 11, pp. 23–32, 1988.

[31] J. A. Lombardi and J. C. Motta-Junior, "Seed dispersal of Solanum lycocarpum St. Hil. (Solanaceae) by the maned wolf, *Chysocyon brachyurus* Illiger (Mammalia, Canidae)," *Ciência e Cultura*, vol. 45, pp. 126–127, 1993.

[32] S. R. M. Elias, R. M. Assis, E. Stacciarini-Seraphin, and M. H. Rezende, "Anatomia foliar em plantas jovens de Solanum lycocarpum A.St.-Hil. (Solanaceae)," *Revista Brasileira de Botânica*, vol. 26, pp. 169–174, 2033.

[33] I. R. Diniz and H. C. Morais, unpublished data.

[34] A. L. T. Souza, G. W. Fernandes, J. E. Cortes Figueira, and M. O. Tanaka, "Natural history of a gall-inducing weevil *Collabismus clitellae* (coleoptera: Curculionidae) and some effects on its host plant *Solanum lycocarpum* (Solanaceae) in Southeastern Brazil," *Annals of the Entomological Society of America*, vol. 91, no. 4, pp. 404–409, 1998.

[35] J. C. Dalponte and E. S. Lima, "Disponibilidade de frutos e a dieta de *Lycalopex vetulus* (Carnivora) em um cerrado do Mato Grosso, Brasil," *Revista Brasileira de Botânica*, vol. 22, pp. 325–332, 1999.

[36] L. M. S. Aguiar, "Primeiro registro do uso de folhas de *Solanum lycocarpum* (Solanaceae) e de frutos de *Emmotum nitens* (Icacinaceae) por *Platyrrhinus lineatus* (E. Geoffroy) (Chiroptera, Phyllostomidae) no Cerrado brasileiro," *Revista Brasileira de Zoologia*, vol. 22, pp. 509–510, 2005.

[37] D. C. Briani and J. P. R. Guimaraes, "Seed predation and fruit damage of *Solanum lycocarpum* (Solanaceae) by rodents in the cerrado of central Brazil," *Acta Oecologica*, vol. 31, no. 1, pp. 8–12, 2007.

[38] L. Sousa-Souto, J. H. Schoereder, and C. E. G. R. Schaefer, "Leaf-cutting ants, seasonal burning and nutrient distribution in Cerrado vegetation," *Austral Ecology*, vol. 32, no. 7, pp. 758–765, 2007.

[39] R. K. Colwell, "EstimateS: statistical estimation of species richness and shared species from samples. Version 8.0.0 User's Guide and Application," 2008, http://viceroy.eeb.uconn.edu/estimates.

[40] M. Ayres, M. Ayres Jr., D. L. Ayres, and A. A. S. Santos, *BioEstat 5.0*, Instituto de Desenvolvimento Sustentável Mamirauá, Belém, Brazil, 2005.

[41] V. Rico-Gray, J. G. García-Franco, M. Palacios-Rios, C. Diaz-Castelazo, V. Parra-Tabla, and J. A. Navarro, "Geographical and seasonal variation in the richness of ant-plant interactions in Mexico," *Biotropica*, vol. 30, no. 2, pp. 190–200, 1998.

[42] B. C. Lopes, "Treehoppers (Homoptera: Membracidae) in the Southeast Brazil: use of host plants," *Revista Brasileira de Zoologia*, vol. 12, pp. 595–608, 1995.

[43] K. Del-Claro and P. S. Oliveira, "Ant-homoptera interactions in a neotropical savanna: the honeydew-producing treehopper, *Guayaquila xiphias* (Membracidae), and its associated ant fauna on *Didymopanax vinosum* (Araliaceae)," *Biotropica*, vol. 31, no. 1, pp. 135–144, 1999.

[44] H. C. P. Silveira, P. S. Oliveira, and J. R. Trigo, "Attracting predators without falling prey: chemical camouflage protects honeydew-producing treehoppers from ant predation," *American Naturalist*, vol. 175, no. 2, pp. 261–268, 2010.

[45] C. V. A. Dansa, *Estratégia de forrageamento de pseudomyrmex gracilis (Fabr.) (Hymenoptera, Formicidae)*, M.S. thesis, Universidade Estadual de Campinas, Campinas, Brazil, 1989.

[46] H. G. Fowler, L. C. Forti, C. R. F. Brandão, J. H. C. Delabie, and H. L. Vasconcelos, "Ecologia nutricional de formigas," in *Ecologia Nutricional de Insetos e Suas Implicações no Manejo de Pragas*, A. R. Panizzians and J. R. P. Parra, Eds., pp. 131–223, Editora Manole e CNPq, São Paulo, Brazil, 1991.

[47] M. A. S. De La Fuente and R. J. Marquis, "The role of ant-tended extrafloral nectaries in the protection and benefit of a neotropical rainforest tree," *Oecologia*, vol. 118, no. 2, pp. 192–202, 1999.

[48] R. Cogni, A. V. L. Freitas, and P. S. Oliveira, "Interhabitat differences in ant activity on plant foliage: ants at extrafloral nectaries of Hibiscus pernambucensis in sandy and mangrove forests," *Entomologia Experimentalis et Applicata*, vol. 107, no. 2, pp. 125–131, 2003.

[49] A. D. Gove, J. D. Majer, and V. Rico-Gray, "Ant assemblages in isolated trees are more sensitive to species loss and replacement than their woodland counterparts," *Basic and Applied Ecology*, vol. 10, no. 2, pp. 187–195, 2009.

[50] F. S. Neves, R. F. Braga, M. M. Do EspíritoSanto, J. H. C. Delabie, G. W. Fernandes, and G. A. Sánchez-Azofeifa, "Diversity of arboreal ants in a brazilian tropical dry forest: effects of seasonality and successional stage," *Sociobiology*, vol. 56, no. 1, pp. 177–194, 2010.

[51] G. D. Weiblen, C. O. Webb, V. Novotny, Y. Basset, and S. E. Miller, "Phylogenetic dispersion of host use in a tropical insect herbivore community," *Ecology*, vol. 87, no. 7, pp. 62–75, 2006.

[52] H. C. Morais, E. R. Sujii, M. Almeida-Neto, P. S. de Carvalho, J. D. V. Hay, and I. R. Diniz, "Host plant specialization and species turnover of caterpillars among hosts in the Brazilian Cerrado," *Biotropica*, vol. 43, no. 4, pp. 467–472, 2011.

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 393486, 6 pages
doi:10.1155/2012/393486

Research Article

Poneromorph Ants Associated with Parasitoid Wasps of the Genus *Kapala* Cameron (Hymenoptera: Eucharitidae) in French Guiana

Jean-Paul Lachaud,[1, 2] Philippe Cerdan,[3] and Gabriela Pérez-Lachaud[2]

[1] *Centre de Recherches sur la Cognition Animale, CNRS-UMR 5169, Université de Toulouse UPS, 118 Route de Narbonne, 31062 Toulouse Cedex 09, France*
[2] *El Colegio de la Frontera Sur, Entomología Tropical, Avenida Centenario km 5.5, Chetumal 77014, Quintana Roo, Mexico*
[3] *Laboratoire Environnement de Petit Saut (HYDRECO), BP 823-97388 Kourou Cedex, France*

Correspondence should be addressed to Jean-Paul Lachaud, jlachaud@ecosur.mx

Received 13 June 2011; Accepted 17 July 2011

Academic Editor: Jacques H. C. Delabie

Eucharitid wasps are specific, specialized parasitoids of ants. The genus *Kapala* Cameron is the most common in the Neotropics but few species are described, and information dealing with their biology, behavior and host associations is scarce. Numerous poneromorph ant colonies were inspected over 4 collection surveys in French Guiana. A diverse fauna of parasites and parasitoids was found, including mermithid nematodes, flies, eucharitids, and another gregarious endoparasitoid wasp. Five new host associations for *Kapala* are reported, all of them involving medium- to large-size poneromorph ant species from 4 genera: *Ectatomma brunneum* Fr. Smith, *Gnamptogenys tortuolosa* (Fr. Smith), *Odontomachus haematodus* (L.), *O. mayi Mann*, and *Pachycondyla verenae* (Forel). Three other associations involving *O. hastatus* (Fabr.), *P. apicalis* (Latreille), and *P. stigma* (Fabr.), already reported for other countries but new for French Guiana, are confirmed. The data extend the number of hosts for *Kapala* to 24 ant species from 7 genera. The high diversity of the ant host genera associated with *Kapala,* combined with the fact that these ant genera are the most widely distributed among Neotropical poneromorph ants, could account for the dominant status of the genus *Kapala* among the eucharitine wasps of Central and South America.

1. Introduction

Within Hymenoptera, the family Eucharitidae (subdivided in three subfamilies: Oraseminae, Eucharitinae, and the Indo-Pacific Gollumiellinae) is the most numerous and diverse group of ant parasitoids [1, 2]. All of the members of this family have a highly modified life cycle [3–6]. Unlike most parasitic wasp species, eucharitid females deposit their eggs away from hosts, in or on plant tissue [2, 7]. The active first-instar larva, termed planidium, is responsible for gaining access to the host ant larvae by using various phoretic behaviors including either attachment to an intermediate host (most often a potential ant prey) or to foraging ant workers, with on occasion the presence of attractive substances in or on the eggs [2, 8]. Within the nest, planidia attach themselves to ant larvae, but development is only completed when the host pupates [6, 7, 9, 10]. In almost all of the cases, adults emerge among ant brood (but see [11]) and have to leave the host nest to reproduce. Ants show only moderate aggression to newly emerged eucharitids [7, 12–17] and transport them outside as if they were refuse [11, 15, 17], ultimately enhancing wasp dispersal. Parasitism is very variable and localized in time and space [13, 18, 19]. A very high local prevalence may lead to only a very low impact at the regional scale, suggesting that these parasitoids do not have a major influence on the dynamics of their host population [19]. However, they constitute a remarkable example of both host-parasitoid coevolution and host behavior manipulation.

The eucharitine genus *Kapala* Cameron is widespread in the New World, with only one species, *K. ivorensis* Risbec, found in the Old World (Ethiopian region and Malagasy). This is one of the eucharitid genera most commonly collected by traps and aerial nets in the Neotropical region [1].

However, taxonomic and systematic studies of the species belonging to this genus have proved difficult because of the high degree of morphological variability both within and among species [20]. Only 17 species have been described up to now, but more than 60 are estimated to exist [1, 10]. This genus is presently under revision (E. Murray and J. M. Heraty, pers. comm). Information dealing with the biology, ecology, and behavior of *Kapala* wasps is still very scarce (but see [10, 16, 18]), even though the number of known associations with ant hosts significantly increased in the past ten years. To date, all of the ant species which have been recorded as reliable hosts for the genus *Kapala* apply to medium to large poneromorph ant genera belonging to two subfamilies: Ponerinae and Ectatomminae [1, 4, 11, 21–24]. As all of the ant larvae attacked by *Kapala* pupate inside a protective cocoon, immature stages of the parasitoids are not easily spotted unless under close scrutiny. Furthermore, accurate host records can only be obtained by direct rearing of the parasitoids from ant brood and need laborious target sampling and collection. This could explain in part why so few associations have been reported before the late 90s. Here we both summarize the results of several collection surveys in French Guiana aimed to contribute to the knowledge of the diversity and distribution of the *Kapala* species in the Neotropics and provide a comprehensive review of ant-host associations for this highly variable genus.

2. Materials and Methods

Several dozen colonies (or portions of colonies) of poneromorph ants were collected in French Guiana, during 4 extensive surveys between 2002 and 2010. Collecting surveys were performed during both dry and rainy seasons and at several biotopes, mainly lowland rainforest fragments but also second growth vegetation. Ants were collected from several forest fragments along the road leading to the Hydroelectric complex at Petit Saut, Sinnamary (5 03 39 N; 53 02 36 W). Samples were obtained by systematically breaking up all of the fallen rotten logs found on the ground or were visually detected in the case of tree-inhabiting ants. Colonies of *Ectatomma brunneum* Fr. Smith were common in a ruderal area running along Route No. 1 from Kourou to Sinnamary (kilometric point 101) and were collected from the soil by excavation. Complete colonies or significant parts of colonies containing cocoons and larvae were taken to the laboratory. Most ants were identified to species level with available keys. Nest composition (presence and number of dealate females, alate females, males, workers, cocoons, and larvae), including the presence of adult eucharitids, was determined, and all of the pupae (cocoons) were dissected under a stereomicroscope and checked for the presence of eucharitids or for evidence of their attack. In particular, we looked both for wasp remains (exuvia) within empty ant cocoons denoting previous eucharitid emergence and for the presence of any abnormal pupa (phthisergate, phthisogyne, or phthisaner, according to the caste) indicating an unsuccessful eucharitid attack [12]. Larvae were also checked for the presence of planidia attached to their cuticle or for the presence of round melanized scars, an evidence of the previous attachment of a planidium [19]. Voucher specimens of ants were deposited in the Arthropod Collection at El Colegio de la Frontera Sur-Chetumal. Eucharitid specimens were sent to the specialist of this group, Dr. John M. Heraty (UCR).

3. Results

A total of 161 complete colonies of poneromorph ants or colony fragments with pupae, representing 26 species from 3 subfamilies, were collected and their contents examined (Table 1). No evidence of eucharitid attack to larvae was found for any of the poneromorph ant species examined, but several species of *Kapala* were found parasitizing the pupae of 8 different ant species. Of these, 5 represent new host associations (Table 1): one for the genus *Ectatomma* Fr. Smith (*E. brunneum* Fr. Smith), one for the genus *Gnamptogenys* Roger (*G. tortuolosa* (Fr. Smith)), and two for the genus *Odontomachus* Latreille (*O. haematodus* (L.), *O. mayi* Mann). The fifth new host record involves the genus *Pachycondyla* Fr. Smith and concerns a *P. verenae* (Forel) colony which was collected by Ronara de Souza Ferreira in the Southwestern part of French Guiana, at Camp Patawa, about 40 km from Roura in the direction of Raw. In addition, the host status of *O. hastatus* (Fabr.)—already reported for Ecuador [1]—and of *P. stigma* (Fabr.) and *P. apicalis* (Latreille)—already reported for Mexico [10, 22, 24]— were confirmed, and this constitutes the first report for French Guiana.

Due to the very reduced number of sampled nests for *O. mayi* and *P. apicalis*, percent parasitism figures (number of infested nests/number of revised nests) for these species are given only as indicative of eucharitid attack. For those species where a significant number of nests could be revised, prevalence of parasitism was generally low to medium (from 14.3% for *P. stigma* to 27.3% for *G. tortuolosa*) but reached up to 50% in the case of *O. hastatus*. However, parasitism rate within parasitized colonies was very low for all of the species, and only few eucharitid specimens were retrieved (Table 1).

Apart from eucharitids, some other parasites were found attacking ant colonies. Pupae of *P. goeldii* (Forel) were parasitized by a gregarious endoparasitoid wasp, and those of *P. commutata* (Roger) and *Paraponera clavata* (Fabr.) were parasitized by two gregarious dipteran species. Finally, a mermithized worker was found in a *P. stigma* colony, and this constitutes the first report of mermithid nematode parasitization for this species. In the absence of any post-parasitic juvenile, the mermithid species identification was not possible. Voucher specimens of both the ants and the mermithid nematode were deposited in the authors' collection.

4. Discussion

A diverse fauna of parasites and parasitoids attacked the different poneromorph ant species present in French Guiana near Petit Saut, including nematodes, flies, a gregarious

Table 1: Poneromorph ants of French Guiana and parasitism by *Kapala*. Ant species revised (n = number of nests containing pupae), presence of eucharitid wasps, parasitism rate by eucharitids (in %), and number and developmental stage of specimens of Eucharitidae retrieved (F: female; M: male; A: adult, damaged specimen; Lif: first-instar larva feeding on host; Lf: last-instar larva; Pht.: phthisergate; Ex.: presence of eucharitid exuvia within an empty cocoon).

Ant species	Parasites and parasitoids
Ectatomminae	
Ectatomma brunneum (n = 46)	*Kapala* sp. (21.7%): 7 F, 1 M, 1 A, 2 Lif, 1 Pht., 1 Ex.
Gnamptogenys pleurodon (n = 5)	—
Gnamptogenys tortuolosa (n = 11)	*Kapala* sp. (27.3%): 1 F, 1 Lf, 1 Lif, 1 Pht.
Gnamptogenys sp. (n = 1)	—
Ponerinae	
Anochetus sp. 1 (n = 1)	—
Anochetus sp. 2 (n = 3)	—
Centromyrmex sp. (n = 1)	—
Hypoponera sp. 1 (n = 4)	—
Hypoponera sp. 2 (n = 1)	—
Leptogenys sp. 1 (n = 2)	—
Leptogenys sp. 2 (n = 1)	—
Odontomachus haematodus (n = 20)	*Kapala* sp. (15.0%): 1 F, 3 M, 1 Pht.
Odontomachus hastatus (n = 6)	*Kapala* sp. (50.0%): 2 F, 1 M, 2 Lf, 1 Lif
Odontomachus mayi (n = 2)	*Kapala* sp. (50.0%): 1 F
Odontomachus sp. 1 (n = 1)	—
Pachycondyla apicalis (n = 2)	*Kapala* sp. (50.0%): 1 F, 2 M, 1 Ex.
Pachycondyla commutata (n = 2)	—(a)
Pachycondyla constricta (n = 6)	—
Pachycondyla crenata (n = 1)	—
Pachycondyla goeldii (n = 2)	—(b)
Pachycondyla harpax (n = 6)	—
Pachycondyla obscuricornis (n = 3)	—
Pachycondyla stigma (n = 21)	*Kapala* sp. (14.3%)(c): 1 F, 1 M, 1 Lif
Pachycondyla verenae (n = 6)	*Kapala* sp. (16.7%): 1 M
Platythyrea sinuata (n = 6)	—
Paraponerinae	
Paraponera clavata (n = 1)	—(a)

(a) Presence of dipteran parasitoids;
(b) Presence of unidentified, gregarious parasitoid wasps;
(c) Presence of a mermithid nematode.

endoparasitoid wasp, and, above all, eucharitids. Several authors have recorded the presence of eucharitids in ant nests, but the information is scattered in the literature and concerns only few ant species. Neotropical eucharitine wasps are represented by approximately 160 species from 16 genera [1], but information on the host plant(s) used for oviposition is extremely scarce, and the identity of the ant host has been clearly established for only a few species belonging to 5 genera (*Dilocantha* Shipp, *Isomerala* Cameron, *Kapala* Cameron, *Obeza* Heraty, and *Pseudochalcura* Ashmead). These ant hosts concern exclusively formicine, ponerine, and ectatommine ants, whose larvae pupate inside a protective cocoon.

With about 60 estimated species, the genus *Kapala* is by far the most diverse and dominant eucharitine genus of Central and South America [1]. All of the hosts reported until now for this genus belong to 7 genera of ectatommine and ponerine ants (Table 2). Only *K. floridana* (Ashmead) has been reported associated with a host from another subfamily, the myrmicine ant *Pogonomyrmex badius* (Latreille) (according to Ashmead, in [12]), but, considering that *Pogonomyrmex* larvae do not spin a cocoon, such an association seems very doubtful [1, 10]. Even if the presence of an undetermined species of eucharitid was already signaled for *Gnamptogenys annulata* (Mayr) and also for *G. horni* (Santschi) in Venezuela [26], and, very likely concerned a *Kapala* species, reliable associations between the genus *Kapala* and the ant genera *Ectatomma* and *Gnamptogenys* have previously been reported only for Mexico [10, 22] and for Colombia [25]. The new associations with these two ectatommine genera reported here for French Guiana, as well as the new associations or confirmations of record for the ponerine genera *Odontomachus* and *Pachycondyla*, support the outstanding importance of these four genera

Table 2: Known ant host species associated with the eucharitid genus *Kapala*.

Host species	Associated *Kapala* species
Ectatomminae	
Ectatomma Fr. Smith	
E. brunneum Fr. Smith	*Kapala* sp. [this work]
E. ruidum Roger	*K. iridicolor* (Cameron) [10, 18, 25], [16, 22] , *K. izapa* Carmichael [10, 18]
E. tuberculatum (Olivier)	*Kapala* sp. [23]
Gnamptogenys Roger	
G. regularis Mayr	*K. iridicolor* (Cameron) [10], [22]
G. striatula Mayr	*K. iridicolor* (Cameron) [10], [22]
G. sulcata (Fr. Smith)	*K. iridicolor* (Cameron) [10], [22] , *Kapala* sp. [24]
G. tortuolosa (Fr. Smith)	*Kapala* sp. [this work]
Typhlomyrmex Mayr	
T. rogenhoferi Mayr	*Kapala* sp. [24]
Ponerinae	
Dinoponera Roger	
D. lucida Emery	*Kapala* sp. [11]
Hypoponera Santschi	
H. nitidula (Emery)	*Kapala* sp. [24]
Odontomachus Latreille	
O. bauri Emery	*Kapala* sp. [1]
O. brunneus (Patton)	*Kapala* sp. [10, 22]
O. haematodus (L.)	*Kapala* sp. [this work]
O. hastatus (Fabr.)	*Kapala* sp. [1], [this work]
O. insularis Guérin-Méneville	*K. terminalis* Ashmead [4]
O. laticeps Roger	*Kapala* sp. [10, 22, 24]
O. mayi Mann	*Kapala* sp. [this work]
O. meinerti Forel	*Kapala* sp. [24]
O. opaciventris Forel	*Kapala* sp. [10, 22]
Pachycondyla Fr. Smith	
P. apicalis (Latreille)	*Kapala* sp. [22, 24], [this work]
P. crassinoda (Latreille)	*K. cuprea* Cameron [21]
P. harpax (Fabr.)	*K. atrata* (Walker) [1] , *Kapala* sp. [24]
P. stigma (Fabr.)	*K. iridicolor* (Cameron) [10], [22] , *Kapala* sp. [24], [this work]
P. verenae (Forel)	*Kapala* sp. [this work]
Myrmicinae	
Pogonomyrmex Mayr	
P. badius (Latreille)	*K. floridana* (Ashmead) [12] (doubtful record) [1, 10]

Referred to as *Kapala sulcifacies*;
Referred to as *Kapala* sp.;
Referred to as *Kapala surgens*.

of medium- to large-size poneromorph ants as potential hosts for *Kapala* wasps, a hypothesis previously formulated on the basis of more limited data [10, 22]. In contrast with other eucharitid genera which have a limited range of potential hosts and a marked specificity towards the host as far as genus is concerned [4–6], the diversity of host genera and species attacked by *Kapala* is impressive. The data reported here for French Guiana extend the number of reliable host species for *Kapala* to 24 (see Table 2), a diversity of host species only comparable to that found for the worldwide distributed orasemine genus *Orasema* Cameron [1, 6]. Such a broad range of potential hosts for *Kapala* is also observed at the species level. For example, *K. iridicolor* (Cameron) (Table 2) parasitizes no less than five different species from three genera and two ant subfamilies [10, 22], and a similar phenomenon is likely to concern also some of the other species reported here as undescribed under the label "*Kapala* sp.". Furthermore, *Kapala* species are known to parasitize ants in very diverse habitats including both highly anthropic modified environments (roadsides, college campus, agroecosystems, pastures) and well-preserved forests [1, 10, 22, 24, 25], [this work]. Combined with the fact that *Ectatomma*, *Gnamptogenys*, *Odontomachus,* and *Pachycondyla* are probably the four most widely distributed genera among the Neotropical poneromorph ants [27–29], the wide host range of *Kapala* species and their ability to attack ants in diverse habitats could account, at least in part, for the dominant status of this genus among the eucharitine wasps of Central and South America. Moreover, though the sampling of ant nests in general is not really adequate to confidently discuss rates of parasitism, for four species (*E. brunneum*, *G. tortuolosa*, *O. haematodus*, and *P. stigma*), the number of collected nests is significant enough (see [18, 19] for a comparison) to give a good idea of the rates of parasitism at the population level. The rate of parasitism is low to medium (from 14.3% to 27.3%, see Table 1) in all of these four cases, but for certain associations, parasitism rate can reach significant values. Half of the nests were parasitized in the case of the association *Kapala* sp. and *O. hastatus* in French Guiana [this work] (but our sample limitation—only 6 nests—could result, in this specific case, in rates of parasitism relatively far from the natural figures) and up to 63% of the nests for the association between *K. iridicolor*/*K. izapa* (Carmichael) and *E. ruidum* Roger in Mexico [18]. Such high parasitism rates certainly contribute to explain why *Kapala* is one of the eucharitid genera most commonly collected by traps and aerial nets in the Neotropical region [1].

All of the eucharitids are parasitoids of ants, but the exact relationship between these wasps and their host is far from being understood, and the scenario might be more complicated than once thought. For example, from the 17 species already described in the genus *Kapala*, the complete life cycle is known for only one of them, *K. iridicolor* [10]. However, even for this species, the way planidia manage to enter ant nests is unknown. Instead of a direct attachment to a foraging ant worker, some *Kapala* planidia have been recently reported attached to different species of scorpions, suggesting the use of alternative phoretic transport [30]. However, such occasional phoretic attachments to scorpions more likely correspond to random attachment to any nearby living object and likely have nothing to do with getting into the ant nest. They would just give evidence in favour of the high mobility of the planidia. Eucharitids are known to attack five subfamilies of ants, and a correlation between the phylogenetic relationships of the parasitoid and host is suggested by both morphological and molecular evidence ([1], E. Murray and J. M. Heraty unpubl. data). Additional information about ant hosts and within-nest biology as well as about oviposition habits throughout the geographical range of *Kapala* is critical for further resolving the limits and phylogenetic relationships of the species of this genus.

Acknowledgments

The authors thank all the team of the Laboratoire Environnement de Petit Saut (HYDRECO) for logistical help and for assistance with local accommodation. They also thank Alain Dejean and Jérôme Orivel (ECOFOG, French Guiana) for their help in ant identification and Sandor Buys and an anonymous refeere for helpful advices and useful suggestions on the paper. Ronara de Souza Ferreira kindly provided material from *P. verenae*. This research was partially supported by a grant from the French Ministère de l'Écologie et du Développement Durable (Program "Recherche de procédés limitant l'activité de fourmis tropicales d'importance écologique et économique"). The experiments comply with the current laws of the country in which they were performed.

References

[1] J. M. Heraty, "A revision of the genera of Eucharitidae (Hymenoptera: Chalcidoidea) of the World," *Memoirs of the American Entomological Institute*, vol. 68, pp. 1–367, 2002.

[2] J. M. Heraty, D. Hawks, J. S. Kostecki, and A. Carmichael, "Phylogeny and behaviour of the Gollumiellinae, a new subfamily of the ant-parasitic Eucharitidae (Hymenoptera: Chalcidoidea)," *Systematic Entomology*, vol. 29, no. 4, pp. 544–559, 2004.

[3] C. P. Clausen, "The biology of *Schizaspidia tenuicornis* Ashm., a eucharid parasite of *Camponotus*," *Annals of the Entomological Society of America*, vol. 16, pp. 195–217, 1923.

[4] C. P. Clausen, "The habits of the Eucharidae," *Psyche*, vol. 48, pp. 57–69, 1941.

[5] G. C. Wheeler and E. W. Wheeler, "New hymenopterous parasites of ants (Chalcidoidea: Eucharidae)," *Annals of the Entomological Society of America*, vol. 30, pp. 163–175, 1937.

[6] J. M. Heraty, "Classification and evolution of the Oraseminae in the Old World, with revisions of two closely related genera of Eucharitinae (Hymenoptera: Eucharitidae)," *Life Sciences Contributions, Royal Ontario Museum*, vol. 157, pp. 1–176, 1994.

[7] C. P. Clausen, "The oviposition habits of the Eucharidae (Hymenoptera)," *Journal of the Washington Academy of Sciences*, vol. 30, pp. 504–516, 1940.

[8] J. M. Heraty and K. N. Barber, "Biology of *Obeza floridana* (Ashmead) and *Pseudochalcura gibbosa* (Provancher) (Hymenoptera: Eucharitidae)," *Proceedings of the Entomological Society of Washington*, vol. 92, pp. 248–258, 1990.

[9] J. M. Heraty, "Phylogenetic relationships of Oraseminae (Hymenoptera: Eucharitidae)," *Annals of the Entomological Society of America*, vol. 93, no. 3, pp. 374–390, 2000.

[10] G. Pérez-Lachaud, J. M. Heraty, A. Carmichael, and J.-P. Lachaud, "Biology and behavior of *Kapala* (Hymenoptera: Eucharitidae) attacking *Ectatomma, Gnamptogenys*, and *Pachycondyla* (Formicidae: Ectatomminae and Ponerinae) in Chiapas, Mexico," *Annals of the Entomological Society of America*, vol. 99, no. 3, pp. 567–576, 2006.

[11] S. C. Buys, R. Cassaro, and D. Salomon, "Biological observations on *Kapala* Cameron 1884 (Hymenoptera Eucharitidae) in parasitic association with *Dinoponera lucida* Emery 1901 (Hymenoptera Formicidae) in Brazil," *Tropical Zoology*, vol. 23, no. 1, pp. 29–34, 2010.

[12] W. M. Wheeler, "The polymorphism of ants, with an account of some singular abnormalities due to parasitism," *Bulletin of the American Museum of Natural History*, vol. 23, pp. 1–93, 1907.

[13] G. L. Ayre, "*Pseudometagea schwarzii* (Ashm.) (Eucharitidae: Hymenoptera), a parasite of *Lasius neoniger* Emery (Formicidae: Hymenoptera)," *The Canadian Journal of Zoology*, vol. 40, pp. 157–164, 1962.

[14] R. K. Vander Meer, D. P. Jouvenaz, and D. P. Wojcik, "Chemical mimicry in a parasitoid (Hymenoptera: Eucharitidae) of

fire ants (Hymenoptera: Formicidae)," *Journal of Chemical Ecology*, vol. 15, no. 8, pp. 2247–2261, 1989.

[15] J.-P. Lachaud, G. Pérez-Lachaud, and J. M. Heraty, "Parasites associated with the ponerine ant *Ectatomma tuberculatum* (Hymenoptera: Formicidae): first host record for the genus *Dilocantha* (Hymenoptera: Eucharitidae)," *The Florida Entomologist*, vol. 81, no. 4, pp. 570–574, 1998.

[16] R. W. Howard, G. Pérez-Lachaud, and J.-P. Lachaud, "Cuticular hydrocarbons of *Kapala sulcifacies* (Hymenoptera: Eucharitidae) and its host, the ponerine ant *Ectatomma ruidum* (Hymenoptera: Formicidae)," *Annals of the Entomological Society of America*, vol. 94, no. 5, pp. 707–716, 2001.

[17] G. Pérez-Lachaud and J.-P. Lachaud, "Comportement de transport de parasitoïdes Eucharitidae par leur hôte: mimétisme chimique et effet de la taille de l'objet à transporter," in *Proceedings of the Colloque Annuel de la Section Française de l'UIEIS*, p. 32, Toulouse, France, 2007.

[18] J.-P. Lachaud and G. Pérez-Lachaud, "Impact of natural parasitism by two eucharitid wasps on a potential biocontrol agent ant in southeastern Mexico," *Biological Control*, vol. 48, no. 1, pp. 92–99, 2009.

[19] G. Pérez-Lachaud, J. A. López-Méndez, G. Beugnon, P. Winterton, and J.-P. Lachaud, "High prevalence but relatively low impact of two eucharitid parasitoids attacking the Neotropical ant *Ectatomma tuberculatum* (Olivier)," *Biological Control*, vol. 52, no. 2, pp. 131–139, 2010.

[20] J. M. Heraty and J. B. Woolley, "Separate species or polymorphism: a recurring problem in *Kapala* (Hymenoptera: Eucharitidae)," *Annals of the Entomological Society of America*, vol. 86, pp. 517–531, 1993.

[21] J. G. Myers, "Descriptions and records of parasitic Hymenoptera from British Guiana and the West Indies," *Bulletin of Entomological Research*, vol. 22, pp. 267–277, 1931.

[22] J.-P. Lachaud and G. Pérez-Lachaud, "Fourmis ponérines associées aux parasitoïdes du genre *Kapala* Cameron (Hymenoptera, Eucharitidae)," *Actes des Colloques Insectes Sociaux*, vol. 14, pp. 101–105, 2001.

[23] G. Pérez-Lachaud, J. A. López-Méndez, and J.-P. Lachaud, "Eucharitid parasitism of the Neotropical ant *Ectatomma tuberculatum*: parasitoid co-occurrence, seasonal variation, and multiparasitism," *Biotropica*, vol. 38, pp. 574–576, 2006.

[24] A. De la Mora and S. M. Philpott, "Wood-nesting ants and their parasites in forests and coffee agroecosystems," *Environmental Entomology*, vol. 39, no. 5, pp. 1473–1481, 2010.

[25] A. A. Vásquez Ordóñez, *Parasitismo de Kapala iridicolor (Hymenoptera: Eucharitidae) sobre Ectatomma ruidum (Hymenoptera: Formicidae) en el Campus Meléndez de la Universidad del Valle, Cali, Colombia*, Tesis de Licenciatura, Universidad del Valle, Santiago de Cali, Colombia, 2010.

[26] J. E. Lattke, "Revisión del género *Gnamptogenys* Roger en Venezuela," *Acta Terramaris*, vol. 2, pp. 1–47, 1990.

[27] B. Hölldobler and E. O. Wilson, *The Ants*, Springer, Berlin, Germany, 1990.

[28] B. Bolton, *Identification Guide to the Ant Genera of the World*, Harvard University Press, Cambridge, Mass, USA, 1994.

[29] B. Bolton, "Synopsis and classification of Formicidae," *Memoirs of the American Entomological Institute*, vol. 71, pp. 1–370, 2003.

[30] L. F. de Armas, "Identity of planidium larvae (Hymenoptera: Chalcidoidea) previously recorded on Antillean scorpions," *Euscorpius*, vol. 66, pp. 1–3, 2008.

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 609106, 8 pages
doi:10.1155/2012/609106

Research Article

Evidence of Competition Between Two Canopy Ant Species: Is Aggressive Behavior Innate or Shaped by a Competitive Environment?

Nádia Barbosa do Espírito Santo,[1,2] Sérvio Pontes Ribeiro,[3] and Juliane Floriano Santos Lopes[1]

[1] *Programa de Pós-Graduação em Comportamento e Biologia Animal, Universidade Federal de Juiz de Fora, Campus Universitário Martelos, 36036-330 Juiz de Fora, MG, Brazil*
[2] *Programa de Pós-Graduação em Ecologia, Universidade Estadual de Campinas, 13083-970 Campinas, SP, Brazil*
[3] *Departamento de Biodiversidade, Evolução e Meio Ambiente, Programa de Pós-Graduação em Ecologia de Biomas Tropicais, Universidade Federal de Ouro Preto, Campus Morro do Cruzeiro, 35400-000 Ouro Preto, MG, Brazil*

Correspondence should be addressed to Nádia Barbosa do Espírito Santo, nadiabarbosa@yahoo.com.br

Received 1 June 2011; Accepted 4 July 2011

Academic Editor: Jonathan D. Majer

Competition occurs in all ecological communities, although it has not always been experimentally tested as a structuring force in the distribution of species. We tested the hypothesis that the aggressiveness exhibited by *Camponotus rufipes* changes according to the pressures of a competitive environment. This is a dominant species in the montane forest of the Itacolomi State Park, Brazil, where *Camponotus sericeiventris* does not occur. Using bait traps in a field site where both species occur, ("Juiz de Fora" site) we showed that *C. sericeiventris* was able to remove *C. rufipes* workers at the same bait. In the laboratory, we used dyadic encounters to test workers from both species taken from colonies found in areas where both occur and where only *C. rufipes* was found. *Camponotus rufipes* from Itacolomi fought significantly less and was killed during the first few minutes in 60% of the events. On the other hand, the workers that co-existed with *C. sericeiventris* in the field were more aggressive, but less efficient fighters than the latter. This investigation demonstrated existence of competition between *C. rufipes* and *C. sericeiventris*, and also the lower aggressiveness of *C. rufipes*' individuals that did not co-exist in the field with *C. sericeiventris*.

1. Introduction

The importance of competition for structuring ecological communities is a matter for debate, and it has been extensively researched in ant assemblages [1]. Exploitation and interference competition in ants involve mutual aggression, which can frequently be observed, often resulting in injuries, death, and the avoidance of one colony by another [1]. The more similar are the species' morphology and niche breadths, the stronger is the competition [2, 3]. Species coexistence is possible when there are diversified strategies for resource usage, namely, time partitioning, feeding-source differentiation, or nesting locations [1, 3]. On the other hand, competition causes hierarchical dominance amongst the species through the use of aggression, food source exclusion, and different foraging strategies [4, 5]. Dominant ant species can influence the occurrence of other species and play a major role in ant assemblage structuring, in which they generate distribution patterns and a mosaic-like species coexistence, especially in forest canopies [6–9].

Territorial defence is related to dominance and occurs widely among canopy ant species in tropical rainforests [5]. Here, we observe the occurrence of a hierarchical competition that is based on their social organization and, ultimately, on foraging workers density. Hence, when a nonterritorial species encounter a territorial one, the former tends to run way from aggressive conflict, which may result in locally improbable species pairs [10, 11].

Camponotus (Myrmothrix) rufipes (Fabricius, 1775) is normally associated with ecotones between forests and open vegetation and is rarely found in great quantities in the canopy of lowland forests [12–18]. However, in the State Park of Itacolomi, a montane forest ecosystem in the borders between the Brazilian Cerrado and the Atlantic rainforest, this species is the most frequent member of this genus in the canopy [18]. In this particular forest the potential competitor, *Camponotus (Myrmepomis) sericeiventris* (Guérin-Menéville, 1838), which has a similar body size and uses the same kinds of food and nesting sites, was absent, unlike in the other areas of Atlantic rainforest and in most other Neotropical arboreal ecosystems [19]. On the contrary of *C. rufipes*, the latter is mostly frequent and dominant in the upper canopy [19, 20].

The present work investigates the degree of *C. rufipes* aggressiveness in contrasting competitive environments by means of direct observation in field and laboratory. We tested the hypothesis that *C. rufipes* shows different behaviours depending on the nature of the competitive environment. The prediction is that levels of aggressiveness of *C. rufipes* vary in response to presence or absence of competition from *C. sericeiventris*.

2. Methods

2.1. Field Experiments. Observations were carried out at two locations in the Atlantic rainforest. The first was Itacolomi State Park (Itacolomi), Minas Gerais State (20 22 30 S and 43 32 30 W), between 1000–1300 metres above sea level, within an area of 7.543 hectares, and belonging to the Espinhaço Mountain Range, which has a tropical montane climate, with rainfall varying from 1000 to 1500 mm per year and the temperatures between 4 C and 33 C [21]; The second was the campus of the Federal University of Juiz de Fora (UFJF) (21 46 47 S and 43 22 24 W), at 818 metres above sea level, also with a well-defined rainy and dry seasons, an annual average temperature of 19.3 C, and a annual precipitation of 1500 mm [22]. Both species, *C. rufipes* and *C. sericeiventris*, were encountered at the UFJF campus, but only *C. rufipes* was found in Itacolomi.

At Itacolomi, three trees were selected because of the high foraging activity of previously observed *C. rufipes* ants [18]. At the UFJF Campus, three trees were also selected in a territorial border where both *C. rufipes* and *C. sericeiventris* coexisted: in two of the trees there was an intense foraging by *C. rufipes* ants, due to the existence of nests closer than 10 metres to their trunk; in the third, there was a *C. sericeiventris* nest. The experiments were conducted during the months of October and November 2007.

Observations were made on one tree per day, thus in 3 days all trees were observed. Afterwards, two new rounds of observations, following the same order, were executed. Hence, in 9 days all trees were observed three times, with 2 days intervals between each observation. As the experiment was conducted within a short and continuous time interval, no relevant change in weather conditions was noticed. On the trunks of each of these trees a paper towel with attractant bait made of sardines (10 g) and honey (1 : 1; g : g) was placed. The behavioural recordings started with the arrival of the first *C. rufipes* ant in Itacolomi, whereas at the UFJF Campus it started when the first *C. rufipes* or *C. sericeiventris* appeared. From that moment on, we used the sequential sampling method [23]. For 4 hours, during five minutes at 10-minute intervals, all ant behaviours were recorded. These recordings include not only the behaviour of the two species in focus but also that of all the other species that appeared. Hence, this experiment was composed of six behavioural recordings per tree, constituting 18 repetitions, that provided 288 records. The observed behavioural acts were then divided into three categories: action, reaction, and nonaggressive.

Access to the tree crowns was achieved by tree-trunk climbing, either with or without a rope, and using safety equipment (see Ribeiro et al. [24]). Contingency tables were created to analyse species superiority in aggressiveness for both action and reaction types of behaviour. The analyses were done using Chi-square at a 5% significance level.

2.2. Laboratory Experiments. Experimental dyadic encounters were manipulated between *C. rufipes* and *C. sericeiventris* workers from different colonies collected in both Itacolomi and UFJF. Approximately 70 workers of *C. rufipes* from an Itacolomi colony were collected. Meanwhile, 50 workers of this species, along with 50 workers of *C. sericeiventris*, were collected from UFJF in an area where they coexisted. These collected ants were kept in a lidded plastic containers (12 cm × 9 cm) with a cotton ball soaked in water-diluted honey and remained isolated (at 25 C and 70% humidity) for 24 hours before performing the experiment. During this period, the samples were exposed to similar stress of collecting and travelling, and subsequent resting in the laboratory. The resting period and the experiments took place at the Myrmecology Laboratory of UFJF during the months of December 2007 and January 2008.

At each dyadic encounter, two ants of the same caste were placed in an arena (6 cm diameter) with Fluon at the edges to prevent their escape. To relieve the stress of transferring, the ants were separated by a partition in the arena for 10 minutes. Afterwards, the partition was removed, and their behaviour was registered during 5 minutes (*ad libitum* [23]). The observed behavioural acts were divided into three categories: action, reaction, and nonaggressive.

We manipulated six types of encounters (Table 1) and each one was repeated 10 times. After each repetition, the experimental arena was cleaned with alcohol 50% to eliminate any ant odour, so as to not interfere with the results of the next repetition. For the repetitions involving ants of the same species, the individuals were marked on the pronotum with nontoxic ink using an Edding 750 pen [25].

Aggression was calculated according to a modified index of aggressiveness from Errard and Hefetz [26]. The assigned values represent degrees of aggressiveness: 0 = “touched antennae and retreated”, 1 = “on alert and charged”, 2 = “bite”, 3 = “torsioned gaster” and 4 = “fight”. The resulting index for each treatment was subjected to the Kruskall-Wallis test, followed by the post-hoc Student-Newman-Keuls test, at 5% significance level (Table 2), using Biostat 4.0 software. This study was performed under licence permission from

Table 1: Dyadic encounters occurring at the laboratory of the Federal University of Juiz de Fora (UFJF) for all treatments and species involved.

	Treatment	Species
1	Control *C. rufipes* Itacolomi	*C. rufipes* Itacolomi × *C. rufipes* Itacolomi
2	Control *C. rufipes* UFJF	*C. rufipes* UFJF × *C. rufipes* UFJF
3	Control *C. sericeiventris* UFJF	*C. sericeiventris* UFJF × *C. sericeiventris* UFJF
4	Neighbours	*C. rufipes* UFJF × *C. sericeiventris* UFJF
5	Same species	*C. rufipes* UFJF × *C. rufipes* Itacolomi
6	Different species	*C. rufipes* Itacolomi × *C. sericeiventris* UFJF

Itacolomi = Itacolomi State Park; UFJF = Campus of the Federal University of Juiz de Fora.

Table 2: Student-Newman-Keuls ($H = 77.1648$) comparisions for each treatment of dyadic encounters listed in Table 1 (significative P-values in evidence).

		1 Control *C. rufipes* Itacolomi	2 Control *C. rufipes* UFJF	3 Control *C. sericeiventris* UFJF	4 Neighbours	5 Same species	6 Different species
1	Control *C. rufipes* Itacolomi	—	**0.0031**	0.7043	**<0.0001**	**<0.0001**	0.4172
2	Control *C. rufipes* UFJF		—	**0.0008**	0.0344	0.0355	**0.0002**
3	Control *C. sericeiventris* UFJF			—	**<0.0001**	**<0.0001**	0.6659
4	Neighbours				—	0.9891	**<0.0001**
5	Same species					—	**<0.0001**
6	Different species						—

Itacolomi: Itacolomi State Park; UFJF: Campus of the Federal University of Juiz de Fora.

the State Forestry Institute, and it followed university's ethic requirements for experiments with alive animals.

3. Results

3.1. Field Experiments. Nine morphospecies of ants were registered in experiments conducted in the Itacolomi State Park and 12 in the UFJF Campus. Fourteen types of behaviours were registered with the bait. The behaviour exhibited by the ants is categorized and described in Table 3.

The most frequent behaviours for the ants in the two experimental sites were "quietly feeding" and "exploring the surroundings" (Table 4). When observing interactive behaviour in Itacolomi, *C. rufipes* was the species that most engaged in the aggressive actions of "charge" and "bite" ($\chi^2 = 88.3$, $P < 0.001$). *Myrmelachista* sp.1 was the one that most engaged the reactions of "flee" and "gaster torsion" ($\chi^2 = 15.65$, $P < 0.05$) (Figure 1). For all the other species together, only two registers were recorded for the "charge" behaviour, while the "avoid", "flee", and "retreat" were the most frequent ones ($\chi^2 = 15.65$, $P < 0.05$), suggesting that they were submissive to the aggressiveness of *C. rufipes*.

In UFJF campus, *C. rufipes* and *C. sericeiventris* frequently showed aggressive behaviour through the actions of "charge" and "bite" ($\chi^2 = 45.78$, $P < 0.05$) with no statistical difference between these species in terms of the amount of these acts performed ($\chi^2 = 3.43$, $P > 0.05$). All other morphospecies showed significantly more defensive behaviour, especially "retreat" and "flee" reactions ($\chi^2 = 18.9$, $P < 0.05$) (Figure 2).

When comparing behaviour of *C. rufipes* workers from the two sites, the UFJF individuals bit more than the Itacolomi individuals, which showed more of "avoid" aggressors act ($\chi^2 = 19.34$, $P < 0.05$) (Figure 3). Concerning reaction behaviours, the *C. rufipes* from the UFJF colony tended to "retreat", especially in the presence of *C. sericeiventris* ($\chi^2 = 23.9$, $P < 0.05$) (Figure 2).

3.2. Laboratory Experiments. Fifteen types of behaviours were registered in the laboratory, which are categorized and described in Table 3. According to the calculated aggressiveness index, the more aggressive encounters were between *C. rufipes* workers from the two areas and between *C. rufipes* from Itacolomi and *C. sericeiventris*, thus, between workers whose colonies are far apart from each other (Figure 4). Colony workers had an average agonistic response significantly larger than that observed between themselves in the control experiment (Table 2).

Considering the mortality at the encounters, we verified that 70% of *C. rufipes* workers were dead in less than 2

Table 3: Description of behavioral acts displayed by the ants on Itacolomi State Park (Itacolomi) and the Campus of Federal University of Juiz de Fora (UFJF) during field experiments ( ) and laboratory experiments (dyadic encounters) occurring at the lab of the Federal University of Juiz de Fora ( ).

Action	Reaction	Nonaggressive
Charge—an ant approaches the other with its mandible open	( ) Remain on the bait—after any types of the listed actions, the ant remains in the area, eating the bait	( ) Quietly eating—when an ant is standing still, only eating the bait
Bite—grips part of the body of another individual with its mandibles	( ) Flee—after any types of these actions it flees not only from the area, but also from the bait	( ) Food transport—the individual carries part of the bait to the colony
Espontaneous gaster torsion—the ant curls its abdomen to emits formic acid	( ) Retreat—after the mentioned actions, it retreats from the other individual, but does not leave the bait and eats it	Autogrooming—cleaning itself
Avoid—when perceiving the proximity of another individual, the first moves away, avoiding the encounter	Defensive gaster torsion—after these actions, it exhibits aggressive behaviour by curling its abdomen to emit formic acid	Trophallaxis—exchange of regurgitated liquid from one individual directly into the crop of the other
( ) Antennal touching—an ant exchanges antennal touches with the other for identification	Fight—after mentioned actions, it grabs the other individual with its jaws and emits formic acid	Exploring the surroundings—walking around, touching its antennae on the whole extension of the paper where the bait was placed
( ) On alert—an ant stands still with its head and antenna raised, and with its gaster torsed in the posterior-anterior position ready to emit formic acid, if necessary	( ) Bite—grips part of the body of another individual with its mandibles in response to any action act	( ) Trying to escape—the ant stays on the border of the arena, trying to climb its wall
	( ) Charge—the ant advances in the direction of the other with its mandible open ready to bite back	

( ) Only in lab experiments; ( ) Only in field experiments.

minutes (mostly in seconds) in the encounters between *C. rufipes* from Itacolomi and *C. sericeiventris.* (Kruskal-Wallis, Student-Newman-Keuls = 23.12, $P < 0.035$). For the remaining 30%, *C. rufipes* killed *C. sericeiventris* in one case, and two other times there were fights without deaths.

Unlike the encounters with the neighbouring *C. rufipes* and *C. sericeiventris* from UFJF, the fight lasted longer and all the repetitions severally resulted in death; 60% of the *C. sericeiventris* and 40% of the *C. rufipes* died. It is worth noting that when *C. rufipes* were killed, the trial was faster than when it was not killed. Finally, in the treatment between *C. rufipes* from the two studied sites, the ants from the Itacolomi colony died in half of the repetitions without causing a single death among the ants from UFJF (Table 1).

4. Discussion

4.1. Field Experiments. Regardless of the advantage of aggressiveness, high costs of competing may mean that its selective advantage is only sustainable if associated with the minimization of conflicts. An evidence is that the behaviours most frequently exhibited by all ants species from both sites were “quietly feeding” and “exploring the surroundings”. According to ethograms found in the literature, the most common behavioural acts are into the categories of grooming, feeding, and exploring surroundings [19, 27–29].

Likewise, the “dear enemy” hypothesis [30] predicts that ant species are capable of recognizing and discriminating their neighbours (species/individuals), and then they are normally more aggressive with the “foreigners”, saving energy by avoiding unnecessary conflicts with species or colonies with which they have already defined their boundaries [31, 32]. The species that live together adjust to the habitat and share resources, while foreigners may threaten this balance [30]. In addition, the constant contact among all coexisting ants followed by autogrooming results in a common Gestalt odour, that decreases the aggressiveness among all the species that share the same space [4]. Finally, for canopy ants, it has been reported that various species have the habit of foraging over great distances, presenting familiarity with the place, and tolerating the presence of neighbour species [33].

Both experiments suggest that these species tend to have a territory which is aggressively protected, and thus are able to dominate numerically in the canopies. Both species seem to have defensive behavior across the complete territory, instead of only at the nest or some particular feeding resource, as aggressive actions have been observed everywhere in the studied forest (pers.obs.) and have been corroborated experimentally. The dominant position could be taken by *C. rufipes* where *C. sericeiventris* does not occur, while in the presence of the latter, *C. rufipes* may still keep high abundance (mainly by combining foraging in different habitats, such as the canopy and in the litter) and codominate the assemblage.

Concerning other observed species, distinct behaviours at the bait reflected their recruiting and foraging strategies and, in many cases, their attack and defence tactics. Many species proved to be opportunists, eating rapidly until being

Table 4: Occurrence of behaviours for the morphospecies of ants in the Itacolomi State Park (Itacolomi) and the Campus of Federal University of Juiz de Fora (UFJF) during field experiments.

Local	Espécie	Quietly eating	Exploring the surroundings	Autogrooming	Food transport	Charge	Bite	Espontaneous torsion gaster	Avoid	Remain on the bait	Flee	Retreat	Fight	Trofalaxis
UFJF	*Acromyrmex* sp.1	100%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
UFJF	*C. rufipes*	42%	21%	14%	0%	9%	10%	0%	0%	1%	0%	2%	0%	0%
UFJF	*C. sericeiventris*	69%	8%	12%	0%	4%	4%	0%	0%	0%	1%	1%	0%	1%
UFJF	*Camponotus* sp.5	82%	8%	2%	0%	0%	0%	0%	1%	0%	3%	3%	0%	0%
UFJF	*Camponotus* sp.6	41%	19%	5%	0%	0%	0%	0%	0%	0%	27%	3%	5%	0%
UFJF	*Camponotus* sp.7	50%	8%	7%	0%	2%	1%	0%	7%	0%	9%	15%	2%	0%
UFJF	*Camponotus* sp.8	100%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
UFJF	*Cephalotes* sp.2	100%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
UFJF	*Crematogaster* sp.1	98%	2%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
UFJF	*Pheidole* sp.2	75%	23%	0%	1%	0%	1%	0%	0%	0%	0%	0%	0%	0%
UFJF	*Pseudomyrmex* sp.2	69%	15%	3%	0%	3%	1%	0%	4%	0%	1%	5%	0%	0%
UFJF	*Solenopsis* sp.1	100%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
Itacolomi	*C. rufipes*	29%	40%	14%	4%	6%	3%	0%	4%	0%	0%	0%	—	—
Itacolomi	*Camponotus* sp.4	86%	7%	0%	0%	0%	0%	0%	0%	0%	0%	7%	—	—
Itacolomi	*Camponotus* sp.2	76%	6%	12%	0%	0%	0%	0%	0%	0%	6%	0%	—	—
Itacolomi	*Camponotus* sp.3	50%	17%	33%	0%	0%	0%	0%	0%	0%	0%	0%	—	—
Itacolomi	*Camponotus* sp.1	65%	22%	8%	0%	1%	0%	0%	3%	0%	0%	0%	—	—
Itacolomi	*Cephalotes* sp.1	80%	20%	0%	0%	0%	0%	0%	0%	0%	0%	0%	—	—
Itacolomi	*Myrmelachista* sp.1	95%	4%	0%	0%	0%	0%	0%	0%	0%	1%	0%	—	—
Itacolomi	*Pheidole* sp.1	100%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	—	—
Itacolomi	*Pseudomyrmex* sp.1	37%	46%	10%	4%	0%	0%	0%	2%	0%	0%	2%	—	—

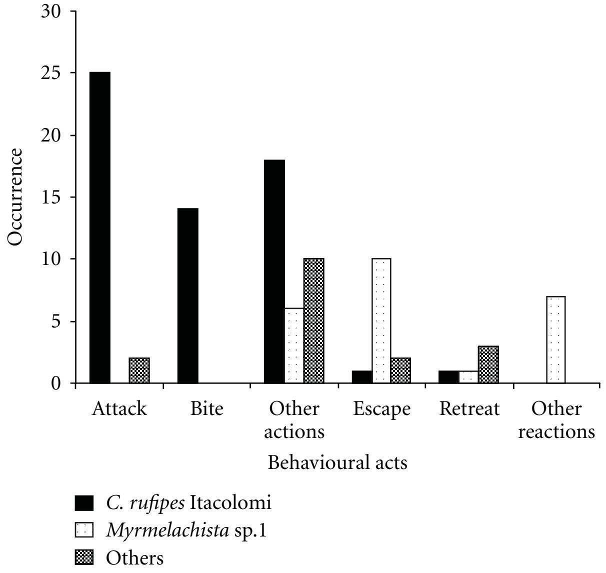


Figure 1: Action and reaction behavioural occurrences for *C. rufipes*, *Myrmelachista* sp.1 ants, and other morphospecies assemblages during field experiments in the Itacolomi State Park (Itacolomi). The "other actions" and "other reactions" are grouped together because of their low frequency.

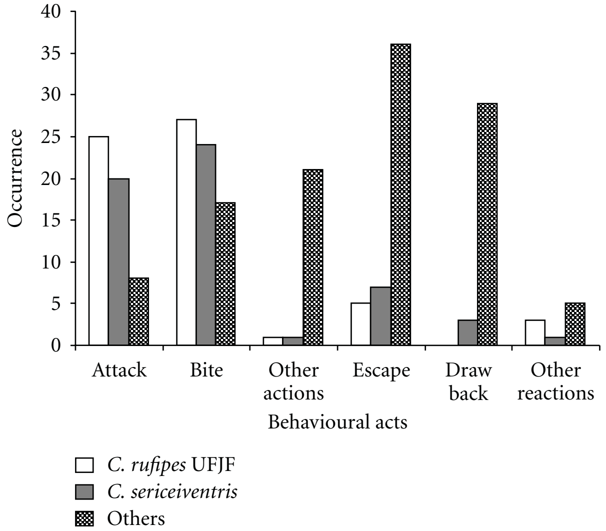


Figure 2: Action and reaction behavioural occurrences for *C. rufipes*, *C. sericeiventris*, and other morphospecies (grouped together) during field experiments at the Campus of Federal University of Juiz de Fora. The "other actions" and "other reactions" behaviours are grouped together because of their low frequency.

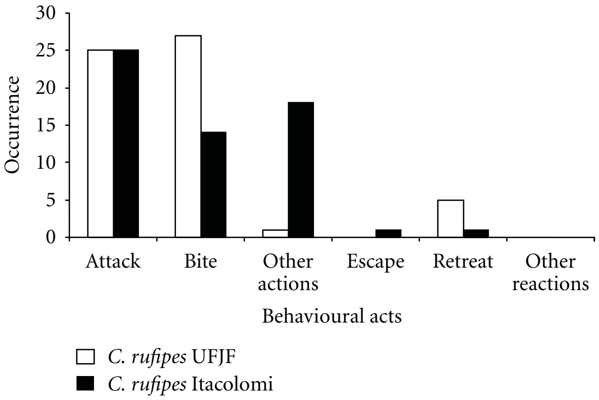


Figure 3: Action and reaction behavioural occurrences for the *C. rufipes* colonies at the Itacolomi State Park (Itacolomi) and campus of Federal University of Juiz de Fora (UFJF) during field experiments. The "other actions" and "other reactions" behaviours are grouped together because of their low frequency.

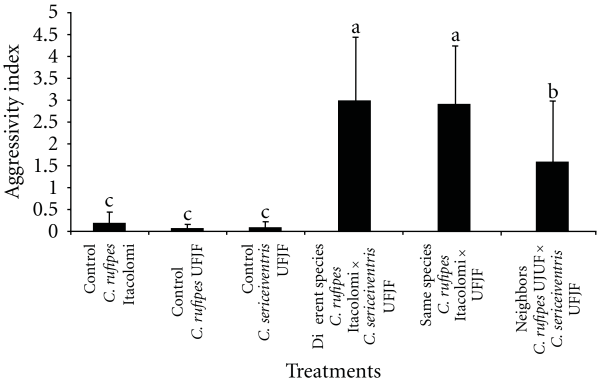


Figure 4: Aggressiveness index (mean and standard deviation) for each treatment of laboratory experiments (dyadic encounters) in which "control" is the manipulation with individuals from the same colony and species; "different species" between *C. rufipes* from Itacolomi State Park (Itacolomi) and *C. sericeiventris* from Campus of Federal University of Juiz de Fora (UFJF); "same species" between *C. rufipes* from both Itacolomi and UFJF; "neighbours" between *C. rufipes* and *C. sericeiventris* from UFJF.

expelled by the dominant species, but avoiding interactive aggressive behaviour. In this study, the genera *Cephalotes* and *Pseudomyrmex*, along with some species of *Camponotus* (*C. crassus* and three nonidentified *Camponotus* species) exhibited this type of behaviour. The opportunistic or cowardly behaviour was previously recorded by *Cephalotes pusillus* in Byk and Del-Claro [34], as the species was never observed attacking any insect, contrary to what is expected for a plan-ant-herbivore system.

To a certain extent, the coexistence of these species was possible due to behavioural diversity. For instance, we observed that different species place themselves almost opposite to the others when eating on the bait, thus avoiding conflicts while sharing the same resource at the same moment. In this study, at various times when the bait was exposed, there were around five ant species on it. An erroneous interpretation of this would be to say that there was no competition in place. However, upon behavioural observation *in locu*, it was evident that species placed themselves strategically on the bait, avoiding visual or chemical contact. Furthermore, when two species meet, there was aggressive behaviour, resulting in fleeing of one of them. It is worth noting, though, that since baits were an energetic, unpredictable, and sufficiently abundant food source, it was possible for various species to eat at the same time without the need to expel or attack the others. Most of natural resources available ought to result in a tougher competitive environment than the one we manipulated.

4.2. Laboratory Experiments. *Camponotus rufipes* and *C. sericeiventris* were able to recognize individuals of their colony and to differentiate them from other colonies and species. For *C. rufipes,* this capacity has already been registered [35]. Most importantly, the present experiment measured the aggressiveness between these species, which was high for *C. sericeiventris*, but also stronger for those individuals of *C. rufipes* that coexisted in the field with *C. sericeniventris*, compared with the Itacolomi's individuals. Since Itacolomi's ants have grown without any substantial competition in nature, they become pacifists.

Similar results were previously described for other systems. Lucas [36] observed three species of *Pachycondyla* (*P. villosa, P. inversa*, and *P. subversa*) during dyadic encounters and found out that they were able to recognize members of the same colony, of the same species and of different species, increasing aggressiveness in the same order. For *C. rufipes* at UFJF, there was no differentiation of aggressiveness between intra- and interspecific encounters, which means that their defensive behaviour against *C. sericeiventris* or a potential invader colony of their own species was similar and may reflect their establishment in a hostile environment.

Combative behaviours are widely described in the myrmecological literature. In the laboratory, *Oecophylla longinoda* (a dominant arboreal genera) was observed while fighting for its territory with two foreign individuals that entered simultaneously the arena [37]. This species was also observed in its natural habitat fighting and excluding other ant colonies in Africa. Similar results were encountered for *Oecophylla smaragdina* in Australia [38, 39]. De Vita [40] measured the aggressiveness of *Pogonomyrmex californicus* populations in their natural habitat and observed that 81% of the encounters resulted in some type of aggression and, in some cases, led to the death of the individuals. In addition, there was evidence that ants of the same species from different colonies showed aggression against each other. Aggression was also shown against potential competitors of another species, which resulted in fights or death in all repetitions.

The lack of aggressiveness from Itacolomi's *C. rufipes* corroborates the assumption that aggressive behaviour is more likely learned than inherited, especially since the same species (*C. rufipes* from UFJF) that coexists with competitors presents a greater level of aggressiveness and a greater capacity to fight with foreign species of the same size (*C. rufipes* from Itacolomi). Also, the data from the encounters among *C. rufipes* from Itacolomi and *C. sericeiventris* show that *C. rufipes* from Itacolomi was almost always attacked and killed. On the other hand, when the encounters were between *C. rufipes* and *C. sericeiventris* that coexisted in the same area (UFJF), the battles were more evensided, registering 40% of the deaths for workers of *C. rufipes* and 60% for *C. sericeiventris*. In these cases, the aggressiveness index was higher; the ants fought for a longer time before one of them died. In the field experiments, there was no occurrence of a fight to death between *C. rufipes and C. sericeiventris*, as had occurred in the dyadic encounters. Nevertheless, a transposing experiment is needed to confirm whether such aggressiveness would be learnt or, otherwise, whether there could be a *C. rufipes* "pacifist genotype".

As generally observed in the field for all species, these two codominant species also avoid combative behaviour, in accordance with the prediction that a strategy of decreasing costs of combat is of great importance in behavioural evolution. This mutual avoidance during the field experiments could also be related to the abundance of food that the bait represents, which implies in no dispute. However, the dominant species was bothered by the presence of other species when they were encountered feeding at the same place in the bait. On the other hand, in the dyadic encounters in a small arena and with no escape route, the ants had no alternative other than to dispute that small space by attacking and killing the other individual.

In conclusion, direct contacts seem to be avoided between *C. rufipes* and *C. sericeiventris*, as is expected, since they are two species with similar feeding habits, nesting location, foraging strategy, and body dimensions. However, *C. rufipes* species from Itacolomi does not have a great fighting capacity, very likely because it does not coexist with any other similar competitor, showing that behavioural plasticity will always favour the cost-saving behaviour, namely avoiding conflict.

Acknowledgments

The authors thank Jacques H. C. Delabie, Fábio Prezoto, and Nathércia Espírito Santo for original paper revision; IEF, the State Institute of Forestry and the administration of Itacolomi State Park for providing permits and logistical facilities for the work. They thank FAPEMIG for financial support and Universidade Federal de Juiz de Fora for a masters grant. Sérvio Pontes Ribeiro is a researcher funded by CNPq.

References

[1] B. Hölldobler and E. O. Wilson, *The Ants*, The Belknap Press of Harvard University Press, Cambridge, Mass, USA, 1990.

[2] R. H. Macarthur and R. Levins, "The limiting similarity, convergence, and divergence of coexisting species," *American Naturalist*, vol. 101, pp. 377–385, 1967.

[3] N. J. Gotelli and A. M. Ellison, "Assembly rules for New England ant assemblages," *Oikos*, vol. 99, no. 3, pp. 591–599, 2002.

[4] E. O. Wilson, *The Insect Societies*, Harvard University Press, Cambridge, Mass, USA, 1971.

[5] D. W. Davidson, "Resource discovery versus resource domination in ants: a functional mechanism for breaking the trade-off," *Ecological Entomology*, vol. 23, no. 4, pp. 484–490, 1998.

[6] P. M. Room, "The relative distribution of ant species in Ghana's cocoa farms," *Journal of Animal Ecolog*, vol. 40, pp. 735–751, 1971.

[7] D. Leston, "The ant mosaic, tropical tree crops and the limiting of pests and diseases," *Pest Articles and News Summaries*, vol. 19, pp. 311–341, 1973.

[8] D. Leston, "A neotropical ant mosaic," *Annals of the Entomological Society of America*, vol. 71, pp. 649–653, 1978.

[9] J. D. Majer, J. H. C. Delabie, and M. R. B. Smith, "Arboreal ant community patterns in Brazilian cocoa farms," *Biotropica*, vol. 26, no. 1, pp. 73–83, 1994.

[10] B. Hölldobler and C. J. Lumsden, "Territorial strategies in ants," *Science*, vol. 210, no. 4471, pp. 732–739, 1980.

[11] R. Savolainen and K. Vepsalainen, "A competition hierarchy among boreal ants: impact on resource partitioning and community structure," *Oikos*, vol. 51, no. 2, pp. 135–155, 1988.

[12] K. Del-Claro and P. S. Oliveira, "Ant-homoptera interactions in a neotropical savanna: the honeydew-producing treehopper, *Guayaquila xiphias* (Membracidae), and its associated ant fauna on *Didymopanax vinosum* (Araliaceae)," *Biotropica*, vol. 31, no. 1, pp. 135–144, 1999.

[13] M. R. Orr, D. L. Dahlsten, and W. W. Benson, "Ecological interactions among ants in the genus *Linepithema*, their phorid parasitoids, and ant competitors," *Ecological Entomology*, vol. 28, no. 2, pp. 203–210, 2003.

[14] R. C. Fonseca and E. Diehl, "Riqueza de formigas (Hymenoptera: Formicidae) epigéicas em povoamentos de *Eucalyptus* spp. (Myrtaceae) de diferentes idades no Rio Grande do Sul, Brasil," *Revista Brasileira de Entomologia*, vol. 48, pp. 95–100, 2004.

[15] E. F. O. Peternelli, T. M. C. Della Lucia, and S. V. Martins, "Espécies de formigas que interagem com sementes de *Mabea fistulifera* Mart. (Euphorbiaceae)," *Revista Árvore*, vol. 28, pp. 733–738, 2004.

[16] J. A. Lutinski and F. R. M. Garcia, "Análise faunística de Formicidae (Hymenoptera: Apocrita) em ecossistema degradado no município de Chapecó, Santa Catarina," *Biotemas*, vol. 18, pp. 73–86, 2005.

[17] M. S. Santos, J. N. C. Louzada, N. Dias, R. Zanetti, J. H. C. Delabie, and I. C. Nascimento, "Litter ants richness (Hymenoptera, Formicidae) in remnants of a semi-deciduous forest in the Atlantic rain forest, Alto do Rio Grande region, Minas Gerais, Brazil," *Iheringia*, vol. 96, no. 1, pp. 95–101, 2006.

[18] N. B. Espírito Santo, *Assembléia de formigas do Parque Estadual do Itacolomi (MG) e relações intra- e interespecíficas entre espécies dominantes*, M.S. thesis, Pós-Graduação em Comportamento e Biologia Animal/Departamento de Biologia Animal/Universidade Federal de Juiz de Fora, 2008.

[19] M. Yamamoto and K. Del-Claro, "Natural history and foraging behavior of the carpenter ant *Camponotus sericeiventris* Guérin, 1838 (Formicinae, Campotonini) in the Brazilian tropical savanna," *Acta Ethologica*, vol. 11, no. 2, pp. 55–65, 2008.

[20] R. I. Campos, J. P. Scares, R. P. Martins, and S. P. Ribeiro, "Effect of habitat structure on ant assemblages (Hymenoptera: Formicidae) associated to two pioneer tree species," *Sociobiology*, vol. 47, no. 3, pp. 721–738, 2006.

[21] M. A. G. Fujaco, *Influência dos diferentes tipos de substrato e geomorfologia na distribuição espacial e arquitetônica do gênero* Eremanthus *no Parque Estadual do Itacolomi, Ouro Preto/MG*, M.S. thesis, Pós-Graduação em Evolução Crustal e Recursos Naturais/Departamento de Geologia/Universidade Federal de Ouro Preto, 2007.

[22] "Banco de dados climáticos do Brasil—Embrapa Monitoramento por Satélite e Esalq—USP," 2007, http://www.bdclima.cnpm.embrapa.br/resultados/.

[23] J. Altmann, "Observational study of behavior: sampling methods," *Behaviour*, vol. 49, no. 3-4, pp. 227–267, 1974.

[24] S. P. Ribeiro, J. P. Soares, R. I. Campos, and R. P. Martins, "Insect herbivores species associated to pioneer tree species: contrasting within forest and ecotone canopy habitats," *Revista Brasileira de Zoociências*, vol. 10, pp. 237–248, 2008.

[25] J. F. S. Lopes, W. O. H. Hughes, R. S. Camargo, and L. C. Forti, "Larval isolation and brood care in *Acromyrmex* leaf-cutting ants," *Insectes Sociaux*, vol. 52, no. 4, pp. 333–338, 2005.

[26] C. Errard and A. Hefetz, "Label familiarity and discriminatory ability of ants reared in mixed groups," *Insectes Sociaux*, vol. 44, no. 3, pp. 189–198, 1997.

[27] J. C. Santos and K. Del-Claro, "Ecology and behaviour of the weaver ant *Camponotus (Myrmobrachys) senex*," *Journal of Natural History*, vol. 43, no. 23-24, pp. 1423–1435, 2009.

[28] C. R. Ferreira Brandão, "Sequential ethograms along colony development of *Odontomachus affinis* Guérin (Hymenoptera, Formicidae, Ponerinae)," *Insectes Sociaux*, vol. 30, no. 2, pp. 193–203, 1983.

[29] J. C. Santos, M. Yamamoto, F. R. Oliveira, and K. Del-Claro, "Behavioral repertory of the weaver ant *Camponotus (Myrmobrachys) senex* (Hymenoptera: Formicidae)," *Sociobiology*, vol. 46, no. 1, pp. 27–37, 2005.

[30] E. O. Wilson, *Sociobiology*, Belknap Press of Harvard University Press, Cambridge, Mass, USA, 1975.

[31] T. A. Langen, F. Tripet, and P. Nonacs, "The red and the black: habituation and the dear-enemy phenomenon in two desert *Pheidole* ants," *Behavioral Ecology and Sociobiology*, vol. 48, no. 4, pp. 285–292, 2000.

[32] T. Delsinne, Y. Roisin, and M. Leponce, "Spatial and temporal foraging overlaps in a Chacoan ground-foraging ant assemblage," *Journal of Arid Environments*, vol. 71, no. 1, pp. 29–44, 2007.

[33] C. R. Carroll and D. H. Janzen, "Ecology of foraging by ants," *Annual Review of Ecology and Systematics*, vol. 4, pp. 231–257, 1973.

[34] J. Byk and K. Del-Claro, "Nectar- and pollen-gathering Cephalotes ants provide no protection against herbivory: a new manipulative experiment to test ant protective capabilities," *Acta Ethologica*, vol. 13, no. 1, pp. 33–38, 2010.

[35] K. Jaffé and C. Sánchez, "On the nestmate-recognition system and territorial marking behaviour in the ant Camponotus rufipes," *Insectes Sociaux*, vol. 31, no. 3, pp. 302–315, 1984.

[36] C. Lucas, *Étude des bases chimiques et comportamentales de la formation du "visa" colonial chez les Ponérines du genre* Pachycondyla, Thèse Docteur, Biologie du Comportement, Universitè Paris XI, Paris, France, 2002.

[37] B. Hölldobler and E. O. Wilson, "The multiple recruitment systems of the african weaver ant *Oecophylla longinoda* (Latreille) (Hymenoptera: Formicidae)," *Behavioral Ecology and Sociobiology*, vol. 3, no. 1, pp. 19–60, 1978.

[38] B. Hölldobler, "Territoriality among *Oecophylla*," *National Geographic Society Research Reports*, vol. 1977, pp. 369–372, 1979.

[39] B. Hölldobler, "Territorial behavior in the green tree ant (*Oecophylla smaragdina*)," *Biotropica*, vol. 15, pp. 241–250, 1983.

[40] J. De Vita, "Mechanisms of interference and foraging among colonies of the harvester ant *Pogonomyrmex californcus* in the Mojave Desert," *Ecology*, vol. 60, pp. 729–737, 1979.

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 870794, 9 pages
doi:10.1155/2012/870794

Research Article

Subterranean Pitfall Traps: Is It Worth Including Them in Your Ant Sampling Protocol?

Renata Pacheco and Heraldo L. Vasconcelos

Instituto de Biologia, Universidade Federal de Uberlândia (UFU), C.P. 593, 38400-902 Uberlândia, MG, Brazil

Correspondence should be addressed to Heraldo L. Vasconcelos, heraldo@umuarama.ufu.br

Received 17 May 2011; Accepted 28 June 2011

Academic Editor: Jonathan D. Majer

The use of subterranean traps is a relatively novel method to sample ants, and few studies have evaluated its performance relative to other methods. We collected ants in forests, savannas, and crops in central Brazil using subterranean pitfall traps and conventional pitfall traps placed on the soil surface. Sampling duration, soil depth, and sprinkling vegetal oil around traps all tended to affect the number of species found in subterranean traps. Sixteen percent of the species collected in subterranean traps were unique, and most of these had cryptobiotic morphology (i.e., were truly hypogaeic species). Surprisingly, however, subterranean and conventional traps were similarly efficient at capturing cryptobiotic species. Furthermore, subterranean traps captured far fewer species in total than conventional traps (75 versus 220 species), and this was true in all three habitats sampled. Sampling completeness increased very little using a combination of conventional and subterranean traps than using just conventional traps.

1. Introduction

Biodiversity inventories seek a characterization of the studied community or the elaboration of a complete species list [1]. In both cases a more efficient inventory is commonly achieved with the use of diverse and complementary sampling techniques, and this is especially true with regard to hyperdiverse groups such as terrestrial arthropods [1–3]. Ants are a particularly important group of arthropods as they are highly abundant and diverse, have a wide geographic distribution, and occupy a variety of niches [4]. Ants play important ecological roles, acting as herbivores, seed dispersers or, commonly, as predators and scavengers of other arthropods [4, 5]. Due to these characteristics, ants have been commonly used as a focal taxon in biodiversity studies or as bioindicators in studies of land management [6].

Diverse methodologies have been used to collect ants, and each of them has its own limitations given that no single method is able to collect all species inhabiting a given area (at least not in tropical and subtropical habitats where ant diversity is typically high), since these species commonly have a wide diversity of foraging and nesting habits [1, 7–9]. As a result, many ant inventories employ more than one sampling technique, as their use in combination often increases sampling efficiency [1, 9, 10]. Pitfall traps, for instance, tend to be more efficient for the collection of relatively large ants that are active on the soil surface, whereas the Winkler method favors the collection of smaller and often cryptic species that forage or nest in the litter layer [11]. The combined use of pitfall traps and the Winkler samples has been proposed in the Ants of Leaf Litter (ALL) sampling protocol, a protocol that has been employed successfully in ecological studies and inventories of tropical forest ants [7, 12, 13]. More recent studies, however, have indicated that many species with subterranean habits (i.e., hypogaeic species with cryptobiotic morphology) may not be collected with the use of the more traditional sampling methodologies such as the Winkler method, pitfall traps, baits, or direct search [12, 14, 15]. One way to collect hypogaeic species is to take soil-core samples and extract ants from soil manually or with the aid of the Berlese or the Winkler extractors [10, 16–18]. An alternative and increasingly used method is subterranean traps, such as the subterranean probe [15, 19] or subterranean pitfall traps [14, 20–23].

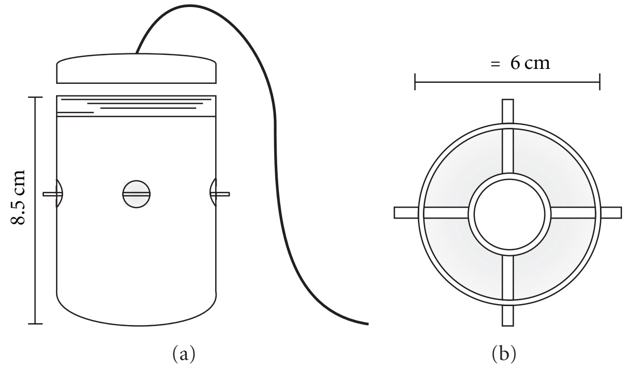
So far, inventories of ant diversity using subterranean traps have been performed in only a small number of sites and habitats including the rain forests of Ecuadorian Amazon [19], the Brazilian Atlantic Forest [22], and the *Eucalyptus*-dominated forests of northern Australia [14]. Therefore, there is a lack of information about the performance of subterranean traps in other types of vegetation. Also, there is only limited information about the best methods to improve the sampling efficiency of subterranean traps (but see [14]). Here we provide results of the first systematic survey of subterranean ants in the Cerrado region of central Brazil. The Cerrado is a biodiversity hotspot and is characterized as a mosaic of vegetation types, which include savannas of variable structure (the dominant vegetation), various types of forests, and grasslands [24, 25]. Most of the original Cerrado vegetation have already been converted to cattle pastures or crop fields, and as a consequence these human-managed ecosystems are now an important feature of the Cerrado landscape and thus have also to be taken into account when assessing diversity at the landscape level.

Pitfall trapping (i.e., pitfall traps placed on the soil surface or, hereafter, conventional pitfalls) is by far the most commonly employed method to sample ants, especially in savanna-dominated landscapes [9, 13, 26]. We thus compared the efficiency of subterranean traps relative to conventional pitfall traps and, most importantly, determined how complementary these two methodologies are. Trap efficiency was measured in terms of the total number of species collected, the number of unique species, and the number of species with cryptobiotic morphology (i.e., species with tiny or absent eyes and small body size). We also evaluated some simple methodologies designed to improve the sampling efficiency of subterranean traps. Finally, we evaluated the efficiency of subterranean traps in collecting hypogaeic ants in different types of ecosystems of the Cerrado region, including forests, savannas, and crop fields.

2. Material and Methods

2.1. Study Site. The study was conducted in 13 sampling sites located near the towns of Uberlândia (18 56 , 48 18 W) and Monte Alegre de Minas (18 52 S, 48 52 W) in the west region of Minas Gerais state in Brazil. The region is characterized by a tropical climate with two well-defined seasons: a dry winter (May–September) and a rainy summer (October–April). The mean annual temperature and precipitation are 22 C and 1650 mm, respectively. Sampling was conducted during the wet seasons of 2008 and 2009.

Soils at our study sites are primarily red latosols. The vegetation at these sites included savannas (locally known as *cerrado sensu stricto*; $n = 2$ sites), forests (semideciduous forests and the forest physiognomy locally known as *cerradão* [25]; $n = 5$ sites), and fields planted with annual crops (maize, sorghum or, most commonly, soybean) ($n = 6$). With a single exception, all sites with natural vegetation were adjacent to the crop fields.



(a) (b)

Figure 1: Schematic external (a) and internal (b) view of the subterranean pitfall trap.

2.2. Description of the Subterranean Trap. Our subterranean pitfall traps (Figure 1) were similar to those employed by other authors [14, 21, 22]. Each trap consisted of a closed plastic container (volume = 250 mL) with four 1 cm holes made in the side of the container (Figure 1). As done in a previous study [22], a 70 cm long rope was attached to the lid of each container to identify its location and facilitate removal. The traps were baited using sardine mixed with vegetable oil. About 5 mL of this mixture was poured onto a small lid (2.5 cm in diameter), and the lid was fixed in the interior of each container suspended by a plastic frame as detailed in Figure 1. About 50 mL of alcohol and glycerin was poured on the bottom of the traps to act as killing and preservative agents.

2.3. Factors Affecting Trap Efficiency. To evaluate if the number of species collected varied with soil depth, we simultaneously buried 60 traps to a depth of 20 cm and 60 traps to a depth of 50 cm. To prevent major alterations on soil structure, we buried traps by first making a cylindrical hole (ca. 8 cm in diameter) using a post hole digger [22] and then filled the holes with the excavated soil. These traps remained in operation for 7 days and were placed along transects in three sites (one forest, one savanna, and one crop field site), keeping a minimum distance of 20 m between traps and alternating the treatments (i.e., 20 or 50 cm). Twenty traps of each type were installed in each site.

We also evaluated if trapping duration affected the number of species collected. For this we compared the number of species collected in 40 of the 60 traps set at 20 cm for the experiment described above with the number of species collected in 40 other traps that were buried to a depth of 20 cm and were left out in the field for just two days. Traps that were left in the field for two days were installed in the same sites and at the same time as those that were left for 7 days. Finally, we evaluated if pouring vegetable oil around the hole made to bury each trap would increase the number of species collected as indicated in previous studies in Malaysia [20, 27, 28]. For this we sprinkled about 20 mL of a mixture consisting of 90% of soybean oil and 10% of palm (*Elaeais guineensis*, known as *dendê* in Brazil) oil on

Table 1: Efficiency of the subterranean pitfall traps as a function of soil depth, time of trap exposure, and addition of vegetable oil on soil around traps.

Factor	Treatment	Number of traps (natural areas + crops)	Observed number of species (SD)	Estimated number of species (SD)	Observed number of cryptobiotic species (SD)	Estimated number of cryptobiotic species (SD)	Total number of ant species records	Traps without ants (%)
Duration	2 days	20 + 20	13 (± 3.1)	21.8 (± 3.0)	2 (± 0.0)	3.0 (± 1.0)	27	50.0
	7 days	20 + 20	17 (± 2.1)	24.8 (± 2.5)	5 (± 1.6)	8.9 (± 1.9)	37	40.0
Depth	20 cm	40 + 20	20 (± 2.6)	29.8 (± 2.9)	6 (± 1.7)	10.9 (± 2.1)	43	53.3
	50 cm	40 + 20	16 (± 3.3)	27.8 (± 3.4)	3 (± 1.9)	4.0 (± 1.0)	27	63.3
Vegetable oil	without	37 + 11	9 (± 1.9)	14.9 (± 2.7)	2 (± 0.6)	3.0 (± 1.0)	24	79.2
	with	38 + 12	13 (± 3.2)	22.8 (± 3.1)	2 (± 0.0)	3.0 (± 1.0)	30	68.0

the soil around each trap. A total of 60 traps received this treatment while another 60 did not. These traps were buried to a depth of 20 cm and remained in operation for 7 days (20 of the 60 traps that received no oil treatment were the same traps used in the experiment about soil depth). As in the previous experiments, traps were spaced 20 m from each other (alternating treatments), with 40 of the traps from each treatment being placed in two forest sites and 20 in a crop field (Table 1).

2.4. Subterranean Traps versus Traps Placed on the Soil Surface. To determine if more species would be collected using a combination of conventional, and subterranean traps than using just conventional traps we installed these two types of traps in our sampling sites ($n = 13$). In addition to traps used in the previous experiments, we installed another 505 subterranean traps and 605 conventional traps in our sampling sites. Within each of these sites, traps were distributed along line transects, keeping a minimum distance of 20 m between traps and alternating the type of trap. Subterranean and conventional traps were installed simultaneously in each transect. Conventional pitfall traps consisted of plastic cups (300 mL volume), filled to one third of its volume with a mixture of alcohol (70%) and glycerin and placed on the ground so that the opening of the trap was leveled off with the soil surface.

All the additional 505 subterranean traps were set at 20 cm of depth (and vegetable oil was poured around the traps as described above) and remained in operation for 7 days. The conventional traps also remained in operation for 7 days, and both types of traps were baited using sardine mixed with vegetable oil.

2.5. Data Analysis. We built sample-based species accumulation curves [29], using the Mao Tau estimator in EstimateS version 8.2 [30], in order to compare the overall number of species collected and the number of cryptobiotic species collected at different depths, after different times of trap exposure, after applying or not vegetable oil around traps, and for comparing subterranean and conventional traps. We used the Jackknife 1 nonparametric richness estimator to determine the number of species expected to be found in different types of traps (or treatments) or in different habitats.

Nonmetric multidimensional scaling (NMDS) was used to evaluate the similarity in ant species composition among samples taken in different habitats or using different sampling methodologies. For this we first constructed a dissimilarity matrix (Sørensen index) using data on species presence or absence for species collected with each of the two sampling methodologies in each sampling site. The resulting ordination scores (two-dimensional solution) were then used in a multivariate analysis of variance (Manova) to test for differences in ant species composition (expressed as ordination scores) in relation to habitat and sampling method.

Of the 260 subterranean traps installed for the first three experiments, 22 were lost to digging animals (most of which in the crop fields) and, therefore, were excluded from our analyses. Of the 505 subterranean traps used in the subsequent experiment (when we protected the traps with a wire mesh fixed on the soil surface), only 6 were lost. Of the 605 conventional traps, 33 were lost and excluded from the analyses.

3. Results

3.1. Improving the Sampling Efficiency of Subterranean Pitfall Traps. The median number of species collected per trap was not significantly affected by soil depth (Mann-Whitney test, $U_{60,60} = 2058$, $P = 0.19$), time of trap exposure ($U_{40,40} = 675$, $P = 0.12$), or the addition of vegetable oil on soil around traps ($U_{48,50} = 1340$, $P = 0.20$). Similar results were obtained when data was analyzed considering only the species with cryptobiotic morphology (Mann-Whitney test, $P > 0.05$ in all cases). Nevertheless, when we compared the cumulative number of species collected (i.e., in all traps from each treatment), there was a clear trend towards finding more ant species, more species records, and less traps with no ants in traps that remained 7 days in operation, in those that were set at 20 cm of depth, and in those around which vegetable oil was poured (Table 1). Traps that remained in the field for 7 days also captured more cryptobiotic species in total than those that remained for two days. Similarly, more cryptobiotic species were found at 20 than at 50 cm of depth. The cumulative number of cryptobiotic species collected in traps with the addition of vegetable oil was equal to the number collected in traps with no oil (Table 1).

3.2. Subterranean Traps versus Traps Placed on the Soil Surface. We collected a total of 75 ant species from 27 genera in the 737 subterranean traps placed in 13 different sites and in three habitats (Table 2). Of all species collected with subterranean traps, 15 were cryptobiotic (20% of the total). Twelve of the 75 species (16%) captured with the subterranean traps were not found in the conventional traps, and most of these (8 out of 12 species) were cryptobiotic.

Using only the conventional traps ($n = 572$ traps), we collected a total of 220 species from 49 genera (a complete list of species/morphospecies is available from the authors upon request). Most of these species (157 species, or 71.3% of the total) were not found in the subterranean traps. Sixteen of the species collected using conventional traps (7.3%) were cryptobiotic (Table 2), and half of these were not captured with the subterranean traps.

The total number of species collected in the conventional traps was much greater than the number collected using subterranean traps, and this difference was detected in all three habitats sampled (forests: 4.3 more species, savannas: 3.7 more species, crop fields: 2.5 more species in the conventional than in the subterranean traps) (Figuers 2(a)–2(c)). When comparing the total number of species collected using just the conventional traps with that collected using both conventional and subterranean traps, we found that the number collected with the latter was only slightly greater than with the former (5.4% greater overall, 4.1% greater in forests, 5.8% greater in savannas, and 4.9% greater in crop fields). Considering only the species with cryptobiotic morphology, we found that conventional traps captured more species in the forest sites (Figure 2(d)), whereas in the crop fields subterranean traps tended to be more efficient (Figure 2(f)). Subterranean and conventional traps captured similar number of cryptobiotic species at the savanna sites (Figure 2(e)).

Overall (i.e., considering the two trapping methods), the proportion of species with cryptobiotic morphology varied a little among habitats, ranging from 9% of all species collected in forests to 8.4% in crops (savannas = 8.7%) (Table 3). The number of cryptobiotic species collected in each habitat represented 64 to 73% of the number of cryptobiotic species expected to be found in these same habitats (Table 3).

Most of the species collected only in the subterranean traps were rare species that were found in only one or two traps (Table 2). These included, for instance, two species of *Acanthostichus*, three species of *Hypoponera*, one species of *Carebara* (*lignata* group), *Oxyepoecus inquilinus*, and the exotic *Tetramorium simillimum* (Table 2). On the other hand, some of the species often collected with subterranean traps were not collected or were rare in the conventional traps. For instance, *Neivamyrmex punctaticeps* was collected 18 times with the subterranean traps but never with the conventional traps, while *Labidus mars* was collected 17 times with the subterranean traps but only once (and only a single individual) with the conventional traps (Table 2). As a result, differences in species composition resulting from collections using different types of traps tended to be even greater than differences in species composition between different habitats sampled with the same type of trap (Figure 3), even though differences in both habitat type (Manova, Pillai trace = 0.783, $F_{4,40} = 6.43$, $P < 0.001$) and trap type were significant (Manova, Pillai trace = 0.821, $F_{2,19} = 43.66$, $P < 0.001$).

4. Discussion

4.1. Increasing Trap Efficiency. Although during the past few years there has been a substantial increase in the use of subterranean traps in ant surveys [14, 15, 19–22], few studies have evaluated how to improve the efficiency of these traps. Our results suggest that extending the time of trap exposure from two to seven days increases trap efficiency in terms of total number of ant species records, total number of ant species, and number of cryptobiotic species. Similarly, Andersen and Brault [14] report that total ant records in subterranean traps were about 40% greater after four days than after just one. However, in their study, the number of species recorded did not change as a result of sampling duration (24 species after four as well as after one day) [14]. Although the number of additional ant species collected in subterranean traps appears to decline strongly as a function of sampling duration (with nearly 80% of the species being collected during the first 24 h of sampling) [19], we recommend that traps should remain in the field for more than two days and ideally for four to seven days. This is because installing the traps is a relatively time-consuming and labor intensive operation, and once the traps are set, few are lost (provided that some protection against digging animals is made). Therefore, unless there is the need to move to another and relatively distant sampling site quickly, there is no point in removing the traps after just one or two days.

Our results also suggest that sprinkling vegetal oil around the traps increases trap efficiency at least in terms of the overall number of species collected. Sprinkling vegetal oil on soil has been found to attract several hypogaeic ant species in Malaysia, especially army ants [20, 27, 28]. In the studies in Malaysia the oil used to attract ants was palm oil, while here we used a mix of palm (*dendê*) and soybean oil, given the elevated price of palm oil in Brazil. Palm oil has a very strong odor, and this odor is not lost after mixing it with soybean oil. Although vegetable oil has been found to increase trap efficiency, future studies should evaluate the use of other types of ant baits (in combination with oil), since vegetable oil is not attractive to all hypogaeic species [20].

As also found in other studies [14, 19], ant species tended to decline with soil depth. Furthermore, no evidence of a vertical stratification of the ant fauna was detected, as basically the same species were collected in different depths (Table 2). Wilkie et al. [19] suggested that in contrast to the situation they found in Ecuador, where the water table is particularly high, studies in dryer landscapes could detect a relatively unique deep-soil (>25 cm in depth) fauna. Our results suggest that this is may not be the case, as even though the water table at our sites is very deep, we found the same species foraging at different depths.

None of the previous studies that used subterranean traps provide data on the proportion of traps with no ant records. Our data indicate that, at least in our study region, this figure can be elevated and that 40% or more of the traps capture no

Table 2: List of all ant species collected with subterranean pitfall traps and list of all cryptobiotic species (marked with an asterisk) found during the study. Shown is the number of records (i.e., number of traps in which the species was present) of each species in different habitats, soil depths, and in total. The total number of records for each species in the conventional traps is also provided.

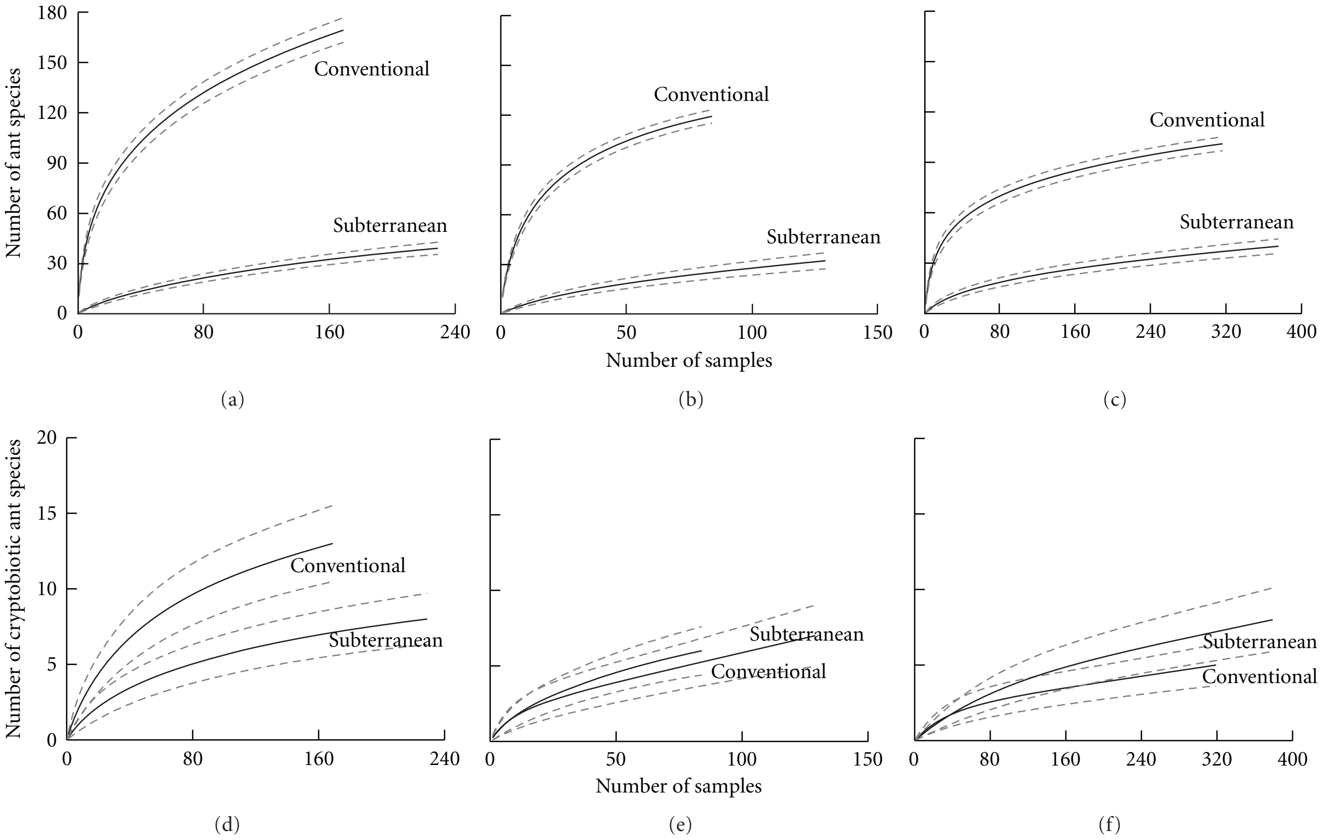
Species	Habitat			Depth		Total subterranean	Total conventional
	Forest	Savanna	Crops	20 cm	50 cm		
Acanthostichus kirbyi		1		1		1	
Acanthostichus sp. nr. *brevicornis*		1		1		1	
Acromyrmex sp.6	1			1		1	1
Acromyrmex subterraneus molestans			1	1		1	73
Acromyrmex subterraneus subterraneus	1			1		1	41
Atta laevigata	1			1		1	135
Brachymyrmex sp.2			1	1		1	100
Camponotus sp.10			1	1		1	26
Camponotus sp.40	1	1		2		2	43
Carebara brevipilosa	3		1	4		4	26
Carebara sp.1 (*lignata* gp.)		1		1		1	
Carebara sp.2 (*lignata* gp.)	1						1
Carebara urichi			1	1		1	5
Cephalotes pusillus	2			2		2	22
Crematogaster rudis		3	1	3	1	4	28
Dorymyrmex brunneus		1	13	14		14	196
Dorymyrmex sp.6			2	2		2	39
Dorymyrmex goeldii			3	3		3	60
Ectatomma sp.5	1		1	2		2	102
Ectatomma brunneum		1	6	6	1	7	96
Ectatomma opaciventri			2	2		2	117
Ectatomma planidens		2		1	1	2	34
Gnamptogenys sp.1			1	1		1	15
Gnamptogenys haenschi	4			4		4	1
Hypoponera sp.2	1				1	1	1
Hypoponera sp.5	1			1		1	
Hypoponera sp.6	1			1		1	
Hypoponera sp.8	1						1
Hypoponera sp.11			1				1
Hypoponera sp.1 (*punctatissima* gp.)			1	1		1	
Hypoponera sp.3 (*punctatissima* gp.)	1						1
Hypoponera cf. *trigona*	4						4
Labidus coecus	1	1	4	6		6	23
Labidus mars	3	7	7	15	2	17	1
Labidus praedator	1			1		1	7
Mycocepurus goeldii		1		1		1	122
Mycocepurus cf. *smithii*		1		1		1	14
Myrmicocrypta sp.3	1			1		1	
Neivamyrmex bruchi	7	21	4	27	5	32	7
Neivamyrmex modestus	3						3
Neivamyrmex cf. *pseudops*		2					2
Neivamyrmex punctaticeps	17		1	17	1	18	
Octostruma jheringi		1		1		1	1
Oxyepoecus inquilinus			1	1		1	
Pachycondyla guianensis	1			1		1	
Pachycondyla obscuricornis		1			1	1	76

Table 2: Continued.

Species	Habitat			Depth		Total subterranean	Total conventional
	Forest	Savanna	Crops	20 cm	50 cm		
Pheidole sp.1	1	6	28	34	1	35	203
Pheidole sp.2	2	4	2	7	1	8	76
Pheidole sp.3		3	7	8	2	10	38
Pheidole sp.A		1		1		1	2
Pheidole sp.4	1	3	8	11	1	12	36
Pheidole sp.5			2	1	1	2	8
Pheidole cf. *fowleri*	9	10	12	31		31	174
Pheidole sp.C (*diligens* gp.)		1		1		1	19
Pheidole sp.10			1	1		1	16
Pheidole sp.D	2			2		2	24
Pheidole sp.12		1	3	3	1	4	93
Pheidole sp.13	1			1		1	21
Pheidole sp.16		4	5	9		9	28
Pheidole sp.17		1	6	7		7	28
Pheidole sp.18			1	1		1	48
Pheidole sp.20	4	3	6	13		13	4
Pheidole sp.21			1	1		1	17
Pheidole sp.24	2			2		2	6
Pheidole sp.25	2			2		2	28
Pheidole sp.33	1			1		1	1
Pheidole sp.36	2			2		2	
Pheidole sp.38	1			1		1	21
Pheidole sp.54			1	1		1	4
Pheidole fimbriata	33			33		33	27
Pheidole oxyops	8	1	32	41		41	281
Pogonomyrmex naegelli			2	2		2	90
Prionopelta cf. *antillana*			1	1		1	14
Sericomyrmex sp.1	1			1		1	15
Sericomyrmex sp.2	2			2		2	23
Solenopsis sp.1	3	1	1	4	1	5	101
Solenopsis sp.2		1	1	2		2	25
Solenopsis iheringi	3			3		3	50
Solenopsis saevissima	2	5	48	49	6	55	97
Tetramorium simillimum		1		1		1	
Trachymyrmex sp.7	1			1		1	3
Typhlomyrmex sp.1	2						2
Wasmannia auropunctata	2	2	1	5		5	32

ants. This indicates that subterranean ants are relatively rare, with low density in the soil. In this sense, we may still need to develop methods to improve trap efficiency. Potential ways to improve trap efficiency include putting various types of baits on the soil around traps (as discussed above), making a large number of perforations in the traps (to facilitate ant access), and/or replacing baits periodically as done in some studies [19, 20].

4.2. Subterranean Traps versus Traps Placed on the Soil Surface. Sixteen percent of the species that we collected with subterranean traps were not collected with conventional pitfalls. Similarly, in Ecuador, 19.1% of the species collected with subterranean probes were not collected with other methods [15, 19], while the use of subterranean traps in Northern Australia resulted in the collection of 13.8% of unique species in one site and of 47% in another [14].



(a) (b) (c)

(d) (e) (f)

Figure 2: Sample-based species accumulation curves of the total number of ant species and the number of cryptobiotic species collected in subterranean or in conventional (i.e., on soil surface) pitfall traps placed in forests (a, d), savannas (b, e), or crop fields (c, f). Dotted lines represent one standard deviation around mean values.

Table 3: Overall ant species richness and richness of cryptobiotic species in three different habitats. Shown is the observed and estimated (± SD) number of species (Jacknife 1 species richness estimator).

	All species		Cryptobiotic species	
Habitat (no. of traps)	Observed species richness	Estimated	Observed species richness	Estimated
Forest (398)	177	190.9 ± 6.1	16	21.0 ± 2.2
Savanna (213)	126	156.9 ± 6.0	11	15.0 ± 2.2
Crops (698)	107	133.0 ± 5.6	9	13.0 ± 2.0
Total (1309)	232	291.0 ± 7.9	23	32.0 ± 3.0

Including subterranean and conventional traps.

Most of the species unique to our subterranean traps had cryptobiotic morphology (i.e., were truly hypogaeic species). However, surprisingly, subterranean traps were not more efficient than conventional traps in collecting cryptobiotic species. In fact, in the forest sites more cryptobiotic species were captured using conventional than subterranean traps (Figure 2). In addition, most of the cryptobiotic species found in the two types of traps (such as *Carebara brevipilosa*, *Carebara urichi*, *Labidus coecus*, *Labidus praedator*, and *Prionopelta* cf. *antillana*; Table 2) were more frequent in the conventional than in the subterranean traps. The only species that we can confidently say that are really more likely to be collected in our sites using subterranean than conventional pitfall traps are the army ants *Labidus mars* and *Neivamyrmex punctaticeps*. Nevertheless, it may well be possible that these two species could perhaps be more easily detected if we had used other methods designed specifically for finding army ants [23].

Overall (i.e., considering all species), subterranean traps collected far fewer species than conventional traps (see also [15] for a comparison between subterranean traps and other more traditional methods), indicating that ant diversity is much greater above- than below-ground. We collected two to four times more (depending on the type of habitat) species using conventional pitfall traps than using subterranean traps. Furthermore, when considering the overall number of species collected using both conventional and subterranean traps (232 species), only 5.2% were not collected using the conventional traps. In other words, the number of species collected by using a combination of subterranean and conventional traps was only slightly greater than the number those collected using just the conventional traps. This raises the question: is it worthwhile to include subterranean pitfall

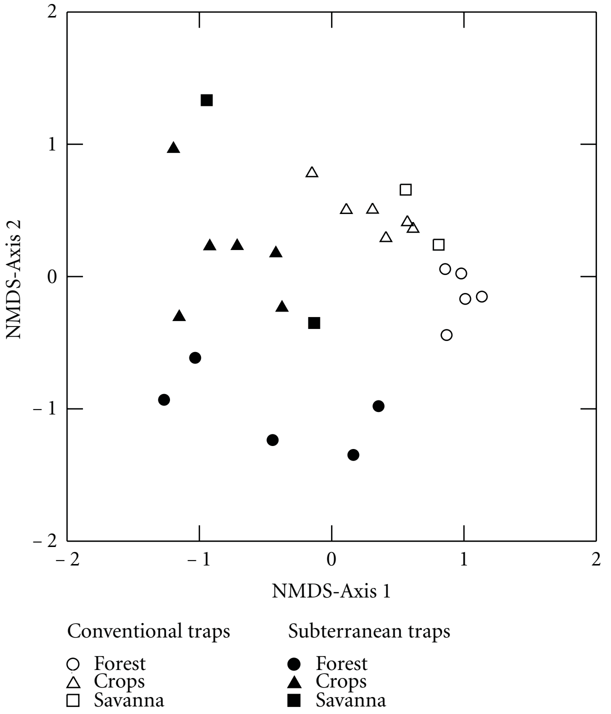


Figure 3: Nonmetric multidimensional scaling (NMDS) ordination of transects placed in different habitats based on the composition of ant species captured in subterranean or in conventional pitfall traps.

traps in your ant sampling protocol? In our view, if the purpose of the sampling is to provide just a general characterization of the studied ant communities, then the response is no. This is because many more species will be collected by using, say, 100 conventional pitfall traps than by using 50 conventional and 50 subterranean traps. In this way, even though a few cryptobiotic species would be missed (or their abundances underestimated), the completeness of the sampling would be much greater. Similarly, subterranean traps would probably not add much more information when the goal of the study is to compare the ant fauna of different habitats, since our results indicate that in most habitats conventional traps are at least as efficient as subterranean traps in collecting cryptobiotic species and, in addition, they collect much more species overall. On the other hand, if the purpose of the sampling is to evaluate the degree of vertical stratification of the ant fauna [31] or, especially, provide a relatively accurate species list (or a more reliable description of the functional composition of the studied community), then the response is yes. This is because some species are less likely to be recorded unless some kind of method to sample hypogaeic ants is employed. Examples include the first record of *Neivamyrmex punctaticeps* and *Labidus mars* in the Cerrado (this study), the rediscovery of *Simopelta minina* in the Atlantic forest [22, 32], the record of a new genus (*Pseudolasius*) for Western Australia [14], and the discovery of new species [19] and even new ant subfamilies [18, 33] by sampling subterranean ants. In this sense, we agree with previous claims that the subterranean ant fauna represents a novel and important frontier in biodiversity inventories [14, 19]. But to better explore this frontier we still need studies that compare the efficiency of the different methods developed so far, including traps, probes [15, 19], sieved buckets [20], and soil-core sampling [10, 16–18], taking into account the costs of each method and their efficiency in terms of the number and uniqueness of the species collected.

Acknowledgments

The authors are grateful to Gabriela P. Camacho and Tiago L. M. Frizzo for assistance with the field and laboratory work and to Scott Powell, Jonathan Majer, and two anonymous reviewers for reading and commenting on a previous view of the manuscript. They also thank UFU for providing logistical support and the farm owners for granting access to collect in their lands. John Longino, Fernando Fernandéz, Scott Powell, Jacques Delabie, and Gordon Snelling kindly identified some of the ant species listed in this study. Financial support was provided by the Brazilian Council of Research and Scientific Development (CNPq Grants 472972/2008-1 and 143112/2008-2).

References

[1] J. T. Longino and R. K. Colwell, "Biodiversity assessment using structured inventory: capturing the ant fauna of a tropical rain forest," *Ecological Applications*, vol. 7, no. 4, pp. 1263–1277, 1997.

[2] K. C. Kim, "Biodiversity, conservation and inventory: why insects matter," *Biodiversity and Conservation*, vol. 2, no. 3, pp. 191–214, 1993.

[3] M. J. Samways, "Insects in biodiversity conservation: some perspectives and directives," *Biodiversity and Conservation*, vol. 2, no. 3, pp. 258–282, 1993.

[4] B. Holldobler and E. Wilson, *The Ants*, Belknap Press of Harvard University, Cambridge, Mass, USA, 1990.

[5] P. J. Folgarait, "Ant biodiversity and its relationship to ecosystem functioning: a review," *Biodiversity and Conservation*, vol. 7, no. 9, pp. 1221–1244, 1998.

[6] A. N. Andersen and J. D. Majer, "Ants show the way down under: invertebrates as bioindicators in land management," *Frontiers in Ecology and the Environment*, vol. 2, no. 6, pp. 291–298, 2004.

[7] B. T. Bestelmeyer, D. Agosti, L. E. Alonso et al., "Field techniques for the study of ground-dwelling ants: an overview, description, and evaluation," in *Ants: Standard Methods for Measuring and Monitoring Biodiversity*, D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz, Eds., pp. 122–144, Smithsonian Institution Press, London, UK, 2000.

[8] B. L. Fisher, "Improving inventory efficiency: a case study of leaf-litter ant diversity in Madagascar," *Ecological Applications*, vol. 9, no. 2, pp. 714–731, 1999.

[9] H. Romero and K. Jaffe, "A comparison of methods for sampling ants (Hymenoptera, Formicidae) in Savannas," *Biotropica*, vol. 21, no. 4, pp. 348–352, 1989.

[10] J. H. C. Delabie, B. L. Fisher, J. D. Majer, and I. W. Wright, "Sampling effort and choice of methods," in *Ants: Standard Methods for Measuring and Monitoring Biodiversity*, D. Agosti,

J. D. Majer, L. E. Alonso, and T. R. Schultz, Eds., pp. 145–154, Smithsonian Institution Press, London, UK, 2000.

[11] D. M. Olson, "A comparison of the efficacy of litter sifting and pitfall traps for sampling leaf litter ants (Hymenoptera, Formicidae) in a Tropical Wet Forest, Costa Rica," *Biotropica*, vol. 23, no. 2, pp. 166–172, 1991.

[12] J. T. Longino, J. Coddington, and R. K. Colwell, "The ant fauna of a tropical rain forest: estimating species richness three different ways," *Ecology*, vol. 83, no. 3, pp. 689–702, 2002.

[13] C. T. Lopes and H. L. Vasconcelos, "Evaluation of three methods for sampling ground-dwelling ants in the Brazilian Cerrado," *Neotropical Entomology*, vol. 37, no. 4, pp. 399–405, 2008.

[14] A. N. Andersen and A. Brault, "Exploring a new biodiversity frontier: subterranean ants in northern Australia," *Biodiversity and Conservation*, vol. 19, no. 9, pp. 2741–2750, 2010.

[15] K. T. R. Wilkie, A. L. Mertl, and J. F. A. Traniello, "Species diversity and distribution patterns of the ants of Amazonian Ecuador," *PLoS ONE*, vol. 5, no. 10, Article ID e13146, pp. 1–12, 2010.

[16] J. F. Lynch, A. K. Johnson, and E. C. Balinsky, "Spatial and temporal variation in the abundance and diversity of ants (Hymenoptera: Formicidae) in the soil and litter layers of a Maryland forest," *American Midland Naturalist*, vol. 119, no. 1, pp. 31–44, 1988.

[17] R. R. Silva and R. Silvestre, "Riqueza da fauna de formigas (Hymenoptera: Formicidae) que habita as camadas superficiais do solo em Seara, Santa Catarina," *Papéis Avulsos de Zoologia*, vol. 44, no. 1, pp. 1–11, 2004.

[18] H. L. Vasconcelos and J. H. C. Delabie, "Ground ant communities from central Amazonia forest fragments," in *Sampling Ground-Dwelling Ants: Case Studies from the World's Rain Forests*, D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz, Eds., pp. 59–70, Curtin University School of Environmental Biology, Perth, Australia, 2000.

[19] K. T. R. Wilkie, A. L. Mertl, and J. F. A. Traniello, "Biodiversity below ground: probing the subterranean ant fauna of Amazonia," *Naturwissenschaften*, vol. 94, no. 9, pp. 725–731, 2007.

[20] S. M. Berghoff, U. Maschwitz, and K. E. Linsenmair, "Hypogaeic and epigaeic ant diversity on Borneo: evaluation of baited sieve buckets as a study method," *Tropical Zoology*, vol. 16, no. 2, pp. 153–163, 2003.

[21] T. Yamaguchi and M. Hasegawa, "An experiment on ant predation in soil using a new bait trap method," *Ecological Research*, vol. 11, no. 1, pp. 11–16, 1996.

[22] F. A. Schmidt and R. R. C. Solar, "Hypogaeic pitfall traps: methodological advances and remarks to improve the sampling of a hidden ant fauna," *Insectes Sociaux*, vol. 57, no. 3, pp. 261–266, 2010.

[23] S. O'Donnell, J. Lattke, S. Powell, and M. Kaspari, "Army ants in four forests: geographic variation in raid rates and species composition," *Journal of Animal Ecology*, vol. 76, no. 3, pp. 580–589, 2007.

[24] C. A. Klink and R. B. Machado, "Conservation of the Brazilian Cerrado," *Conservation Biology*, vol. 19, no. 3, pp. 707–713, 2005.

[25] A. T. Oliveira-Filho and J. A. Ratter, "Vegetation physiognomies and woody flora of the Cerrado biome," in *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*, P. S. Oliveira and R. J. Marquis, Eds., pp. 91–120, Columbia University Press, New York, NY, USA, 2002.

[26] C. T. Parr and S. L. Chown, "Inventory and bioindicator sampling: testing pitfall and winkler methods with ants in a South African Savanna," *Journal of Insect Conservation*, vol. 5, no. 1, pp. 27–36, 2001.

[27] S. M. Berghoff, A. Weissflog, K. E. Linsenmair, R. Hashim, and U. Maschwitz, "Foraging of a hypogaeic army ant: a long neglected majority," *Insectes Sociaux*, vol. 49, no. 2, pp. 133–141, 2002.

[28] A. Weissflog, E. Sternheim, W. H. O. Dorow, S. Berghoff, and U. Maschwitz, "How to study subterranean army ants: a novel method for locating and monitoring field populations of the South East Asian army ant *Dorylus (Dichthadia) laevigatus* Smith, 1857 (Formicidae, Dorylinae) with observations on their ecology," *Insectes Sociaux*, vol. 47, no. 4, pp. 317–324, 2000.

[29] N. J. Gotelli and R. K. Colwell, "Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness," *Ecology Letters*, vol. 4, no. 4, pp. 379–391, 2001.

[30] R. K. Colwell, "EstimateS: Statistical estimation of species richness and shared species from samples," 2009, http://viceroy.eeb.uconn.edu/estimates.

[31] J. H. Delabie and H. G. Fowler, "Soil and litter cryptic ant assemblages of Bahian cocoa plantations," *Pedobiologia*, vol. 39, no. 5, pp. 423–433, 1995.

[32] C. R. F. Brandão, R. M. Feitosa, F. A. Schmidt, and R. R. D. C. Solar, "Rediscovery of the putatively extinct ant species *Simopelta minima* (Brandão) (Hymenoptera, Formicidae), with a discussion on rarity and conservation status of ant species," *Revista Brasileira de Entomologia*, vol. 52, no. 3, pp. 480–483, 2008.

[33] C. R. F. Brandão, M. Verhaag, and J. L. M. Diniz, "A new ant subfamily from central Amazon soil samples," in *Proceedings of the 14th International Congress of IUSSI*, Hokkaido University, Sapporo, Japan, 2002.

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 342623, 9 pages
doi:10.1155/2012/342623

Research Article

The Ant Genus *Sphinctomyrmex* Mayr (Hymenoptera, Formicidae, Cerapachyinae) in the Neotropical Region, with the Description of Two New Species

Rodrigo M. Feitosa,[1] Carlos Roberto F. Brandão,[1]
Fernando Fernández,[2] and Jacques C. H. Delabie[3, 4]

[1] *Museu de Zoologia da Universidade de São Paulo, Avenida Nazaré 481, Ipiranga,*
04263-000 São Paulo, SP, Brazil
[2] *Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Carreira 30, No. 45-03, Apartado 7495,*
Bogotá, DC, Colombia
[3] *Laboratório de Mirmecologia, Centro de Pesquisas do Cacau (CEPEC/CEPLAC), Caixa Postal 7,*
45600-000 Itabuna, BA, Brazil
[4] *Departamento de Ciências Agrárias e Ambientais, Universidade Estadual de Santa Cruz, Km 16 Rodovia Ilhéus-Itabuna,*
45650-000 Ilhéus, BA, Brazil

Correspondence should be addressed to Rodrigo M. Feitosa, rfeitosa@usp.br

Received 20 May 2011; Accepted 13 June 2011

Academic Editor: Jonathan D. Majer

The ant genus *Sphinctomyrmex* has been represented in the Neotropical Region until now by a single species, *S. stali*, known only from sparse localities in southeastern Brazil. Two new neotropical species are herein described, *S. marcoyi* sp. n. and *S. schoerederi* sp. n. from workers collected in the Brazilian Amazon and Atlantic Forest, respectively. New records for *Sphinctomyrmex stali* are presented, and the species is redescribed together with discussions on its high morphological variation and the identity of its type specimen. A key for the neotropical *Sphinctomyrmex* workers, images of all species presently known, and a distribution map are supplied.

1. Introduction

Sphinctomyrmex is a pantropical and distinctive group of cerapachyine ants, originally described by Mayr [1] with *S. stali* as its type species by monotypy, based on a single gyne collected in Brazil. Borgmeier [2] provided taxonomic notes and described the worker caste of *S. stali*. Brown [3] revised the genus and provided an identification key for the species known at that time.

Morphologically, the genus is characterized by the unique arrangement of the gastric segments, which are nearly equal in length and separated from each other by distinct constrictions. *Sphinctomyrmex* is best represented in number of species in the Indo-Australian region compared to other parts of the world [4]. Until now, this genus remained known in the Neotropical region only by the rarely collected *S. stali*.

Very little is known on the natural history of *Sphinctomyrmex*. The few observations so far suggest that ants of this genus are nomadic predators of other ants [3, 5, 6].

Recent surveys of leaf litter ants in Brazilian biomes revealed several *Sphinctomyrmex* specimens, extending considerably the known distribution range of the genus. Moreover, these surveys have yielded specimens that do not fit the *S. stali* diagnosis and which are here described as two new species. In addition, we redescribe *S. stali* commenting on its extreme morphological variation and the identity of its type specimen. We hope that this paper will encourage further examination and revision of this biogeographically interesting ant genus.

2. Material and Methods

Observations were made at 60x magnification with a Leica MZ95 stereomicroscope. Measurements were made with a micrometer and recorded to the nearest 0.01 mm. Ranges between brackets are always presented as minimum–maximum values. All measurements are given in millimeters, and the abbreviations used are:

HL: head length—the maximum measurable length of head capsule excluding mandibles, measured in full-face view, in a straight line from the mid-point of the anterior clypeal margin to the midpoint of the vertexal margin;

HW: head width—the maximum width of the head capsule measured in full-face view, excluding the compound eyes;

SL: antennal scape length—the chord length of the antennal scape, excluding the basal condyle and its peduncle;

EL: eye length—the maximum measurable length of eyes in profile;

WL: mesosomal length (Weber's length)—the diagonal length of mesosoma in profile, from the midpoint of the anterior pronotal declivity to the posterior margin of the propodeal lobes;

PL: petiole length—in dorsal view, the maximum length of the petiole;

PW: petiole width—in dorsal view, the maximum width of the petiole;

GL: gaster length—the maximum length of gaster in lateral view, excluding the sting;

TL: total length—the summed length of HL, WL, PL, and GL;

CI: cephalic index—HW × 100/HL;

SI: scape index—SL × 100/HW;

OI: ocular index—EL × 100/HW;

Depository collections are referred to by the following acronyms.

CPDC: Centro de Pesquisas do Cacau, Itabuna, BA, Brazil;

MCZC: Museum of Comparative Zoology, Harvard University, Cambridge, Mass, USA;

MZSP: Museu de Zoologia da Universidade de São Paulo, São Paulo, SP, Brazil;

NHRS: Naturhistoriska Riksmuseet, Stockholm, Sweden;

UFV: Laboratório de Ecologia de Comunidades, Universidade Federal de Viçosa, Viçosa, MG, Brazil.

High resolution digital images of *Sphinctomyrmex schoerederi* sp. n. and *S. stali* (workers) are here presented thanks to the kind permission of Dr. B. L. Fisher (California Academy of Sciences). These images are available at the AntWeb webpage (http://www.antweb.org/). Images of *Sphinctomyrmex marcoyi* sp. n. and *S. stali* (gyne) were obtained under a stereomicroscope Leica M205C attached to a video camera Leica DFC 295. The photos were then combined using the software Leica Application Suite V3.Ink. Combined photos were edited in PhotoShop (Adobe) to enhance parameters of brightness and contrast. The distribution map was generated by the software Quantum GIS 1.5.0 (Tethys) with coordinates imported from Google Earth (Google).

The terms for external morphology and surface sculpturing follow, respectively, [7], [8]. The reproductive females are here called "gynes" [9].

3. Results

3.1. Revised Diagnosis for the Neotropical Species of Sphinctomyrmex

3.1.1. Sphinctomyrmex *Mayr, 1866. Sphinctomyrmex* Mayr, 1866: 895. Type species: *Sphinctomyrmex stali*, by monotypy. (for the complete taxonomic synopsis, see [4]).

Worker. Size highly variable (TL 2.04–4.64). Body yellowish to black, commonly reddish-brown, with appendages slightly lighter. Pilosity relatively dense, composed mainly by long whitish hairs, which are suberect on head, mesosoma, and petiole, and subdecumbent on the gaster dorsum; appendages densely covered by short suberect hairs; antennal funiculi and leg tarsomeres with dense pubescence. Mandibular surface smooth, with sparse piligerous punctures; antennal scapes densely punctuate; body dorsum variably foveolate, with a single filiform hair projected from each fovea; declivous face of propodeum smooth to faintly areolate; dorsal surface of pygidium shallowly and densely areolate.

Head as long as to longer than broad; posterior margin mostly straight with a discrete median concavity; mandibles subtriangular, without intramandibular space when fully closed; mandibular dentition inconspicuous; antennae with 12 segments; antennal scapes clavate, distinctly curved at the base and relatively short; funicular segments length gradually increasing towards the apex; eyes strongly reduced to vestigial.

Mesosoma subrectangular in lateral view, relatively elongate, with a flat and continuous dorsal profile; inferior corners of pronotum rounded; anepisternum and katepisternum separated by a distinct suture; dorsal and posterior margins of propodeum meeting in a distinct angle, never projected as teeth or spines; propodeal spiracles set very low in the segment, bellow the midheight of propodeum in lateral view, with the opening directed posterad; propodeal lobes well developed and subquadrate; declivous face of propodeum straight in lateral view.

Petiole not pedunculate, slightly higher than long in lateral view, with dorsal face weakly convex; in dorsal view, petiole barely longer than broad; subpetiolar process developed, rounded apically, and in general with a conspicuous elliptical to rounded fenestra. In dorsal view, first gastral segment (abdominal III) notably narrower than the posterior ones, separated from the second gastral segment (abdominal IV) by a wide and deep constriction; abdominal segment IV with a relatively large pretergite; segments V to VII nearly equal in length, separated from each other by distinct constrictions.

Gyne. See comments under *S. stali* description.

3.2. Identification Key to Neotropical Species of Sphinctomyrmex *(Workers).*

(1) Size relatively small (HW <0.40 mm); head notably elongate (CI <70); dorsum of mesosoma with a median longitudinal smooth stripe (Brazil: AM) ... *S. marcoyi* sp. n.

\- Size relatively large (HW >0.40 mm); head moderately elongate to subquadrate (CI >70); dorsum of mesosoma without a median longitudinal smooth stripe . . . (2)

(2) Head slightly to considerably elongate; clypeus narrowly inserted between the frontal lobes, so that the frontal carinae are placed close to each other (Figures 2(a) and 2(d)); lateral lobes of the anterior margin of clypeus absent or vestigial; abdominal segments IV to VII with comparatively short pretergites; gastral dorsum devoid of appressed hairs (Brazil: BA, MG, RJ, SC, SP) ... *S. stali* Mayr

\- Head distinctly subquadrate; clypeus broadly inserted between the frontal lobes, so that the frontal carinae are well separated from each other (Figure 1(d)); anterior margin of clypeus with two lateral lobes projecting over the mandibles; abdominal segments IV to VII with strongly developed pretergites; gastral dorsum with short appressed hairs (Brazil: MG) ... *S. schoerederi* sp. n.

3.3. Species Accounts

3.3.1. Sphinctomyrmex marcoyi *sp. n. (Figures 1 and 4).*

Holotype Worker. Brazil. Amazonas; Manaus, Rs 2206; in soil, 01.11.1993; A.B. Casimiro col. no. 6 (4832) [CDPC].

Diagnosis. Sphinctomyrmex marcoyi can be easily separated from other species in the genus by its comparatively diminutive size (HW <0.40 mm, TL <3.00 mm), conspicuously elongate head, comparatively short scapes, and by the presence of a smooth longitudinal stripe on the dorsum of mesosoma, which is otherwise covered by foveolae and subdecumbent to erect hairs.

Holotype Measurements. HL 0.53; HW 0.35; SL 0.21; EL 0.025; WL 0.61; PL 0.23; PW 0.21; GL 1.24; TL 2.04; CI 66; SI 60; OI 7.14.

Worker Description. Relatively small size (TL about 2.00 mm). Body reddish-brown with slightly lighter appendages. Body dull; dorsum of mesosoma and petiole shiny. Pilosity comparatively dense; dorsum of head with short suberect to subdecumbent hairs; dorsum of mesosoma with short suberect hairs and a few long, sparsely distributed erect hairs, except for a longitudinal median stripe devoid of pilosity; petiole densely covered by suberect hairs; gastral dorsum with short appressed hairs mixed with sparse, longer hairs. Posterior area of head (nuchal area) opaque; dorsum of body densely foveolate; dorsum of mesosoma with a longitudinal, smooth, and shining, median stripe; sides of mesosoma and petiole with faint irregular reticulation; declivous face of propodeum without discernible sculpture; dorsal surface of the apical segments of gaster finely foveolate, the foveolae separated by wide interspaces (wider than the foveolae).

Head elongate (CI 66), slightly broader anteriorly; lateral margins faintly convex; clypeus narrowly inserted between the frontal lobes; anterior margin of clypeus devoid of lateral lobes, with a distinct median incision; antennal scapes short, with the apices well below the level of eyes; antennal club formed only by the apical segment, which is longer than the four preceding segments combined; eyes strongly reduced, as small as or smaller than the adjacent foveae of the head surface, with two small facets at it's maximum diameter. In dorsal view, lateral margins of mesosoma subparallel; pronotum with evenly rounded humeral corners; promesonotal suture not impressed dorsally. In dorsal view, petiole slightly longer than broad, with lateral margins slightly divergent; subpetiolar process moderately developed. Abdominal segments IV to VII with short pretergites, separated from each other by deeply impressed, short constrictions.

Gyne. Unknown.

Male. Unknown.

Etymology. The specific epithet honors Laurent Saint-Cricq (1815–1888), who published several papers and books between 1853 and 1876 on his voyages to South America (under the pseudonym of Paul Marcoy or Paul de Carmoy). His writings were particularly humanistic and naturalistic; his most important book is "Voyage à travers l'Amérique du Sud, de l'Océan Pacifique à l'Océan Atlantique" published in 1869 and translated into different languages.

Comments. Sphinctomyrmex marcoyi is known only from the holotype. The specimen was collected from a soil sample (25 cm depth). Nothing is known about its biology. As far as we know this is the only *Sphinctomyrmex* species recorded in the Amazon Forest [10], extending the distribution range of the genus more than 2,500 km to the north-west.

3.3.2. Sphinctomyrmex schoerederi *sp. n. (Figures 1 and 4).*

Holotype Worker. Brazil. Minas Gerais; Viçosa; ii.1994; Sperber, Louzada and Lopes cols [MZSP].

Diagnosis. This species can hardly be confounded with other congeners given the combination of subquadrate head,

(a) (b) (c) (d) (e) (f)

Figure 1: *Sphinctomyrmex marcoyi*. (a)–(c): Holotype worker from Manaus, AM, Brazil: (a) head in full face view, (b) lateral view, (c) dorsal view. Image by Ricardo Kawada, specimen CPDC 6(4832). *Sphinctomyrmex schoerederi*. (d)–(e): Holotype worker from Viçosa, MG, Brazil: (d) head in full face view, (e) lateral view, (f) dorsal view. Image by April Nobile, specimen CASENT 0178849.

anterior margin of clypeus with two lateral lobes projecting over the mandibles, abdominal segments IV to VII with strongly developed pretergites, and the presence of short appressed hairs on the dorsal surface of gaster.

Holotype Measurements. HL 0.72; HW 0.65; SL 0.43; EL 0.05; WL 1.01; PL 0.44; PW 0.41; GL 2.31; TL 4.48; CI 90.11; SI 65.81; OI 7.32.

Worker Description. Size comparatively large (TL 4.48 mm). Body reddish-brown with appendages slightly lighter. Pilosity dense; gaster covered by short appressed hairs.

Posterior area of head (nuchal area) smooth and shiny; body dorsum foveolate; space between the foveae mostly smooth, with fine longitudinal striation on the anterior portion of head; declivous face of propodeum shallowly punctuate-reticulate; sides of mesosoma and petiole strongly sculptured, with shallow foveae and irregular reticulation; sides of gaster predominantly smooth and shiny, with a few coarse punctures.

Head subquadrate (CI 90.11); lateral margins gently convex; clypeus broadly inserted between the frontal lobes, so that the frontal carinae are well separated from each other; anterior margin of clypeus with two lateral lobes projecting over the mandibles; antennal scapes reaching the level of eyes; apical segment of antennae longer than the three preceding ones together; antennal club formed only by the apical segment; eyes strongly reduced, as large as the adjacent foveae of head surface, with about three small facets at its maximum diameter. In dorsal view, lateral margins of mesosoma convex; pronotum with humeral corners rounded; promesonotal suture distinct in dorsal view but not impressed. In dorsal view, petiole a little longer than broad, with lateral margins slightly divergent; subpetiolar process

FIGURE 2: *Sphinctomyrmex stali*. (a)–(c): worker of morphotype 1 from São Bonifácio, SC, Brazil (a) head in full face view, (b) lateral view, (c) dorsal view. Image by Michele Esposito, specimen CASENT 0178866. (d)–(f): ergatoid from São Bento do Sul, SC, Brazil (d) head in full face view, (e) lateral view, and (f) dorsal view. Image by Ricardo Kawada.

moderately developed. Abdominal segments IV to VII with strongly developed pretergites, separated from each other by comparatively shallow and wide constrictions.

Gyne. Unknown.

Male. Unknown.

Etymology. The specific epithet honors our colleague Dr. José Henrique Schoereder, a prominent ant ecologist working at Universidade Federal de Viçosa, MG, Brazil. Dr. Schoereder kindly allowed us to describe this species formerly deposited in the ant collection of his laboratory.

Comments. Sphinctomyrmex schoerederi is known only from the holotype. The specimen was collected in a leaf litter sample from a forest remnant in the campus of Universidade Federal de Viçosa, MG, Brazil, where it occurs in sympatry with *S. stali*. Nothing is known about its biology.

3.3.3. Sphinctomyrmex stali *Mayr, 1866 (Figures 2, 3, and 4). Sphinctomyrmex stali* G. Mayr, 1866: 895, pl. 20, Figure 8. Holotype gyne: Brazil, Rio de Janeiro, F. Sahlberg coll., HEVA000000012 [NHRS] (high-resolution images examined); Borgmeier [2, page 105], (distribution records and worker description); Brown [3], (world revision and key to species).

Diagnosis. The distinctly elongate head, the narrow insertion of the clypeus between the frontal lobes, the absence of lateral lobes from the anterior margin of clypeus, and the absence of appressed hairs on the dorsum of gaster separate *S. stali* from *S. schoerederi*. This species can be separated from *S. marcoyi* by its much larger size and the absence of a median smooth longitudinal stripe on the dorsum of mesosoma.

Worker Measurements ($n = 20$). HL (0.60–0.79); HW (0.44–0.68); SL (0.31–0.50); EL (0.02–0.08); WL (0.71–1.12); PL (0.28–0.43); PW (0.29–0.41); GL (1.66–2.39); TL (3.33–4.64); CI (71.79–86.00); SI (68.42–77.50); OI (3.33–12.50).

Figure 3: *Sphinctomyrmex stali*. (a)–(c): worker of morphotype 2 from Ubatuba, SP, Brazil (a) head in full-face view, (b) lateral view, and (c) dorsal view. Image by Michele Esposito, specimen CASENT 0178865. (d)–(f): worker of morphotype 3 from Viçosa, MG, Brazil (d) head in full-face view, (e) lateral view, (f) dorsal view. Image by April Nobile, specimen CASENT 0178850.

Worker Description. Size highly variable (TL 3.33–4.64). Body yellowish to black, commonly reddish-brown with slightly lighter appendages. Pilosity dense; gaster devoid of appressed pilosity. Posterior area of head (nuchal area) smooth to coarsely striate; dorsum of body sparsely foveolate; space between the foveae predominantly smooth and shiny; declivous face of propodeum smooth and shiny to shallowly punctuate-reticulate; sides of meso- and metasoma predominantly smooth and shiny, with a few coarse punctures.

Head slightly to considerably longer than broad, (CI 71.79–86.00); lateral margins subparallel to gently convergent; clypeus narrowly inserted between the frontal lobes, so that the frontal carinae are close to each other; lateral lobes of the anterior margin of clypeus absent or vestigial; antennal scape apices not reaching the level of the compound eyes; apical segment of antennae as long as the three preceding sgments combined; antennal club formed by the apical segment or by the two apical segments; compound eyes strongly reduced to vestigial, as large as or slightly larger than the adjacent foveae of head surface. In dorsal view, lateral margins of mesosoma subparallel; pronotum with humeral corners angled but not forming teeth or spines; promesonotal suture distinct to vestigial in dorsal view, not impressed. In dorsal view, petiole as long as to gently longer than broad with lateral margins feebly divergent; subpetiolar process well developed. Abdominal segments IV to VII with relatively short pretergites, separated from each other by deeply impressed, short constrictions.

Gyne (Ergatoid) Measurements (n = 3). HL (0.66–0.68); HW (0.52–0.55); SL (0.36–0.38); EL (0.08–0.11); WL (0.91–0.98); PL (0.36–0.41); PW (0.32–0.36); GL (1.95–2.17); TL (3.89–4.20); CI (78.57–81.40); SI (65.71–72.73); OI (15.15–20.00).

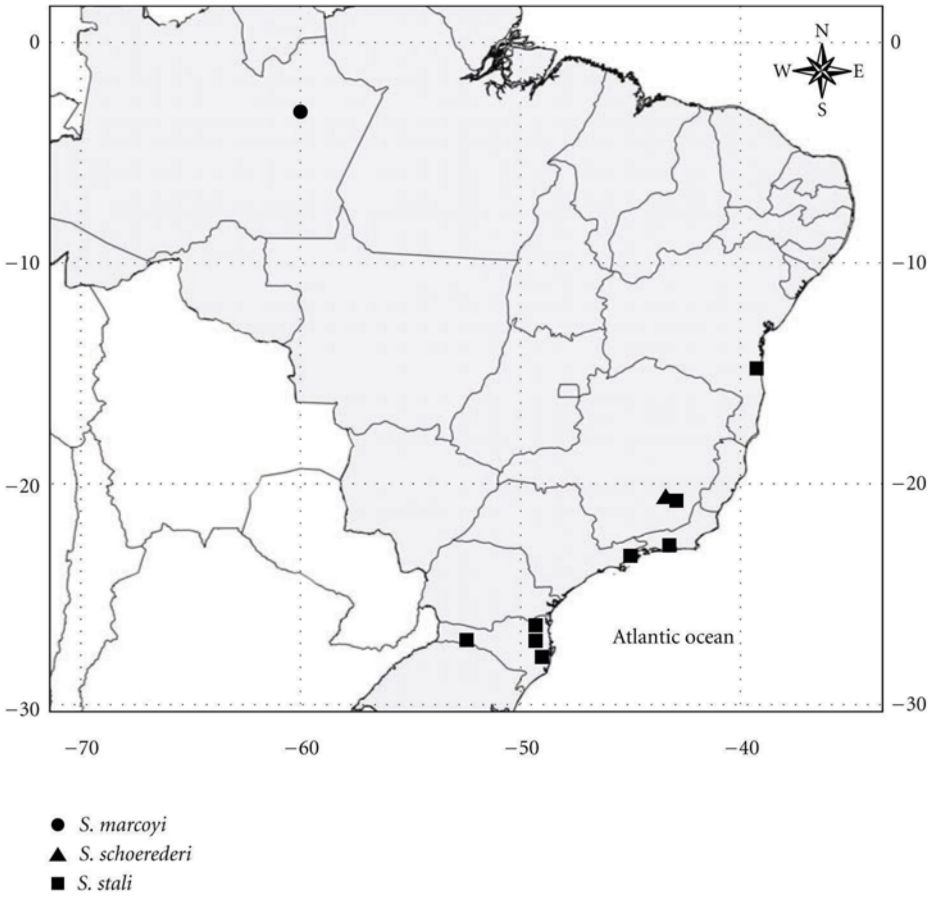


Figure 4: Distribution map for the neotropical species of *Sphinctomyrmex*.

Gyne Description. Two forms are recognized, alates and ergatoids (but see comments below). The alate form is known from a single specimen, the holotype. This gyne differs from workers by the typical characters expected for ant reproductive females: size significantly larger (TL *ca.* 6.00); ocelli well developed; compound eyes considerably large, occupying almost one third of the lateral margin of head. Pronotumis well developed, without projections; scutum large and trapezoidal; notauli shallow, almost indistinct; parapsidial lines feebly visible and convergent towards scutellum; scutoscutellar sulcus impressed; scutellum relatively narrow and set at the same level as the scutum, in lateral view; propodeum large in dorsal view, with dorsal face meeting the declivous face in a blunt angle; wings unknown. Petiole and gaster comparatively larger than in conspecific workers.

The ergatoids (Figures 2(d)–2(f)) differ from the conspecific workers only by the presence of three equally developed ocelli and by the compound eyes being comparatively well developed (OI 15.15–20.00).

Male. Unknown.

Etymology. Dr. Gustav Mayr named this species after the Swedish entomologist Dr. Carl Stål (1833–1878), who was a professor of the Zoological Department of the Royal Swedish Museum of Natural History in Stockholm. Although he published mostly on Hemiptera and was regarded as its world's foremost scholar, Dr. Stål also published on Orthoptera and to a lesser extent on Coleoptera and Hymenoptera.

Variation. At least three different morphotypes of this highly variable species can be distinguished. Categorization of these morphotypes is somewhat arbitrary as they are not entirely distinct from each other. Therefore, they are not to be recognized as distinct units, but rather as belonging to a gradient. The following comparison, however, simplifies the description of morphological variation and allows for the recognition of possible geographic patterns.

Morphotype 1 (Figures 2(a)–2(c)). Medium size (HW 0.48–0.55, TL 3.51–4.00). Color reddish-brown to blackish. Posterior area of head (nuchal area) predominantly smooth and shiny. Head distinctly longer than broad (CI 75.50–81.40), with lateral margins weakly convex; eyes reduced but distinctly larger than the adjacent foveae of head surface. Promesonotal suture distinct in dorsal view.

This morphotype conforms most closely with the first workers described for this species [2]. Despite its distribution being restricted to scattered localities in the state of Santa

Catarina, southern Brazil, it is the most common morphotype of *S. stali* in museum collections.

Morphotype 2 (Figures 3(a)–3(c)). Large size (HW 0.60–0.69, TL 4.05–4.64). Color reddish to dark brown. Posterior area of head (nuchal area) predominantly smooth and shiny. Head moderately longer than broad (CI 81.63–86.00), with lateral margins weakly convex; eyes reduced but distinctly larger than the adjacent foveae of head surface. Promesonotal suture variably impressed in dorsal view.

In his initial description of *S. stali* workers [2], the author stated: "*…The specimens collected in October 3, 1953 are somewhat larger than the other …*" We examined these workers mentioned by Borgmeier; in fact, they are considerably larger than the other workers, and even larger than the ergatoids examined here. However, except for the exceptional size, the individuals of this morphotype are very similar to those of morphotype 1. Additional workers of morphotype 2 were collected in the Brazilian states of Bahia, Minas Gerais, and São Paulo.

Morphotype 3 (Figures 3(d)–3(f)). Small size (HW 0.44–0.47, TL 3.33–3.41). Color pale yellow to reddish-brown. Posterior area of head (nuchal area) irregularly striate, with sparse punctures. Head notably longer than broad (CI 71.79–75.00), with lateral margins subparallel; eyes vestigial, feebly convex; in some cases only discernable by a dark spot on the sides of head, of the same size as the adjacent foveae of the head surface. Promesonotal suture obsolete, almost indistinct in dorsal view.

This is the most distinctive morphotype of *S. stali*, known so far only from Viçosa, state of Minas Gerais, southeastern Brazil where it occurs in sympatry with *S. schoerederi*.

Comments. Mayr [1] described *Sphinctomyrmex* with *S. stali* as its type species, based on a single dealate gyne. However, except for the holotype, there are no records of normal (alate) gynes for *S. stali*. All reproductive females collected after the original description are ergatoids. Dr. H. Vårdal, Hymenoptera curator of the NHRS collection, kindly sent us images of the *S. stali* holotype. We confirm that it is a typical dealate ant gyne given the wing scars and the structure of mesosoma. Therefore, there are at least three possibilities: (1) *Sphinctomyrmex stali* can possess both forms of reproductive females, alates and ergatoids, as already recorded for other ant species [11, 12, Christian Peeters (pers.com.)]; (2) our current conception of *S. stali* includes more than a single species, not entirely distinguishable by morphology, and each species may present a different gyne form, or (3) the initial suspicion by Brown (see below) may prove correct, and the Brazilian locality record for the dealate gyne designated as holotype by Mayr may be in error. Hypotheses 1 and 2 seem to be the more plausible based on the label information of the type specimen. The collector of the type, the Finish entomologist Reinhold Ferdinand Sahlberg, probably captured this specimen while collecting insects in his visit to Rio de Janeiro in the middle 1800's [R.F. Sahlberg's field book; Hege Vårdal (pers.com.)]. Incidentally, this possibility is supported by Kempf's decision [13] to treat Rio de Janeiro as the type locality of *Sphinctomyrmex stali*. The nature of *S. stali* reproductive females will only be solved with the collection of additional material associated with workers.

Sphinctomyrmex stali is known from sparse localities along the southeastern portion of the Brazilian Atlantic Forest, from Santa Catarina to southern Bahia. Recent collections suggest that this species can be most commonly found in submontane forests (above 600 m) of the states of Santa Catarina and São Paulo, from whence come most of the specimens in collections. In correspondence between William Brown Jr. and Father Thomas Borgmeier in 1954 [2], Brown mentions: "*The thing that really surprised me about the paper was your mention of Plaumann's discovery of* Sphinctomyrmex *in Santa Catarina! As matter of fact, I have just finished examining the type of* S. ståli [SIC] *Mayr (Stockholm Museum), and just send it back to Sweden. I had concluded that the Brazilian locality must be in error, but if your specimens are the same, then I must revise my opinion! I could discover no characters of generic significance between* S. ståli *and the known winged females of certain Australian* "Notosphinctus", *and I tentatively conclude that these two names are synonyms. I have seen the type of* furcatus *Emery, from Burma, and also a winged female of a species (undescribed?) marked as from "Sierra Leone/Afzelius" which is surely of the same genus as* ståli *on female characters alone, but which is blackish in color ….*"

In a single leaf-litter sample collected in São Bonifácio, Santa Catarina, six workers and two ergatoids, very similar to the workers, were captured, which suggests that *S. stali* is polygynous, as already described for other *Sphinctomyrmex* species [3, 6].

Material Examined. Brazil: *Bahia*: Ilhéus, Área Zoolog., CEPEC, Ilhéus-Itabuna km 22, x.1986, J. Delabie leg., no. 56 (1 worker) [MZSP]; *Minas Gerais*: Viçosa, Mata da Prefeitura. 07.i – 09.xi.1994, P.S.P. Ferreira col. (1 worker) [CDPC]; Mata do Paraíso, xii.1993–xii.1994, Ferreira, P.S.F. col. (3 workers) [CPDC]; same locality, 1997/1998, Soares, S.M. col., no. 5245 (1 worker) [CPDC]; same locality, Fragment P14, Winkler extractor, 08.iv.1998, Soares, S.M. col. (1 worker) [UFV]; same locality, same data, no. 116, Soares, S.M. col. (1 worker) [MZSP]. *Santa Catarina*: Blumenau, P.E. das Nascentes, 27 06 15 S 49 09 14 W, 20–27.x.2000, R.R. Silva & F. Eberhardt cols, no. 50 (1 worker) [MZSP]; Nova Teutônia [currently Seara], 27 11 S 52 23 W, x.1953, Fritz Plaumann col. (1 worker) [MZSP]; same locality, iv.1954, Fritz Plaumann col. (4 workers) [MZSP]; same data (1 worker) [MCZC]; same locality, xi.1957, Fritz Plaumann col. (2 workers) [MZSP]; same locality, v.1960, Fritz Plaumann col. (1 gyne) [MZSP]; same locality, iii.1971, Fritz Plaumann col., no. 7055 (1 worker) [MZSP]; same locality, iv.1972, Fritz Plaumann col., no. 7983 (1 worker) [MZSP]; same locality, xii.1974, Fritz Plaumann col., Kempf collection, no. 11627 (3 workers) [MZSP]; São Bento do Sul, A.P.A. Rio Vermelho, 26 21 51 S 49 16 16 W, 30.iii–4.iv.2001, R.R. Silva & F. Eberhardt cols, nos. 28/50 (6 workers and 2 ergatoid gynes) [MZSP]; São Bonifácio, P.E. da Serra do

Tabuleiro, 27 49 06 S 48 54 41 W, 8–13.iii.2004, R.R. Silva, B.H. Dietz & N.L. Albuquerque cols, nos. 2/6/23 (5 workers) [MZSP]. *São Paulo*: Ubatuba, P.E.S.M., N. Picinguaba, 600 m, 23 17 54.4 S 44 47 49.2 W, 23.i.2006, Scott-Santos, C.P. & Santos, E.F. cols, no. 4 (1 worker) [MZSP].

Acknowledgments

The authors thank Brian Fisher, Erin Prado, and April Nobile (CASC) for the preparation of and permission to use the automontage figures, and Muriel Oliveira for technical support. Ricardo Kawada (MZSP) kindly prepared the images of *Sphinctomyrmex marcoyi* and of the *S. stali* gyne. Two anonymous reviewers critically read and greatly improved the manuscript. The authors are deeply indebted to Dr. Hege Vårdal (NHRS) and Dr. Larry Huldén for the invaluable information on the *S. stali* holotype and on the expeditions of R.F. Sahlberg to Brazil. Christian Peeters provided them with important information on ergatoids. The authors acknowledge the research grant received from Fundacão de Amparo à Pesquisa do Estado de São Paulo, Biota-FAPESP Program (no. 98/05083-0 to C.R.F. Brandão), the project PRONEX FAPESB-CNPq PNX 0011-2009, and for the grant to R.M. Feitosa (no. 07/01310–2). J.H.C. Delabie and C.R.F. Brandão are research fellows of CNPq. In accordance with section 8.6 of the ICZNs International Code of Zoological Nomenclature, printed copies of the edition of Psyche containing this article are deposited at the following six publicly accessible libraries: Green Library (Stanford University), Bayerische Staatsbibliothek, Library—ECORC (Agriculture & Agri-Food Canada), Library—Bibliotheek (Royal Belgium Institute of Natural Sciences), Koebenhavns Universitetsbibliotek, University of Hawaii Library.

References

[1] G. L. Mayr, “Diagnosen neuer und wenig gekannter formiciden,” *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien*, vol. 16, pp. 885–908, 1866.

[2] T. Borgmeier, “Myrmecologische studien I,” *Anais da Academia Brasileira de Ciências*, vol. 29, pp. 103–128, 1957.

[3] W. L. Brown Jr, “Contributions toward a reclassification of the Formicidae. V. Ponerinae, Tribes Platythyreini, Cerapachyini, Cylindromyrmecini, Acanthostichini, and Aenictogitini,” *Search Agriculture*, vol. 5, pp. 1–116, 1975.

[4] B. Bolton, G. Alpert, P. S. Ward, and P. Naskrecki, *Bolton’s Catalogue of Ants of the World: 1758–2005*, Harvard University Press, Cambridge, Mass, USA, 2006.

[5] E. O. Wilson, “Observations on the behavior of the Cerapachyine ants,” *Insectes Sociaux*, vol. 5, no. 1, pp. 129–140, 1958.

[6] A. Buschinger, C. Peters, and R. H. Crozier, “Life-pattern studies on an Australian *Sphinctomyrmex* (Formicidae; Ponerinae; Cerapachyini): functional polygyny, brood periodicity, and raiding behavior,” *Psychology*, vol. 96, pp. 287–300, 1989.

[7] B. Bolton, *Identification Guide to the Ant Genera of the World*, Harvard University Press, Cambridge, Mass, USA, 1994.

[8] R. A. Harris, “A glossary of surface sculpture,” *Occasional Papers of the Bureau of Entomology of the California Department of Agriculture*, vol. 28, pp. 1–32, 1979.

[9] R. M. Feitosa and C. R. F. Brandão, “A taxonomic revision of the neotropical myrmicine ant genus *Lachnomyrmex* Wheeler (Hymenoptera: Formicidae),” *Zootaxa*, no. 1890, pp. 1–49, 2008.

[10] H. L. Vasconcelos and J. H. C. Delabie, “Ground ant communities from central Amazonia forest fragments,” in *Sampling Ground-dwelling Ants: Case Studies from the World’s Rain Forests*, D. Agosti, J. D. Majer, L. T. Alonso, and T. Schultz, Eds., pp. 59–70, Curtin University, School of Environmental Biology Bulletin, Perth, Australia, 2000.

[11] R. Fersch, A. Buschinger, and J. Heinze, “Queen polymorphism in the Australian ant *Monomorium* sp.10,” *Insectes Sociaux*, vol. 47, no. 3, pp. 280–284, 2000.

[12] A. Buschinger and M. Schreiber, “Queen polymorphism and queen-morph related facultative polygyny in the ant, *Myrmecina graminicola* (Hymenoptera, Formicidae),” *Insectes Sociaux*, vol. 49, no. 4, pp. 344–353, 2002.

[13] W. W. Kempf, “Catálogo abreviado das formigas da Região Neotropical,” *Studia Entomologica (N.S.)*, vol. 15, pp. 3–344, 1972.

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 306925, 15 pages
doi:10.1155/2012/306925

Research Article

Community Structure of Leaf-Litter Ants in a Neotropical Dry Forest: A Biogeographic Approach to Explain Betadiversity

Rogério Silvestre,[1] Manoel F. Demétrio,[2] and Jacques H. C. Delabie[3]

[1] *Laboratório de Ecologia de Hymenoptera (HECOLAB), Universidade Federal da Grande Dourados, Rodovia Dourados, Itahum, km 12, Cidade Universitária, 79.804-970 Dourados, MS, Brazil*
[2] *Programa de Pós-Graduação em Entomologia e Conservação da Biodiversidade, Universidade Federal da Grande Dourados (UFGD), Cidade Universitária, 79.804-970 Dourados, MS, Brazil*
[3] *Laboratório de Mirmecologia, Centro de Pesquisas do Cacau, Convênio UESC/CEPLAC, 45.651-630 Ilhéus, BA, Brazil*

Correspondence should be addressed to Rogério Silvestre, rogeriosilvestre@ufgd.edu.br

Received 16 March 2011; Revised 9 May 2011; Accepted 8 June 2011

Academic Editor: Jonathan D. Majer

This paper describes habitat and geographic correlates of ant diversity in Serra da Bodoquena, a poorly surveyed region of central-western Brazil. We discuss leaf-litter ant diversity on a regional scale, with emphasis on the contribution of each of the processes that form the evolutionary basis of contemporary beta diversity. The diversity of leaf-litter ants was assessed from a series of 262 Winkler samples conducted in two microbasins within a deciduous forest domain. A total of 170 litter-dwelling ant species in 45 genera and 11 subfamilies was identified. The data showed that the study areas exhibited different arrangements of ant fauna, with a high turnover in species composition between sites, indicating high beta diversity. Our analysis suggests that the biogeographic history of this tropical dry forest in the centre of South America could explain ant assemblage structure more than competitive dominance. The co-occurrence analysis showed that species co-occur less often than expected by chance in only two of the localities, suggesting that, for most of the species, co-occurrences are random. The assessment of the structure of the diversity of litter-dwelling ants is the first step in understanding the beta diversity patterns in this region of great biogeographic importance.

1. Introduction

The highly diverse ant fauna of the leaf litter in tropical forests has been the focus of many studies investigating the structure of ecological communities, particularly in the last twenty years [1–3]. Approximately 60% of the entire ant species that are currently known live in leaf litter, where the ant fauna is especially diverse, taxonomically, morphologically, and ecologically [4–6]. Studies on the biogeography and diversity of Formicidae, as well as the processes affecting their maintenance, can be of great interest for planning effective conservation of the biota at a regional scale. Such studies can also contribute to producing new ecological and taxonomic data, particularly in areas where no previous records exist for the group [7, 8].

The Serra da Bodoquena, within the Chacoan subregion, borders the provinces Chaco, Cerrado, Pantanal and Parana Forest [9, 10] and is a place with no previous ant records. Prado and Gibbs [11] pointed out that seasonal deciduous forests are remnants of a broader continuous distribution that was present in the past, ranging from north-eastern Brazil to Argentina in the Pleistocene dry period. This currently fragmented structure is the result of the dry, cold climate that caused the retraction of wet forests to riversides and the spread of seasonal forests [12]. Deciduous forests comprise discontinuous patches along fertile valleys and basaltic and calcareous rocks in a matrix of Cerrado on the Brazilian Central Plateau. This matrix, intersected by riparian forests, acts as a connection among dry forests in north-eastern Brazil, east of Minas Gerais and São Paulo States, and forest remnants in Pantanal. The vegetation has some floristic similarities to the Amazon and the Paraguayan Chaco [13, 14].

We investigated whether the leaf-litter ant assemblages at Serra da Bodoquena could be explained by current factors, such as ant dominance and competition, or if the community structure was influenced by its geography, which differs between the northern and southern portions of Park.

Some hypotheses regarding the array of situations found in the region could be tested, assuming that the vegetation properties are also valid for the ant assemblage. Despite the biogeographic relationships of the vegetation, current and evolutionary effects of environmental formations may be reflected in the structure of the ant community. Interspecific competition is usually associated with significant divergence and with the principle of limiting similarity [15]. Although niche differentiation is undoubtedly an important concept, it seems insufficient to wholly determine the high levels of local diversity commonly observed in warm climates [5, 6, 16, 17].

Significant aggregations of assemblages have been associated with the presence of environmental filters [18]. The coexistence of species would be more frequent than expected if randomly organized, because of environmental conditions that act as environment filters, allowing only a narrow spectrum of species to survive. We discuss the possibility that the structure of the leaf-litter ant community in Serra da Bodoquena could be influenced by neighbouring landscapes, as it is situated at the intersection between the Pantanal, Chaco, Cerrado, Brazilian Atlantic Forest, and Amazon Forest biomes. Alternatively, the fauna could be completely different and specific to this Seasonal Deciduous Forest.

The following issues were based on three sets of arguments; namely, (i) if the similarity between the sampling sites is high, the ant fauna of the north and south portions of the dry forest could be derived from the same historic processes and by the same selective ecological pressures and could be driven by a single colonisation process (this argument assumes that all species have an equal probability of colonisation in all sites); (ii) if the north and south portions of the forest have a distinct fauna, this suggests that the geographic basis is important to the formation of the ant assemblages once the different portions attained a distinct physiographic structure. (Therefore, the question is whether the faunistic similarity of ant communities between the northern and southern portions of Serra da Bodoquena is low, blocks are likely to be formed through different colonisation processes;) or (iii) if the samples are dissimilar among sites, a series of distinct ecological, spatial, and temporal situations may have contributed to the formation of leaf-litter ant assemblage in the region, and the surrounding environments influence the faunistic colonisation.

The goal in the present study was thus to identify associating parameters between the community structure of leaf-litter ants and the phytophysionomic matrix within the two distinct land portions in Serra da Bodoquena National Park.

In central-western Brazil, the expansion of agriculture and intensive cattle farming has led to a dramatic loss of forests. Thus, it is likely, this insect diversity has already been affected before it is has been thoroughly evaluated. Therefore, the assessment of the structure of the diversity of leaf-litter ants is the first step in understanding these patterns in this region of great biogeographic importance.

2. Materials and Methods

This study was carried out in a seasonal deciduous forest area in Serra da Bodoquena National Park (core coordinates: 21 07 16 S 56 28 55 W). This is the only fully protected Federal Reserve of Mato Grosso do Sul, Brazil. It harbours significant portions of seasonal deciduous and semideciduous forests, transitional areas between Cerrado and Brazilian Atlantic Forest, Cerrado and Tropical Seasonal Deciduous Forest, marshes, rocky fields, and anthropic lands with cattle farms.

The western region of the Bodoquena mountain range is formed by a mosaic of vegetational types; lowlands, including savannas steppe, arborous and gramineous Chaco, plus xeromorphic and mesoxeromorphic forests. To the east, there are many cattle farms within what used to be Cerrado vegetation, to the south, there are soybean farms and islands of semi-deciduous forest, and to the north, there are the Pantanal plains. The island of preserved dry forest areas in this region is the largest of those in the centre of South America.

The Serra da Bodoquena National Park has an area of 77,200 ha, made up of a steep plateau in the west, and comprising two distinct land portions that together cover a 300 × 50 km area. The area is preserved because it is a watershed that supplies the drainage basins of the Western region of Brazil [19]. The region divides important water catchments. Salobra River, in the Northern land portion, fuels the Miranda River on Pantanal plains, and Perdido River, in the Southern land portion, fuels the Apa River. Both rivers are tributaries of the Paraguay River, although their respective waters only mix after a thousand kilometres (Figure 1).

The locality is sustained by calcareous rocks of the Corumbá group-Neoproterozoic III. It is characterised by a high rocky massif, with altitudes varying between 200 m and 770 m asl. Exposed limestone from the Tamengo formation predominates in this karstic region, where rivers are found within canyons [20, 21].

The annual average temperatures of the area vary between 22 C and 26 C. The minimum temperature can be as low as 0 C. The relative humidity is low and rarely reaches 80%, and rainfall varies between 1300 mm and 1700 mm a year. The hot and rainy season occurs between October and April, and the cold and dry season from May to September [22].

The survey was carried out from September 2005 to February 2008, with samples taken in the dry and wet seasons, at 10 selected sites, in eight collecting expeditions (in two expedictions has two sites) along the Bodoquena ridge (Table 1), covering the microbasin of Salobra River in the Northern land portion, including the Kadiwéu Indian Reserve, and the microbasin of Perdido River, in the Southern land portion (Figure 2).

The leaf-litter sampling ant was carried out according to the ALL protocol [2], with a few adaptations due to

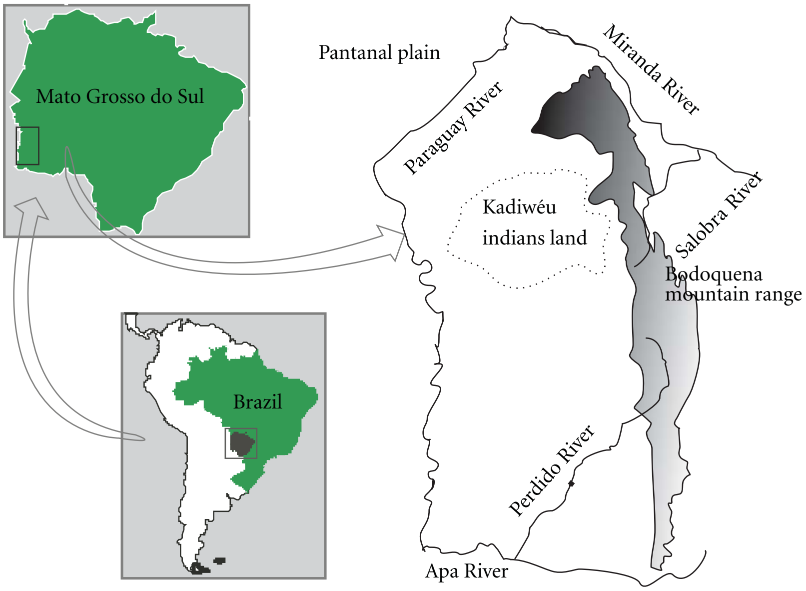


Figure 1: Map of Serra da Bodoquena (Chacoan sub-region), bordering the Pantanal province, State of Mato Grosso do Sul, Brazil.

Sites of capture

Image chart of study area: Serra da Bodoquena National Park

Polyconic projection-South American datum 1969

Cartographic base: landsat mosaic, path/rows 266/74 + 75;

acquisition dates: 2/Sept/07 + 13May/07

1 : 750000

(1) Balneário Perdido River

(2) Sta Maria Farm-Perdido River

(3) Harmonia Farm

(4) Boqueirão Farm

(5) DaMata Farm

(6) Sta Laura Farm and Salobra River-left and right margin

(7) California Farm

(8) Kadiwéu reserve

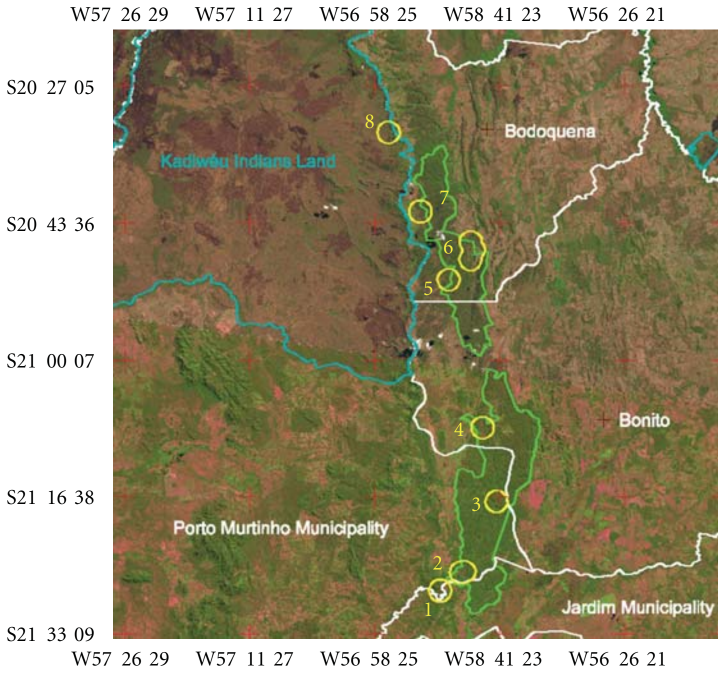


Figure 2: Landsat image indicating eight localities studied in Serra da Bodoquena National Park, Brazil. Obs: in Salobra river (site 6) three sampling points were performed (III, IV, and IX).

the habitat being composed of limestone rock floors which made it impossible to use pitfall traps in most areas. A total of 262 leaf-litter samples of 1 m^2 were extracted using mini-Winkler sacks [23]. A high diversity of microhabitats with a stratified structure was observed in the study areas. Inside the forest, there are calcareous floors and rocks with little-litter accumulation. The sampled points were chosen randomly along each transect of 40 m × 500 m but set at minimum intervals of 20 m. In each transect a minimum of 25 samples were taken. We searched for microhabitats in dry forest with sufficient leaf-litter accumulation so as to obtain approximate 2 kg. The sample exposure time of the material inside the extractor was 24 hours.

The ant identifications follow Bolton [24, 25], Fernández [26], Baroni-Urbani and De Andrade [27], and LaPolla et al. [28]. Voucher specimens were deposited at the Museu de Biodiversidade da Universidade Federal da Grande Dourados (MuBio-UFGD, Mato Grosso do Sul, Brazil) under the

Table 1: Sampling localities, number of samples per site, altitude above sea level, sampling season, and geographic coordinates.

Points/sites	Number of samples	ASL	Portion	Season	Coordinates
(I) Balneário Perdido river	25	357 m	South	Dry	21 27 55.00 S 56 48 34.31 W
(II) Boqueirão farm	32	511 m	South	Wet	21 08 13.94 S 56 43 28.00 W
(III) Salobra river-left margin	25	221 m	North	Dry	20 46 48.87 S 56 44 32.78 W
(IV) Salobra river-right margin	25	248 m	North	Dry	20 47 59. 94 S 56 44 54.05 W
(V) Harmonia farm-Perdido river	25	460 m	South	Wet	21 17 09.8 S 56 41 45.5 W
(VI) Califórnia farm	25	464 m	North	Wet	20 42 11.81 S 56 50 57.56 W
(VII) Kadiweu reserve	25	306 m	North	Wet	20 32 41.48 S 56 54 44.66 W
(VIII) Da Mata farm	25	578 m	North	Dry	20 50 26.16 S 56 47 31.85 W
(IX) Sta Laura farm-Salobra river	30	233 m	North	Wet	20 45 53.6 S 56 44 53.11 W
(X) Sta Maria farm-Perdido river	25	402 m	South	Wet	21 25 39.24 S 56 45 48.90 W

reference numbers Hym00108F to Hym02332F, at the Laboratório de Mirmecologia, Cocoa Research Centre, (CPDC, Ilhéus, Bahia, Brazil), and at the Museu de Zoologia da Universidade de São Paulo (MZ-USP, São Paulo, Brazil).

The data were considered for sites independently and grouped by land portions, South (presumably under Atlantic Forest influence- Paraná subregion), and North (presumably under Pantanal influence- Amazonian subregion).

The data analysis was based on the species occurrence in samples (frequency), as accepted for quantifying social insects [29]. To estimate species richness, the Chao 2 and Jackknife 2nd-order estimators were calculated using-EstimateS 7.5 [30], which are widely used in ant diversity studies [31–33].

Rarefaction curves showing the expected species richness versus species occurrence were used to assess the sampling efficiency for each sample area [34]. From the observed species richness per site, we estimated the number of species remaining to be sampled using the second-order Jackknife estimator (incidence based). The expected number of species was plotted against number of species records on the x-axis (individual-based accumulation curve). This plot provides a measure of species diversity which is robust to sample size effects.

In order to verify if there are differences in betadiversity increasing between northern and southern land portions, the two data sets were compared following a north-south axis and were plotted by increasing ant diversity against the distance between successive sample series in the eight localities.

To analyse site similarity, we used a principal coordinate analysis (PCO) using the Bray-Curtis dissimilarity index [35, 36]. The similarity among the ant assemblages at the different seasons and altitude was assessed using a cluster analysis (Jaccard coefficient of similarity). The resulting similarity matrix was analysed through a sequential, agglomerative, hierarchical, and nested clustering algorithm, described by Sneath and Sokal [37]. The option used was the Unweighted Pair-Group Method, arithmetic average (UPGMA). This analysis was conducted using the MVSP 3.1 software [38].

The diversity and similarity analyses were run using EstimateS 7.5 [30]. Similarity and distance matrices (Euclidian distance) were compared using a Mantel's test [39]. The data set was analysed using R software [40], using the Vegan package [41]. The graphic design was constructed with Statistica for Windows 6 [42]. The Morisita-Horn index was used too to evaluate the similarity among the localities, pairwise, because this index is not affected by the number of samples or the species richness, except for very small sampling niches [43, 44].

We used EcoSim (version 7.72) to compute random matrices of species co-occurrences [45] to determine whether the mean and variance C-score among samples is larger or smaller than expected by chance. Co-occurrences based on averages that were calculated across all possible pairs of species were randomised (5,000 repetitions) within the constraint of fixed marginal totals, which is an appropriate null model for detecting patterns caused by species interactions [46].

3. Results

More than 20,000 ants were captured in the seasonal deciduous forest. We recorded 170 species from 45 genera and

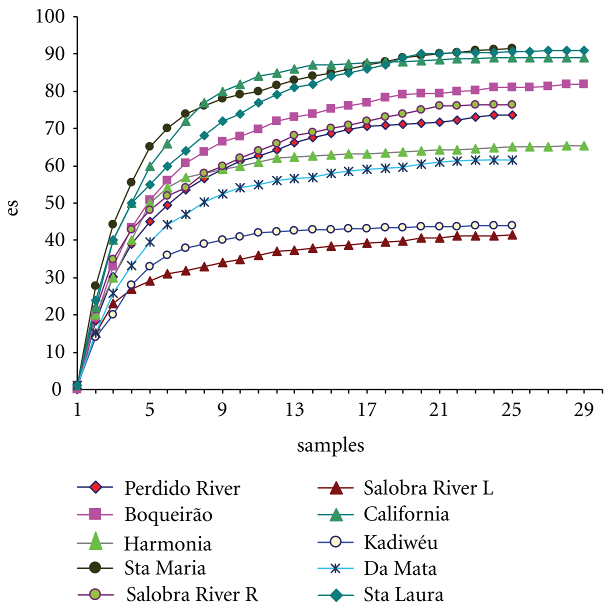


Figure 3: Comparison of incidence-based ant species rarefactions curves showing expected species richness (es) versus sampling effort in ten sampling sites (samples) in the Bodoquena mountain range.

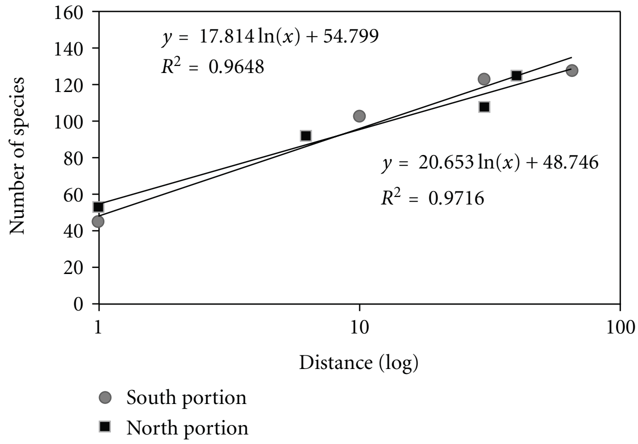


Figure 4: Ant species accumulation (logarithmic scale) in northern and southern portions in Serra da Bodoquena, Mato Grosso do Sul, Brazil. Obs: eight localities were considered, as collecting points III, IV, and IX were grouped as a single sample.

11 subfamilies out of the 15 subfamilies of Formicidae known to occur in the Neotropical Region (Table 2).

The most frequently observed species were *Solenopsis* (*Diplorhoptrum*) sp. 1 (91 occurrences), *Cyphomyrmex* (gr. *rimosus*) sp. 1 (85), *Solenopsis* sp. 2 (81), and *Hypoponera* sp. 7 (77). The most speciose genera were: *Hypoponera* (21 species), *Pheidole* (17), *Cyphomyrmex* (12), *Strumigenys* (13), *Solenopsis* (11), and *Basiceros* (9). We recorded the first observations of the genus *Cryptomyrmex* in the central-west Brazilian region. Three new species were found in deciduous forest: *Asphinctanilloides* sp. new, *Amblyopone* sp. new, and *Probolomyrmex* sp. new.

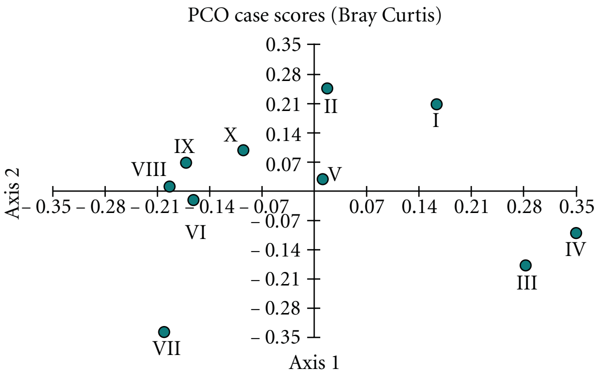


Figure 5: PCO analysis of the sites located in the northern and southern portions of Serra da Bodoquena using the Bray-Curtis dissimilarity index (eigenvalues: 0001).

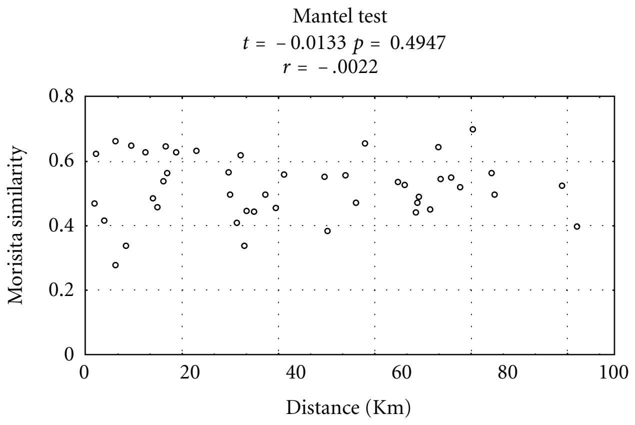


Figure 6: Mantel's test analysis between the values obtained using the Morisita-Horn similarity index and the distance between sites (km).

A total of 37 species were recorded only once (singletons). The total number of singletons represents approximately 20% of all ant species collected in the present study (Table 3).

Rarefaction curves (Figure 3) show the sampling effort in each sample site, for each land portion. Evidence of asymptotes indicates that most leaf litter ant species were sampled with the number of samples used.

The comparison of northern and southern data sets did not reveal any difference in the betadiversity of the ant communities. The two distributions follow more or less the same pattern of species substitution in relation to increasing the distance of sample sites (Figure 4).

The PCO analysis (Figure 5) shows a consistency of groups between northern and southern land portions. The analysis grouped areas of southern (I, II, and V) and also grouped the sites of northern (VI, VIII, and IX); the site X (southern) is close with this group. The samples most similar were taken in the Salobra River (III and IV) in the same season (dry).

There was no correlation between the similarity (Morisita-Horn) among species frequencies in the communities

Table 2: Records of occurrences of the 170 species collected at 10 sampling sites in Serra da Bodoquena National Park, Mato Grosso do Sul, Brazil.

Species	I	II	III	IV	V	VI	VII	VIII	IX	X
Amblyoponinae										
Tribe Amblyoponini										
Amblyopone elongata (Santschi 1912)	—	—	—	—	2	—	—	—	—	—
Amblyopone lurilabes Lattke 1991	—	5	—	—	—	—	1	—	—	—
Amblyopone sp. new	1	—	—	—	—	—	—	—	—	—
Cerapachyinae										
Tribe Cerapachyini										
Cerapachys splendens Borgmeier 1957	—	—	—	—	—	1	—	—	—	1
Dolichoderinae										
Tribe Dolichoderini										
Azteca alfari Emery 1893	4	3	2	1	4	3	—	1	4	—
Dolichoderus sp. 1	1	—	—	—	—	—	—	—	—	—
Dorymyrmex sp. 1	1	—	—	—	—	—	—	—	—	—
Linepithema humile (Mayr 1868)	2	—	1	—	4	—	—	—	—	—
Ecitoninae										
Tribe Ecitonini										
Neivamyrmex sp. 1	—	—	2	—	—	2	—	1	2	2
Neivamyrmex sp. 2	—	1	—	—	—	—	—	—	—	—
Ectatomminae										
Tribe Ectatommini										
Ectatomma brunneum Smith 1858	—	—	—	—	—	—	—	—	—	1
Ectatomma edentatum Roger 1863	—	—	—	—	—	—	—	—	1	—
Gnamptogenys striatula Mayr 1884	—	—	—	—	3	—	—	—	2	2
Gnamptogenys (gr. *striatula*) sp. 1	—	—	1	—	—	—	—	—	—	1
Gnamptogenys sulcata (Smith 1858)	—	—	—	—	—	—	—	—	1	—
Tribe Typhlomyrmecini										
Typhlomyrmex rogenhoferi Mayr 1862	—	—	1	—	—	—	—	—	—	—
Typhlomyrmex sp. 1	—	—	—	1	—	—	—	—	—	—
Formicinae										
Tribe Camponotini										
Camponotus crassus Mayr 1862	—	—	—	—	—	—	—	—	1	—
Camponotus sp. 1	—	—	—	—	—	1	—	—	—	—
Camponotus sp. 2	—	—	—	—	—	—	—	—	—	1
Tribe Plagiolepidini										
Brachymyrmex sp. 1	4	3	1	2	—	3	1	—	—	3
Brachymyrmex sp. 2	7	—	4	—	—	—	—	3	—	—
Brachymyrmex sp. 3	1	1	—	—	—	—	—	—	2	—
Brachymyrmex sp. 4	—	—	—	—	—	—	—	3	—	—
Nylanderia fulva (Mayr 1862)	—	1	—	—	3	2	—	1	—	1
Nylanderia sp. 1	—	—	2	—	1	1	3	1	—	—
Nylanderia sp. 2	1	—	1	—	3	1	—	3	1	1
Nylanderia sp. 3	—	—	—	—	—	—	2	—	—	2
Nylanderia sp. 4	—	—	—	—	—	1	—	—	—	—
Nylanderia sp. 5	—	—	—	—	—	1	—	—	—	—
Paratrechina longicornis (Latreille 1802)	1	3	—	2	3	—	—	2	4	1

Table 2: Continued.

Species	I	II	III	IV	V	VI	VII	VIII	IX	X
Leptanilloidinae										
Asphinctanilloides sp. new	—	—	—	—	—	1	—	—	—	—
Myrmicinae										
Tribe Adelomyrmecini										
Cryptomyrmex boltoni (Fernández 2003)	—	—	—	—	1	—	—	—	—	—
Tribe Attini										
Acromyrmex subterraneus (Forel 1893)	—	3	—	—	—	—	—	—	—	—
Acromyrmex sp. 1	2	—	—	—	—	—	—	—	—	—
Acromyrmex sp. 2	—	4	—	—	—	—	—	—	—	—
Apterostigma manni Weber 1938	—	1	—	—	—	—	—	—	—	—
Apterostigma pilosum Mayr 1865	1	1	—	—	—	—	—	—	—	—
Apterostigma wasmanni Forel 1892	4	1	—	—	—	—	—	—	—	9
Atta sp. 1	2	—	—	—	—	—	—	—	—	—
Cyphomyrmex lectus (Forel 1911)	—	—	5	—	—	—	—	—	—	—
Cyphomyrmex olitor Forel 1893	—	1	—	—	—	—	—	—	—	—
Cyphomyrmex (gr. *rimosus*) sp. 1	11	9	7	4	6	13	8	3	10	14
Cyphomyrmex (gr. *rimosus*) sp. 2	6	8	5	—	8	4	—	6	7	6
Cyphomyrmex (gr. *rimosus*) sp. 3	—	2	—	—	—	6	—	1	4	5
Cyphomyrmex (gr. *rimosus*) sp. 4	—	1	—	—	2	1	—	—	—	—
Cyphomyrmex (gr. *rimosus*) sp. 5	—	2	—	—	—	1	—	—	—	5
Cyphomyrmex (gr. *rimosus*) sp. 6	—	—	—	—	—	2	—	—	—	—
Cyphomyrmex (gr. *rimosus*) sp. 7	—	1	—	—	—	2	—	—	3	—
Cyphomyrmex (gr. *rimosus*) sp. 8	—	2	—	—	—	—	—	2	2	—
Cyphomyrmex (gr. *strigatus*) sp. 1	—	—	—	—	8	—	—	—	—	—
Cyphomyrmex (gr. *strigatus*) sp. 2	—	—	—	—	—	—	—	—	—	3
Mycocepurus goeldii (Forel 1893)	—	1	12	11	3	5	5	2	6	6
Mycocepurus smithii (Forel 1893)	—	1	—	—	—	—	—	—	—	—
Mycocepurus sp. 1	1	—	—	—	—	—	—	—	—	—
Myrmicocrypta sp. 1	—	3	—	1	1	—	—	—	—	—
Sericomyrmex (gr. *amabilis*) sp. 1	—	—	3	2	—	2	—	2	—	—
Sericomyrmex (gr. *amabilis*) sp. 2	—	—	—	—	—	—	—	1	—	—
Sericomyrmex sp. 1	—	4	—	—	—	3	—	—	—	—
Trachymyrmex sp. 1	4	—	—	—	—	—	—	—	—	—
Trachymyrmex sp. 2	1	1	—	—	—	—	—	—	—	—
Tribe Blepharidattini										
Wasmannia auropunctata (Roger 1863)	—	2	3	2	—	9	—	3	—	1
Wasmannia lutzi Forel 1908	1	2	1	—	—	—	—	4	1	4
Wasmannia sp. 1	—	—	—	—	3	4	5	1	—	1
Wasmannia sp. 2	—	—	—	—	—	2	—	3	1	4
Wasmannia sp. 3	—	—	—	—	—	—	—	1	2	—
Tribe Cephalotini										
Cephalotes atratus (Linnaeus 1758)	1	—	—	—	—	—	—	—	—	—
Cephalotes sp. 1	—	—	—	—	—	—	—	—	1	1
Cephalotes sp. 2	—	—	—	—	—	—	—	1	1	—
Procryptocerus alternatus Smith 1876	1	—	—	—	—	—	—	—	—	—
Tribe Crematogastrini										
Crematogaster curvispinosa Mayr 1862	—	—	4	—	—	1	1	—	—	—
Crematogaster sp. 1	—	—	3	—	2	—	—	—	—	—

Table 2: Continued.

Species	I	II	III	IV	V	VI	VII	VIII	IX	X
Crematogaster sp. 2	1	—	—	2	4	—	1	—	—	—
Crematogaster sp. 3	—	2	—	—	—	—	—	—	—	—
Crematogaster sp. 4	—	3	—	—	—	—	—	—	—	—
Tribe Dacetini										
Basiceros disciger (Mayr 1887)	—	—	—	—	1	—	—	—	—	—
B. stenognathum (Brown & Kempf 1960)	4	9	—	13	11	11	4	—	8	7
Basiceros (*Octostruma*) *balzani* (Emery 1894)	7	—	10	14	12	10	—	—	7	3
Basiceros (*Octostruma*) *simoni* (Emery 1887)	—	—	—	—	7	7	—	—	7	4
Basiceros (*Octostruma*) *rugifera* (Mayr 1887)	—	—	—	—	6	6	6	—	3	6
Basiceros (*Octostruma*) sp. 1	—	—	—	—	5	—	—	4	2	4
Basiceros (Octostruma) sp. 2	—	—	—	—	2	—	—	—	2	—
Basiceros (*Octostruma*) sp. 3	—	5	—	—	—	—	—	—	—	—
Basiceros (*Octostruma*) sp. 4	4	—	—	—	—	2	—	—	—	—
Strumigenys eggersi Emery 1890	3	3	7	—	12	9	5	3	16	4
Strumigenys (*gr. elongata*) sp. 1	—	—	2	—	—	3	—	—	—	—
Strumigenys xenochelyna (Bolton 2000)	3	4	—	—	14	—	—	—	—	—
Strumigenys sp. 1	—	—	—	7	2	—	—	—	—	2
Strumigenys sp. 2	—	2	—	—	2	4	—	—	2	4
Strumigenys sp. 3	—	—	—	—	—	—	3	—	—	—
Strumigenys sp. 4	1	—	—	—	—	—	—	—	—	—
Strumigenys sp. 5	3	6	—	—	8	—	—	—	—	—
Strumigenys sp. 6	—	5	9	2	5	4	6	1	14	—
Strumigenys sp. 7	—	—	1	—	—	2	—	—	1	—
Strumigenys sp. 8	—	—	4	—	—	—	—	—	2	—
Strumigenys sp. 9	—	—	1	—	2	3	—	—	—	2
Strumigenys sp. 10	—	—	—	—	—	—	1	—	—	—
Tribe Myrmicini										
Hylomyrma balzani (Emery 1894)	—	—	—	—	1	—	—	—	—	—
Hylomyrma sp. 1	—	—	2	—	—	—	—	—	—	—
Tribe Pheidolini										
Pheidole (gr. flavens) sp. 1	—	—	—	—	—	—	—	—	—	1
Pheidole gertrudae Forel 1886	—	—	—	1	—	—	—	—	1	2
Pheidole sp. 1	4	3	2	2	6	7	5	5	8	4
Pheidole sp. 2	2	11	3	2	5	5	7	5	—	3
Pheidole sp. 3	—	4	2	13	8	—	—	4	14	3
Pheidole sp. 4	1	3	1	4	7	—	—	—	4	3
Pheidole sp. 5	2	—	2	—	5	—	—	—	11	2
Pheidole sp. 6	2	—	1	—	—	—	—	—	3	2
Pheidole sp. 7	—	—	2	2	2	—	—	—	—	—
Pheidole sp. 8	—	—	—	—	—	—	—	—	1	—
Pheidole sp. 9	—	—	—	—	1	2	2	—	2	—
Pheidole sp. 10	—	—	2	3	—	—	—	—	1	—
Pheidole sp. 11	—	—	—	—	—	3	3	—	—	—
Pheidole sp. 12	—	—	—	—	—	1	3	—	—	—
Pheidole sp. 13	—	—	—	—	—	4	2	—	—	—
Pheidole sp. 14	—	—	—	—	—	—	—	1	—	—
Pheidole sp. 15	—	—	—	—	—	9	6	—	1	—

Table 2: Continued.

Species	I	II	III	IV	V	VI	VII	VIII	IX	X
Tribe Solenopsidini										
Carebara sp. 1	8	10	6	3	6	9	2	3	9	3
Carebara sp. 2	2	3	1	—	7	4	6	—	8	2
Megalomyrmex silvestrii Wheeler 1909	—	—	—	—	—	3	—	3	—	—
Megalomyrmex wallacei Mann 1916	—	—	—	—	—	—	3	—	—	—
Monomorium sp. 1	—	—	14	2	—	—	—	—	—	—
Oxyepoecus sp. 1	—	—	1	—	—	—	—	—	—	—
Solenopsis (gr. *geminata*) sp. 1	—	—	1	—	—	—	—	—	—	—
Solenopsis (gr. *invicta*) sp. 1	4	2	—	—	—	4	—	1	3	14
Solenopsis (gr. *invicta*) sp. 2	1	—	—	—	—	—	—	—	1	—
Solenopsis (*Diphorhoptrum*) sp. 1	10	8	6	10	10	12	5	8	7	15
Solenopsis sp. 2	5	6	4	2	3	9	—	22	20	10
Solenopsis sp. 3	3	2	5	4	2	4	9	3	2	4
Solenopsis sp. 4	8	6	8	9	—	4	—	3	1	2
Solenopsis sp. 5	1	—	—	—	—	4	—	—	5	4
Solenopsis sp. 6	—	—	—	—	—	9	—	3	3	3
Solenopsis sp. 7	2	6	—	—	—	4	—	4	4	1
Solenopsis sp. 8	—	—	—	—	—	—	—	—	10	—
Tribe Stenammini										
Rogeria alzatei Kugler 1994	—	—	—	—	—	—	1	—	—	—
Rogeria lirata Kugler 1994	—	1	—	—	—	1	7	—	—	—
Rogeria sp. 1	—	—	1	—	—	—	—	—	2	—
Rogeria sp. 2	—	—	1	—	—	—	—	—	2	—
Ponerinae										
Tribe Ponerini										
Anochetus diegensis Forel 1912	2	—	7	4	3	5	6	2	9	10
Hypoponera sp. 1	10	11	8	11	15	6	—	—	—	8
Hypoponera sp. 2	4	13	9	9	7	—	4	—	7	9
Hypoponera sp. 3	—	—	7	6	—	17	6	3	—	4
Hypoponera sp. 4	—	6	—	—	3	8	2	—	7	4
Hypoponera sp. 5	—	1	—	—	4	—	—	—	—	6
Hypoponera sp. 6	2	3	—	—	—	18	7	8	11	11
Hypoponera sp. 7	4	5	—	—	13	6	13	12	17	7
Hypoponera sp. 8	—	9	—	—	2	3	—	—	3	6
Hypoponera sp. 9	5	2	—	—	—	—	—	—	2	4
Hypoponera sp. 10	—	3	—	—	6	1	3	1	9	2
Hypoponera sp. 11	—	—	—	—	—	—	—	—	1	1
Hypoponera sp. 12	—	—	—	—	—	—	—	—	—	1
Hypoponera sp. 13	—	—	—	—	—	—	—	—	—	4
Hypoponera sp. 14	—	—	—	—	—	6	—	—	—	2
Hypoponera sp. 15	—	—	—	—	—	1	—	—	—	1
Hypoponera sp. 16	—	—	—	—	3	—	—	—	—	—
Hypoponera sp. 17	—	—	—	—	—	—	—	—	—	2
Hypoponera sp. 18	—	—	—	—	1	3	—	2	—	—
Hypoponera sp. 19	—	2	—	—	—	2	—	3	—	—
Hypoponera sp. 20	—	1	—	—	—	1	—	—	—	—
Hypoponera sp. 21	—	6	—	—	—	4	—	—	—	—

Table 2: Continued.

Species	I	II	III	IV	V	VI	VII	VIII	IX	X
Leptogenys sp. 1	—	1	1	—	1	—	—	—	—	—
Odontomachus bauri Emery 1892	—	—	2	—	—	2	—	—	—	—
Odontomachus chelifer (Latreille 1802)	—	—	—	—	—	2	—	—	—	—
Odontomachus meinerti Forel 1905	2	—	4	—	2	2	1	—	3	1
Pachycondyla harpax (Fabricius 1804)	—	—	—	—	—	—	—	—	4	—
Pachycondyla lunaris (Emery 1896)	—	—	—	—	—	—	—	—	—	1
Pachycondyla marginata (Roger 1861)	—	—	—	—	—	—	—	—	1	—
Pachycondyla ferruginea (Smith 1858)	—	—	12	2	—	—	—	1	—	—
Proceratiinae										
Tribe Probolomyrmecini										
Probolomyrmex sp. new	—	—	—	4	—	—	—	—	1	7
Probolomyrmex petiolatus Weber 1940	—	—	1	—	—	—	—	—	—	—
Pseudomyrmecinae										
Tribe Pseudomyrmecini										
Pseudomyrmex gracilis (Fabricius 1804)	2	—	—	—	—	—	—	—	—	3

Table 3: Species richness, estimated richness (Chao 2, Jackknife 2), diversity index, and the number of “singletons” and “doubletons”.

Sites	Number of observed species	(Chao 2)	Jackknife2^{a}. order	Shannon-Wiener index	Singletons	Doubletons
I	52	65.14	74.26	3.67	17	11
II	62	73.64	82.52	3.85	16	11
III	54	67.14	76.26	3.66	17	11
IV	33	33.67	29.94	3.18	4	12
V	57	59.91	62.29	3.79	8	11
VI	72	80.65	88.80	3.98	15	13
VII	36	39.60	42.87	3.39	6	5
VIII	45	61.33	66.03	3.45	14	6
IX	69	79.80	89.68	3.86	18	15
X	70	82.04	91.38	3.96	17	12
Total	170	231.70	250.38	4.40	37	17

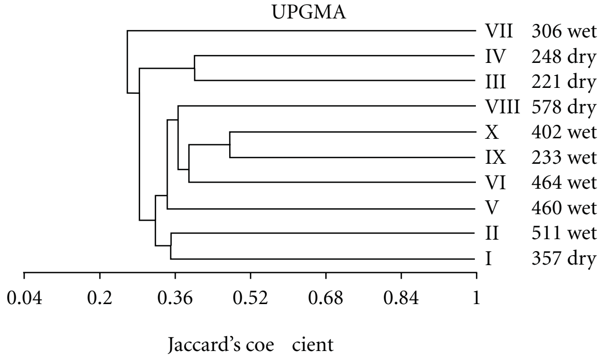


Figure 7: Dendrogram of the similarities (Jaccard coefficient, UPGMA cluster analysis) among 10 sampling sites in the Bodoquena mountain range to leaf-litter ant's fauna. Wet and dry mean seasons, and numbers mean altitude (als).

and the geographical distance (km) between the sites ($r = -0.002$; $P = 0.49$) (Table 4; Figure 6).

The similarity was compared between areas in relation to season and altitude. The samples made during wet season were richer in species, and samples performed in same seasons (VI, IX, and X) appeared grouped. There was no consistent pattern between the assemblages according the altitude ($r = 0.214$; $P = 0.55$) (Figure 7).

The co-occurrence analysis indicated that species co-occurred less often than expected by chance in only two of the localities sampled P (observed expected) = 0.003, for the Balneário Perdido river, and P (observed expected) = 0.042 for the Santa Maria Perdido River, both in the southern micro-basin, suggesting that species co-occurrences are random (Figure 8).

4. Discussion

Our results suggest that the studied sites exhibit different arrangements of ant fauna with a replacement in abundant species across sampling units, which results in high beta diversity. Gotelli and Ellison [47] suggested that species-energy relationships, in addition to other factors that are

Table 4: Similarity analysis, richness, species shared and distance between sample sites in a pairwise comparison of the leaf-litter ant assemblages from Serra da Bodoquena, Brazil.

Localities		Shared species	Chao shared (estimator)	Morisita-Horn	Distance (Km)
Balneário	Boqueirão	30	36.14	0.67	30.05
	Salobra left margin	25	30.02	0.54	76
	Salobra right margin	18	21.14	0.54	73.77
	Harmonia	26	29.18	0.63	23
	Califórnia	25	25.83	0.56	84.4
	Kadiweu reserve	16	16.59	0.39	102
	Da Mata	20	23.02	0.47	69
	Sta Laura	30	36.44	0.51	77.73
	Sta Maria	32	35.76	0.66	6.2
Boqueirão	Salobra left	22	24.69	0.45	39.5
	Salobra right	20	21.49	0.49	37.3
	Harmonia	31	33.99	0.64	16.7
	Califórnia	36	40.73	0.55	49.7
	Kadiweu reserve	18	19.14	0.44	68.6
	Da Mata	26	30.15	0.44	33.5
	Sta Laura	32	34.93	0.55	41.3
	Sta Maria	35	39.71	0.61	32.2
Salobra left	Salobra right	25	26.48	0.62	2.25
	Harmonia	28	32.67	0.47	56.13
	Califórnia	30	34.48	0.48	13.96
	Kadiweu reserve	17	18.28	0.40	31.46
	Da Mata	24	26.26	0.33	8.43
	Sta Laura	29	38.81	0.46	1.81
	Sta Maria	29	37.35	0.45	71.5
Salobra right	Harmonia	22	24.07	0.55	54
	Califórnia	19	19.22	0.45	14.95
	Kadiweu reserve	14	14.23	0.33	33
	Da Mata	18	20.67	0.27	6.28
	Sta Laura	20	23.23	0.41	3.88
	Sta Maria	23	24.24	0.49	69.3
Harmonia	Califórnia	33	35.42	0.52	66.34
	Kadiweu reserve	22	22.82	0.49	85
	Da Mata	23	28.73	0.38	50.3
	Sta Laura	33	33.54	0.65	58
	Sta Maria	36	37.78	0.56	17
Califórnia	Kadiweu reserve	29	31.70	0.62	18.84
	Da Mata	33	37.57	0.53	16.26
	Sta Laura	37	40.34	0.62	12.5
	Sta Maria	43	48.18	0.69	80.5
Kadiweu	Da Mata	16	18.11	0.44	35
	Sta Laura	20	20.42	0.56	29.7
	Sta Maria	22	22.97	0.52	98.9
Da Mata	Sta Laura	30	39.10	0.64	9.56
	Sta Maria	30	33.74	0.53	64.9
Sta Laura	Sta Maria	45	52.68	0.64	73.22

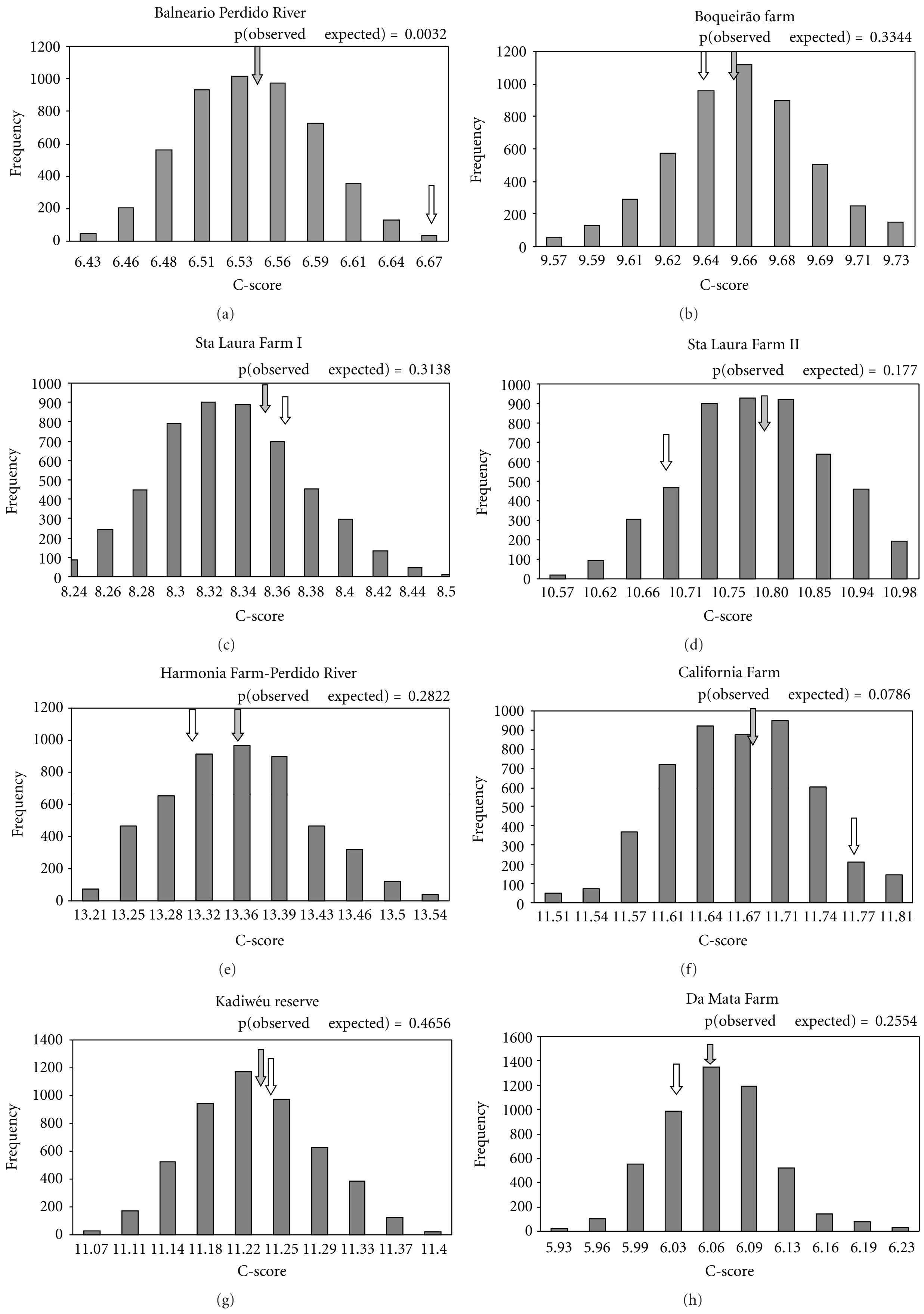
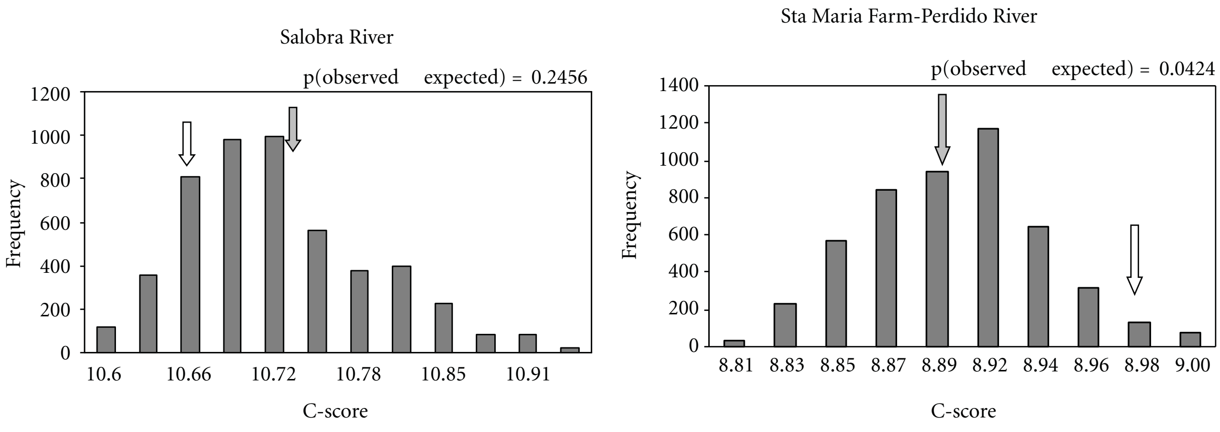


Figure 8: Continued.



(i) (j)

Figure 8: Co-occurrence analysis comparing 262 Winkler's samples of leaf-litter ants in Serra da Bodoquena. (Full arrow represents the expected values, and empty arrow represents the observed values for C-score measures.)

strongly associated with latitude, elevation, light availability, and vegetation composition, are important at regional spatial scales. Local and regional effects can mask or amplify larger-scale latitudinal patterns of species richness.

The differences in species diversity among the study sites could be related to Pleistocene events, such as biota interpenetration between two geologically distinct environments, and the phytophysionomic mosaic occurring in the region. According to Johnson and Ward [48], the topography of an ecotone and adjacent ecosystems is the most important factor affecting ant species richness. Here, each area could similarly allow the entrance of species coming from the surrounding matrix, affecting in turn the distribution of species in the core of the study sites.

There are several possible explanations for the inverse relationship between the observed low alpha diversity and high beta diversity, such as the particular characteristics of the forest fragments. The conservation status and potential connections between forest sites affect species persistence and colonisation in each site. These potential connections have a direct influence on the structure delimited by a buffer (considering the establishment of an influence zone for each area), which leads to an increase in species richness in interconnected forest fragments.

The absence of correlation between similarity and distance suggests that the ant species and assemblages are randomly distributed over the region. The low similarity between consecutive sampled sites suggests a strong formation effect and the influence of adjacent areas, which are evidenced by high beta diversity, with different arrangements of the ant fauna and a high turnover in species dominance across samples.

In forest fragments, ant richness depends on the diversity of local microhabitats and other factors acting at a local scale, such as physical and vegetation structure [33, 49], relief, humidity, and amount of leaf litter available at the location of the food resources and nesting sites used by ants [50, 51]. Significant variance in species composition can be explained by notable features that shape leaf litter ant communities, namely, litter biomass, soil stoichiometry, heterogeneous distribution of nutrients, soil moisture, invasive species, ecological disturbance at a small scale, and competition dynamics [52–56]. However, it is the ecological and historical biogeography that determines the current composition of the ant assemblages that colonize these micro-habitats (biotic and abiotic filters in the historical evolution of habitats), and also patchiness in space and time which are originated from different sources.

Our results suggest that estimated richness (Chao 2 = 231.7, Jackknife 2 = 250.4) is highly affected by the number of species that were only recorded once ("rare species" = 37). This pattern is in agreement with other studies in the Neotropical Region [5, 32, 57], which have found a high incidence of rare species in ant communities.

The Kadiwéu indigenous reserve, bordering the Pantanal plain, was the locality with lowest similarity conjunct dataset. The deciduous forest in this area forms an enclave of vegetation, influenced by the transition to Cerrado in this area. Transition zones are located at the boundaries between biogeographic regions and represent areas of biotic overlap, which are promoted by historical and ecological changes that allow the mixture of different biotic elements [9, 10].

The pattern observed suggests that the structure of the local community is directly affected by the landscape matrix in each region and that it is in fact an ecotone of the Chaco, Cerrado, Atlantic Forest, Amazonian Forest, and Pantanal.

The co-occurrence analysis of leaf-litter ant species indicates that competitive interactions are not the only factors responsible for organising ant assemblages. There is no reason to reject the null hypothesis that the number of checkerboard pairs in the samples is random.

Our results corroborate Andersen [16], agreeing that species coexistence is determined to a significant extent by processes operating during the colonization phase, rather than just by interactions between established colonies, and that competitive outcomes are highly conditioned by environmental variation, which severely limits competitive exclusion.

In spite of changes in the extant ant species along a latitudinal gradient in the Cerrado biome [17], community functionality remains similar; this suggests a similar evolutionary ecological history in response to this matrix. In cases where the functionality of a community is distinct, we can assume that the evolutionary history of colonisation came from particular processes and not from a common process (monophyletic). Regarding the functional structure of the community, we suggest that further studies should investigate whether the same guilds are found in the northern and southern portions of Serra da Bodoquena.

Acknowledgments

The authors thank the members of the “Exército de Libertação da Natureza”, our research group from the Hymenoptera Ecology Laboratory (Hecolab/UFGD); Adílio A. Vadadão de Miranda, Fernando Correia Villela and Ivan Salzo “Instituto Chico Mendes de Biodiversidade” in Bonito, Mato Grosso do Sul state; they thank Kadiwéu people to permit them the access to their land. they are also grateful to Jonathan Majer, Carlos Roberto Brandão, Wedson Desidério Fernandes, Rogério Rosa da Silva, Rodrigo Feitosa, Joelson Gonçalves Pereira, Yzel R. Súarez, Sébastien Lacau, Benoît Jahyny, Sarah Groc, and Wesley DaRocha for assistance. This study was carried out under a collection permit from IBAMA (number 10674-11/09/2007). We would also like to thank the Fundação de Apoio ao Desenvolvimento do Ensino, Ciência e Tecnologia do Mato Grosso do Sul—FUNDECT for granting the second author an MSc scholarship (process 41/100.270/2006). JHCD acknowledges his research grant from CNPq.

References

[1] E. O. Wilson, “A global biodiversity map,” *Science*, vol. 289, no. 5488, p. 2279, 2000.

[2] D. Agosti and L. E. Alonso, “The ALL protocol: a standard protocol for the collection of ground-dwelling ants,” in *Standard Methods for Measuring and Monitoring Biodiversity*, D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz, Eds., pp. 204–206, Smithsonian Institution, Washington, DC, USA, 2000.

[3] L. Lach, C. Parr, and K. Abbott, *Ant Ecology*, Oxford University Press, Oxford, UK, 2009.

[4] D. H. Wall and J. C. Moore, “Interactions underground,” *BioScience*, vol. 49, no. 2, pp. 109–117, 1999.

[5] R. R. Da Silva and R. Silvestre, “Riqueza da fauna de formigas (Hymenoptera: Formicidae) que habita as camadas superficiais do solo em Seara, Santa Catarina,” *Papeis Avulsos de Zoologia*, vol. 44, pp. 1–11, 2004.

[6] R. R. Silva and C. R. F. Brandão, “Morphological patterns and community organization in leaf-litter ant assemblages,” *Ecological Monographs*, vol. 80, no. 1, pp. 107–124, 2010.

[7] L. E. Alonso, “Ants as indicators of diversity,” in *Standard Methods for Measuring and Monitoring Biodiversity*, D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz, Eds., pp. 80–88, Smithsonian Institution, Washington, DC, USA, 2000.

[8] H. M. André, X. Ducarme, and P. Lebrun, “Soil biodiversity: myth, reality or conning?” *Oikos*, vol. 96, no. 1, pp. 3–24, 2002.

[9] J. J. Morrone, “Biogeographic areas and transition zones of Latin America and the Caribbean Islands based on panbiogeographic and cladistic analyses of the entomofauna,” *Annual Review of Entomology*, vol. 51, pp. 467–494, 2006.

[10] J. J. Morrone, “What is the Chacoan subregion?” *Neotropica*, vol. 46, pp. 51–68, 2000.

[11] D. E. Prado and P. E. Gibbs, “Patterns of species distributions in the dry seasonal Forest of South America,” *Annual Missouri Botanical Garden*, vol. 80, pp. 902–927, 1993.

[12] R. Toby Pennington, D. E. Prado, and C. A. Pendry, “Neotropical seasonally dry forests and Quaternary vegetation changes,” *Journal of Biogeography*, vol. 27, no. 2, pp. 261–273, 2000.

[13] J. M. Felfili, “Fragmentos florestais estacionais do Brasil Central: diagnóstico e proposta de corredores ecológicos,” in *Fragmentação Florestal e Alternativas Para o Desenvolvimento Rural na Região Centro-Oeste*, R. B. Costa, Ed., pp. 139–160, UCDB, Campo Grande, MS, Brasil, 2003.

[14] A. Pott and V. J. Pott, “Espécies de fragmentos florestais em Mato Grosso do Sul,” in *Fragmentação Florestal e Alternativas Para o Desenvolvimento Rural na Região Centro-Oeste*, R. B. Costa, Ed., pp. 26–52, UCDB, Grande, MS, Brasil, 2003.

[15] E. Weiher, G. D. P. Clarke, and P. A. Keddy, “Community assembly rules, morphological dispersion, and the coexistence of plant species,” *Oikos*, vol. 81, no. 2, pp. 309–322, 1998.

[16] A. N. Andersen, “Not enough niches: non-equilibrial processes promoting species coexistence in diverse ant communities,” *Austral Ecology*, vol. 33, no. 2, pp. 211–220, 2008.

[17] R. Silvestre, C. R. F. Brandão, and R. R. Da Silva, “Grupos funcionales de hormigas: el caso de los gremios del Cerrado, Brasil,” in *Introdución a Las Hormigas de la Región Neotropical*, F. Fernández, Ed., pp. 113–143, Instituto Humboldt, Bogotá, Colômbia, 2003.

[18] W. J. Stubbs and J. B. Wilson, “Evidence for limiting similarity in a sand dune community,” *Journal of Ecology*, vol. 92, no. 4, pp. 557–567, 2004.

[19] MMA- Ministério do Meio Ambiente Brasil, “Biodiversidade Brasileira: Avaliação e identificação de ações prioritárias para a conservação, utilização sustentável e repartição dos benefícios da biodiversidade brasileira,” Brasília, Secretaria de Biodiversidade e Florestas. 2007 http://www.mma.gov.br.

[20] P. C. Boggiani, T. R. Fairchild, and A. M. Coimbra, “O grupo corumbá (Neoproterozóico - Cambriano) na região Central da Serra da Bodoquena, Mato Grosso do Sul (Faixa Paraguai),” *Revista Brasileira de Geociências*, vol. 23, no. 3, pp. 301–305, 1993.

[21] T. Piacentini, P. C. Boggiani, J. K. Yamamoto, B. T. Freitas, and G. A. C. Campanha, “Formação ferrífera associada à sedimentação glaciogênica da Formação Puga (Marinoano) na Serra da Bodoquena, MS,” *Revista Brasileira de Geociências*, vol. 37, pp. 530–541, 2007.

[22] M. Uetanabaro, F. L. Souza, P. Landgref Filho, A. F. Beda, and R. A. Brandão, “Anfíbios e répteis do Parque Nacional da Serra da Bodoquena, Mato Grosso do Sul, Brasil,” *Biota Neotropica*, vol. 7, no. 3, pp. 279–289, 2007.

[23] B. T. Bestelmeyer, D. Agosti, L. E. Alonso et al., “Field techniques for the study of ground-dwelling ants,” in *Standard Methods for Measuring and Monitoring Biodiversity*, D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz, Eds., pp. 122–144, Smithsonian Institution, Washington, DC, USA, 2000.

[24] B. Bolton, *Identification Guide to the Ant Genera of the World*, Harvard University Press, Cambridge, Mass, USA, 1994.

[25] B. Bolton, "Synopsis and classification of formicidae," *Memoirs of the American Entomological Institute*, vol. 71, pp. 1–374, 2003.

[26] F. Fernández, *Introducción a Las Hormigas de la Región Neotropical*, Instituto de Investigación de Recursos Biológicos "Alexander von Humboldt", Bogotá, Colombia, 2003.

[27] C. Baroni Urbani and M. L. de Andrade, "The ant tribe Dacetini: limits and constituent genera, with descriptions of new species," *Annali del Museo Civico di Storia Naturale "Giacomo Doria"*, vol. 99, pp. 1–192, 2007.

[28] J. S. Lapolla, S. G. Brady, and S. O. Shattuck, "Phylogeny and taxonomy of the Prenolepis genus-group of ants (Hymenoptera: Formicidae)," *Systematic Entomology*, vol. 35, no. 1, pp. 118–131, 2010.

[29] J. T. Longino, J. Coddington, and R. K. Colwell, "The ant fauna of a tropical rain forest: estimating species richness three different ways," *Ecology*, vol. 83, no. 3, pp. 689–702, 2002.

[30] R. K. Colwell, "EstimateS: statistical estimation of species richness and shared species from samples," Version 7.5. User's Guide and application, 2005, http://purl.oclc.org/estimates.

[31] M. Leponce, L. Theunis, J. H. C. Delabie, and Y. Roisin, "Scale dependence of diversity measures in a leaf-litter ant assemblage," *Ecography*, vol. 27, no. 2, pp. 253–267, 2004.

[32] R. R. Silva, R. S. M. Feitosa, and F. Eberhardt, "Reduced ant diversity along a habitat regeneration gradient in the southern Brazilian Atlantic Forest," *Forest Ecology and Management*, vol. 240, no. 1–3, pp. 61–69, 2007.

[33] S. Groc, J. Orivel, A. Dejean et al., "Baseline study of the leaf-litter ant fauna in a French guianese forest," *Insect Conservation and Diversity*, vol. 2, no. 3, pp. 183–193, 2009.

[34] R. K. Colwell, X. M. Chang, and J. Chang, "Interpolating, extrapolating, and comparing incidence-based species accumulation curves," *Ecology*, vol. 85, no. 10, pp. 2717–2727, 2004.

[35] R. L. Chazdon, R. K. Colwell, J. S. Denslow, and M. R. Guariguata, "Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of NE Costa Rica," in *Forest Biodiversity Research, Monitoring and Modeling: Conceptual Background and Old World Case Studies*, F. Dallmeier and J. A. Comiskey, Eds., pp. 285–309, Parthenon Publishing, Paris, France, 1998.

[36] P. Legendre and L. Legendre, *Numerical Ecology*, Elsevier, Amsterdam, The Netherlands, 2nd edition, 1998.

[37] P. H. A. Sneath and R. R. Sokal, *Numerical Taxonomy*, W. H. Freeman, San Francisco, Calif, USA, 1973.

[38] W. L. Kovach, *MVSP—A Multivariate Statistical Package for Windows ver. 3.1*, Kovach Computing Services, Pentraeth, Wales, UK, 2005.

[39] N. Mantel, "The detection of disease clustering and a generalized regression approach," *Cancer Research*, vol. 27, no. 2, pp. 133–153, 1967.

[40] R Development Core Team, *R: A Language and Environment for Statistical Computing*, R Foundation for Statistical Computing, Viena, Austria, 2009.

[41] J. Oksanen, R. Kindt, P. Legendre, and B. O'Hara, "Vegan: community ecology package," Version 1.8.2, 2005, http://cc.oulu.fi/ jarioksa.

[42] StatSoft, Inc., "Statistica (data analysis software system), version 6," 2001, www.statsoft.com.

[43] B. D. Coleman, M. A. Mares, M. R. Willig, and Y. H. Hsieh, "Randomness, area, and species richness," *Ecology*, vol. 63, no. 4, pp. 1121–1133, 1982.

[44] A. E. Magurran, *Ecological Diversity and Its Measurement*, Princeton University Press, Princeton, NJ, USA, 1988.

[45] N. J. Gotelli and G. L. Entsminger, "EcoSim: null models software for ecology, version 7," Acquired Intelligence Inc. and Kesey-Bear. Jericho, VT 05465, 2011, http://garyentsminger.com/ecosim/index.htm.

[46] N. J. Gotelli, "Null model analysis of species co-occurrence patterns," *Ecology*, vol. 81, no. 9, pp. 2606–2621, 2000.

[47] N. J. Gotelli and A. M. Ellison, "Biogeography at a regional scale: determinants of ant species density in New England bogs and forests," *Ecology*, vol. 83, no. 6, pp. 1604–1609, 2002.

[48] R. A. Johnson and P. S. Ward, "Biogeography and endemism of ants (Hymenoptera: Formicidae) in Baja California, Mexico: a first overview," *Journal of Biogeography*, vol. 29, no. 8, pp. 1009–1026, 2002.

[49] S. A. Lassau and D. F. Hochuli, "Effects of habitat complexity on ant assemblages," *Ecography*, vol. 27, no. 2, pp. 157–164, 2004.

[50] C. A. Brühl, G. Gunsalam, and K. E. Linsenmair, "Stratification of ants (Hymenoptera, Formicidae) in a primary rain forest in Sabah, Borneo," *Journal of Tropical Ecology*, vol. 14, no. 3, pp. 285–297, 1998.

[51] N. L. Hites, M. A. N. Mourão, F. O. Araújo, M. V. C. Melo, J. C. De Biseau, and Y. Quinet, "Diversity of the ground-dwelling ant fauna (Hymenoptera: Formicidae) of a moist, montane forest of the semi-arid Brazilian "Nordeste"," *Revista de Biologia Tropical*, vol. 53, no. 1-2, pp. 165–173, 2005.

[52] S. M. Alvarenga, A. E. Brasil, and D. M. Del Arco, "Projeto RADAM/BRASIL," *Geomorfologia*, vol. 28, pp. 125–138, 1982.

[53] A. York, "Long-term effects of frequent low-intensity burning on ant communities in coastal blackbutt forests of southeastern Australia," *Austral Ecology*, vol. 25, no. 1, pp. 83–98, 2000.

[54] T. P. McGlynn, R. M. Fawcett, and D. A. Clark, "Litter aiomass and nutrient determinants of ant density, nest size, and growth in a Costa Rican tropical wet forest," *Biotropica*, vol. 41, no. 2, pp. 234–240, 2009.

[55] F. B. Baccaro, S. M. Ketelhut, and J. W. De Morais, "Resource distribution and soil moisture content can regulate bait control in an ant assemblage in Central Amazonian forest," *Austral Ecology*, vol. 35, no. 3, pp. 274–281, 2010.

[56] A. E. Dunham and A. S. Mikheyev, "Influence of an invasive ant on grazing and detrital communities and nutrient fluxes in a tropical forest," *Diversity and Distributions*, vol. 16, no. 1, pp. 33–42, 2010.

[57] J. H. C. Delabie, D. Agosti, and I. C. Nascimento, "Litter ant communities of the Brazilian Atlantic rain forest region," *Curtin University School of Environmental Biology Bulletin*, vol. 18, pp. 1–17, 2000.

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 153862, 7 pages
doi:10.1155/2012/153862

Research Article

Division of Labor in *Pachycondyla striata* Fr. Smith, 1858 (Hymenoptera: Formicidae: Ponerinae)

Adolfo da Silva-Melo and Edilberto Giannotti

Departamento de Zoologia, Instituto de Biociências, Universidade Estadual Paulista (UNESP), Campus Rio Claro SP, Caixa Postal 199, 13506-900, Rio Claro, SP, Brazil

Correspondence should be addressed to Adolfo da Silva-Melo, adolfoants@yahoo.com.br

Received 26 March 2011; Revised 19 May 2011; Accepted 19 May 2011

Academic Editor: Jacques H. C. Delabie

Four colonies of the ant *Pachycondyla striata* were used to analyze the specie behavioral repertoire. Forty-six behavioral acts were recorded in laboratory. Here, we present the record the division of labor between the castes and the temporal polyethism of monomorphic workers. The queens carried out many of the behavioral traits recorded in this work however; they performed them less frequently compared to the worker. The workers activity involved chasing and feeding on fresh insects and usingthem to nourish larvae besides laying eggs in the C-posture, an activity also performed by queens, which is similar to that of wasps of the subfamily *Stenogastrinae*. The young workers were involved in activities of brood care, sexuate care, and nest maintenance, and the older workers were involved in defense, exploration, and foraging.

1. Introduction

The evolution of social behavior may be defined as the combination of care for young individuals by adults, overlapping generations, and division of labor in the reproductive and nonreproductive castes [1–4]. The ants are eusocial, and their behavior differs from that one of other social insects in three respects: (a) they have a varied diet, (b) nest building retains characteristics unique to this group, parental care in galleries, and workers performing tasks according to their age or size, and (c) adults remaining long time with their brood [5].

Among the aspects covered in ethologic studies of ants, division of labor (when individuals within a group perform different roles) or polyethism comprehends a widely explored subject and may present two divisions: (a) physical polyethism, when individuals show distinct morphological characteristics to perform specific tasks and (b) temporal polyethism, when the variation of tasks occurs according to age [1, 2, 4, 6]. Therefore, temporal polyethism may occur both in populations of monomorphic workers and in polymorphic workers [7, 8]. The ants of the genus *Pachycondyla* have a wide pantropical distribution with about 270 species being described [9]. The *Pachycondyla species* are diverse in their morphology and their behavior [10].

Pachycondyla striata Smith 1858 [11], classified into the subfamily Ponerinae [12], presents relatively large individuals (13.2–16.7 mm long). The castes are slightly different. The workers are different from the queens by the absence of ocelli and wing scars. This species is distributed through northern Argentina, Paraguay, Uruguay, and Brazil [13–15].

The aim of this study was to verify whether there is division of labor among castes and age polyethism in *P. striata*. The results will contribute to better understanding and interpretation of its social organization and allow comparison with other species of the family Formicidae.

2. Materials and Methods

Four colonies were collected on the campus of the University UNESP—Universidade Estadual Paulista, Rio Claro (22 32 40 S/47 32 44 W), São Paulo State. The ethological analysis began two days after the collection. Observations were done in the foraging area and plaster nest.

Table 1: Composition of the colonies of *Pachycondyla striata*.

Colony	Number of individuals							Date of collection
	eggs	larvae	pupae	workers	winged females	males	queens	
N. 2	—	—	—	20	5	—	—	04/13/2006
N. 3	—	—	37	178	38	33	—	04/14/2006
N. 7	264	65	—	382	7	8	—	08/06/2006
N. 8	30	231	240	384	—	—	1	11/17/2006

The colonies selected in field contained queens and/or winged females. The latter were regarded as queens after wing loss. The colonies were transferred to a laboratory and placed in plastic containers (width: 30.0 cm; length: 48.0 cm; height: 12.0 cm). In each container, there was a plaster nest consisting of three chambers in different sizes, interconnected by tunnels of 1.0 cm in width and 3.0 cm in depth, covered with glass to avoid disturbance and red cellophane paper to prevent the passage of the full spectrum of light.

The diet of the ants consisted of sugar and water in a ratio of 1:1 (offered in test tubes, with cotton wool in the opening), termites, worms, cockroaches, larvae of Coleoptera (*Tenebrio molitor*), flies, and papaya seeds.

Previous observation was performed for 20 hours to obtain behavioral data, with the aim of identifying queens and workers. The ants were differentiated by covering their thorax with quick-drying paint for model airplanes (Revel), allowing the identification of the individuals by age group just after their emergence. Young workers are known for having a paler color in relation to older ones. Later, the scan sampling method described by Altmann [16] was used to qualify the acts.

The quantitative observation of the behavioral acts of the individuals in each colony was performed for five minutes, with one-minute intervals. The observation time was one hour a day, four times a week, during six months, for a total of 94 hours. A comparative ethogram for the individuals was developed. Sample coverage was defined by the formula $= \mathbf{1} - (\mathbf{N1}/\mathbf{i})$, where **N1** = number of behavioral acts observed once and **i** = total number of behavioral acts, the more this value approaches to 1, the more complete the sample [17]. The behavioral catalog was divided into ten categories and used to build histograms and a dendrogram with clustering method (UPGMA) of Euclidean distance [18] (Table 1).

3. Results

3.1. Division of Labor. When introduced in laboratory, the individuals of *P. striata* immediately occupied the artificial nest. The ants carried the immature from the foraging area and accommodated them in the first and minor chamber for 12 hours. Only after this, they carried them to the last and bigger chamber. In the nest seven, the workers distributed randomly the immature to the chambers and tunnels of the nest.

As previously announced for this study, we considered the existence of two castes morphologically and subtly differentiated, containing monomorphical workers. In Table 2 the different categories, are distributed and quantified and behavioral acts of queens, workers, winged females, and males of *P. striata are defined as well.*

The sample coverage value (   ) was 0. 981 meeting the expectations of Fagen and Goldman [17]. The dissimilarity dendrogram informs a great ethological difference between the castes. (Figure 1).

The inactivity of the males into the nest suggests their action to be more prevalent in the mating season, but this was not verified in this study (Table 2).

The behavorial acts supposedly regarded as less derived have been identified in the castes, such as feeding larvae and adults on fresh insects, and laying eggs in the C-posture. Furthermore, the queens performed activities that are exclusively carried out by workers in other more derived species, such as brood care, exploring, foraging, and nest maintenance (Table 2).

The dominance behavior involved both individuals for recruiting and reproductive labor. The latter case, the interaction of dominance occurred between queen and worker and among workers. Some workers developed ovaries to lay eggs. However, this data were not quantified.

3.2. Temporal Polyethism. Some activities were preferably carried out by younger workers or older workers. This suggests division of labor by age (Figure 2).

The younger workers (7 to 56 days of age) stayed in the nest for approximately 27.03 ± 12.72 days (7–56, N = 27). For this time, took they care the pupae, larvae, eggs, males, and winged females (Figure 2). However, some newly hatched ants did not taken care for the young individuals. This might be related the presence of physiological problems, because they died within two or three days.

The older workers (those at more than 56 days of age) performed several categories, but they pointed in the activities out of the nest, as defense, foraging, and exploring (Figure 2). Furthermore, the dominance is a category that deserves attention. It may be linked to the maintenance of the colony, as a measure of protection from the nest and obtaining food, or reproduction.

The intermediate group (queens, virgin queens, and winged females), which is regarded as a caste, showed clear transition tasks. The quantitative results of the group are

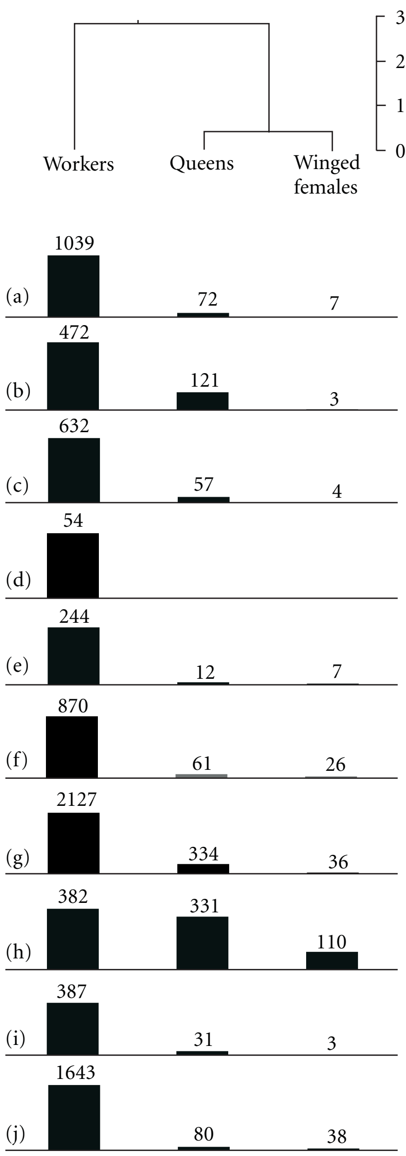


FIGURE 1: Dissimilarity dendrogram of individuals of *P. striata*. Behavioral categories: (a) feeding, (b) communication, (c) brood care, (d) sexuate care, (e) defense, (f) exploring and foraging, (g) grooming, (h) inactivity, (i) dominance, and (j) nest maintenance.

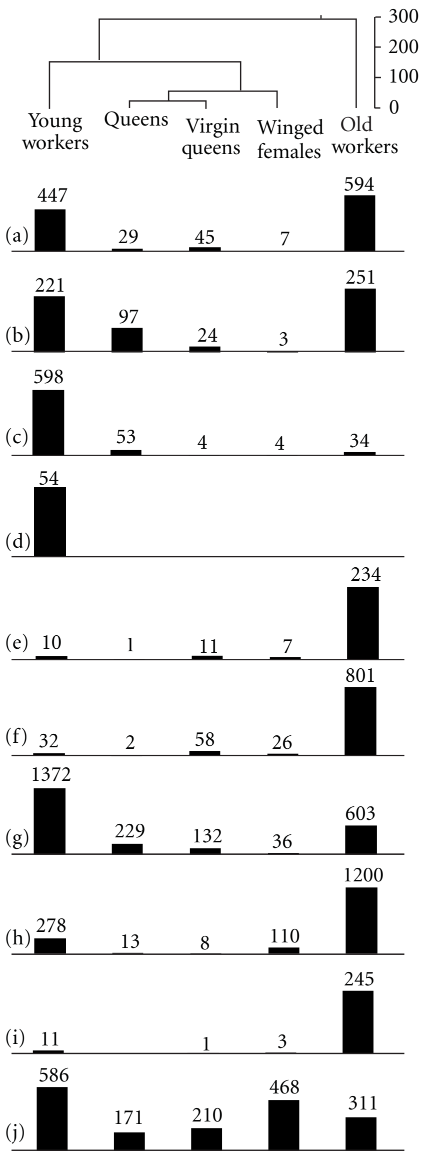


FIGURE 2: Dissimilarity dendrogram of individuals of *P. striata* showing the division of labor by age. Behavioral categories: (a) feeding, (b) communication, (c) brood care, (d) sexuate care, (e) defense, (f) exploring and foraging, (g) grooming, (h) inactivity, (i) dominance, and (j) nest maintenance.

smaller when compared to workers, and the activties have been concentrated within the nest.

4. Discussion

It is interesting to note that a small portion of behavioral acts is performed by queens within the nest. This type of occurrence is mentioned to the species of *P.* (*Neoponera*) *villosa*, *P.* (*Neoponera*) *apicalis*, and *P.* (*Neoponera*) *obscuricornis* [19]. The queens of *P. striata* presented more care for eggs than to the other immature individuals, while *P. (Neoponera) villosa* spends more energy caring for eggs and pupae, *P. (Neoponera) apicalis* and *P. (Neoponera) obscuricornis* invest more energy in caring for larvae and pupae [19]. The involvement of queens in brood care seems to be a little derived characteristic [20].

Feeding was a behavioral act frequently observed in the queens of *P. striata*, while the queen of *Nothomyrmecia macrops* was seen feeding once [21].

The queens and workers which to perform the laying eggs, retained the position in the form C. *Ectatomma planidens* [22, 23] and *Platythyrea punctata* [24], also acquired the same position.

This is characteristic of wasps of the genera *Listenogaster* [25] and *Eustenogaster* [26]. This condition may be an evidence of an attribute that might have been preserved.

Table 2: Behavioral catalog of *Pachycondyla striata*.

Category and behavioral acts	Queens	Workers	Winged females	Males
(A) Feeding				
01-Feeding on prey	0.0355	0.0700	0.0128	
02-Intake of liquids	0.0264	0.0587	0.0171	0.0116
44-Cannibalism	0.0030	0.0020	0.0059	
(B) Communication				
03-Antennate workers	0.0755	0.0549	0.0128	0.0516
04-Antennate queens	0.0345	0.0052		
(C) Brood care				
05-Antennate egg	0.0218	0.0129		
06-Antennate larvae	0.0010	0.003		
07-Antennate pupae		0.004		
08-Standing on eggs		0.0006		
09-Standing on larvae	0.0010	0.0014		
10-Standing on pupae		0.0009		0.0058
11-Handling eggs	0.0127	0.0045		
12-Handling larvae		0.0063	0.0043	
13-Handling pupae		0.0015		
15-Feeding larvae		0.0058		
16-Cleaning larvae		0.0085	0.0043	
18-Carrying eggs	0.0063	0.0126	0.0086	
19-Carrying pupae		0.0071		
20-Carrying larvae		0.0031		
22-Standing and holding an egg	0.0045	0.0061		
23-Standing and holding a pupa		0.0012		
24-Egg laying	0.0045	0.0004		
(D) Sexuate care				
14-Handling winged females		0.0003		
17-Cleaning males		0.0059		
21-Carrying males		0.0006		
(E) Defense				
25-Guarding the nest entrance	0.0110	0.0310	0.0210	
(F) Exploring and foraging				
26-Capturing prey	0.0118	0.0582		
27-Walking in the foraging arena	0.0427	0.0478	0.1070	0.0580
28-Tanden running	0.0010	0.0047	0.0043	
(G) Grooming				
29-Self-grooming their antennae	0.1164	0.082	0.059	0.0860
30-Self-grooming their 1st pair of legs	0.0582	0.03	0.0043	0.0660
31-Self-grooming their antennae and 1st pair of legs	0.0282	0.0252	0.0259	0.0233
32-Self-grooming their 2nd and 3rd pairs of legs	0.0591	0.0722	0.0212	0.0290
33-Self-grooming their anus	0.0054	0.0200		0.0260
34-Social grooming	0.0363	0.0062	0.0530	
(H) Inactivity				
38-Inactivity in the nest	0.3700	0.0323	0.4369	0.5000
39-Inactivity in the foraging arena	0.0219	0.0163	0.0350	0.0630
(I) Dominance				
35-Antennal boxing	0.0218	0.0405	0.0027	
36-Blocking	0.0054	0.0005		
37-Immobilization	0.0010	0.0081		0.0160

Table 2: Continued.

Category and behavioral acts	Queens	Workers	Winged females	Males
(J) Nest maintenance				
40-Carrying a dead ant	0.0010	0.1512		
41-Handling a dead ant		0.133		
42-Carrying garbage	0.0010	0.0103		
43-Handling garbage	0.0010	0.0085		
45-Exploring the plaster nest	0.0700	0.0160	0.1639	0.0643
46-Digging in the plaster nest		0.0080		
Total frequency	1	1	1	1
Total categories	9	10	9	8
Total behavioral acts	31	46	19	13

The agonistic behavioral acts were almost always related to reproduction or foraging activities. Antennal boxing occurred with winged females, queens, and workers. This behavior may be related to the recruitment of workers, as the measure was implemented in the nest, and a larger number of workers moved to the foraging arena. The same happens to *P. bertholudi* [27].

In nest 8, after the queen's death, one worker started laying eggs. Afterwards, agonistic encounters became frequent, and another worker that started laying eggs was mutilated. This suggests that *P. striata* presents a reproductive dominance, as does *P. crassinoda* [28]. Agonistic encounters were also reported for *P. (Neoponera) obscuricornis* [29, 30] and *P. bertholudi* [27].

Chagas and Vasconcelos [31] described the fighting behavior between workers of *P. striata* and *P. (Neoponera) obscuricornis* in the field. According to these researchers, this event occurred because *P. striata* invaded the foraging and/or life area of *P. obscuricornis*.

The agonistic behavioral acts observed in *P. striata* were also reported for *Dinoponera quadriceps* [32], *P. (Neoponera) apicalis* [33], *P. (Neoponera) obscuricornis* [29], *Rhytidoponera* sp. 12 [34], *P. inversa* [35], and *P. bertholudi* [27].

We checked that the workers ate larvae, pupae, other workers, and males. Some alive males had their abdominal region pulled off by workers. These behaviors may indicate stress or cannibalism. Wilson [1] reported that dead workers might be used as food or were discarded.

The eggs of *P. striata* collected from the natural environment and those laid by queens and workers in laboratory did not develop. They were predated by dominant individuals or by the whole group under stress. Egg predation was reported in *Ectatomma planidens* [22, 23] and *E. vizottoi* [36] although it has been absent or not observed in *Pachycondyla bertholudi* [37]. The eggs laid by workers are usually eaten by queens and larvae, which represents a stereotyped, conspicuous behavior pattern [1].

Oophagy is indispensable to the social Hymenoptera [1]. It is important because workers do not regurgitate food either for larvae or for queens, so they can use their own resources to produce immature oocytes [38]. This event seems restricted to some genera in the subfamily Ponerinae [38].

In the presence of a large number of eggs, the workers gathered them and stood still on them. They standing motionless on eggs, pupae, and larvae. This may suggest warming and protection of the immature individuals. When the number of eggs in the nest was small, the ants of this species kept the eggs clustered between their mandibles.

The behavioral act *tandem running* was carried out to recruit workers into the foraging arena. Medeiros and Oliveira [39] observed this as well. This behavior is common in several species such as *Pachycondyla (Brotoponera) tesserinoda* [40] and *Pachycondyla obscuricornis* [31].

The larvae of *P. striata* display a characteristic behavior to order food. They shake their necks and heads several times towards the ventral region of their body until a worker answers. This behavior is similar to that one of larvae of *Gnamptogenys striatula* [41]. The workers moved the larvae towards the prey. In some cases, the workers held the prey between their mandibles, while the larvae inserted their head into the sectioned part of the mealworm and fed on hemolymph. The workers feed preferentially larvae closer to them. Asking for food was a behavioral act observed more often in larvae in the last instar. The workers touched the buccal apparatus of the larvae with their mandibles open, but it was not possible to see the food transfer or the projection of the glossa of the workers. A similar behavioral act was described for *P. crassinoda* [28].

Small pieces of mealworm were placed in the ventral region of the larvae of ants by the workers. The larvae curved their necks and fed in the same manner as described for *Gnamptogenys horni* [42], *Ponera pennsylvannica* [43], and *Pachycondyla crassinoda* [43]. According to Wilson [1] and Traniello and Jayasuriya [44], feeding larvae on small fragments of prey is a less derived characteristic.

P. striata use their stinger to paralyze their prey. The sting might be stimulated by sudden movements of the prey, similar to way what happens to workers of *P. caffraria* [45]. According to Traniello and Jayasuriya [44], using the stinger to paralyze prey is a less derived characteristic.

The state of inactivity or deep sleep exhibited by *P. striata* is similar to one that described by Cassill et al. [46]. Many workers remained motionless in foraging area. This category may reflect the restricted space of the arena or, as Miguel and Del-Claro [47], the state, containment of spent energy. The inactivity behavior was observed in *Pachycondyla (Neoponera) villosa*, *P. (Neoponera) apicalis*, *P. (Neoponera) obscuricornis* [19], *P. crassinoda* [48], *Nothomyrmecia macrops* [21], *E. planidens* [22, 23], and *E. opaciventre* [47].

The monomorphic workers of *P. striata* present specialized task division, forming work groups to performing tasks linking to individuals with similar ages. Young individuals provide parental care, whereas older individuals carry out the activities of defense, exploration, and foraging.

Young workers stayed in the nest for 56 days, but some left earlier. They were recruited into the foraging area according to the necessity of food or to substitute the dead workers. In the first 45 days after emergence, *Ectatomma tuberculatum* performs tasks progressively according to the age of the individuals [49]. The same happens to workers of *Platythyrea lamellosa*, which after hatching (0–5 days of age) present association with pupae and later take care of eggs and larvae, performing specific tasks influenced by their age [50]. Unlike *P. striata*, newly hatched individuals of the species *Pachycondyla caffraria* (0–5 days of age) present four types of behavioral acts and are capable of foraging early at this age [51]. Each colony of this species has precise requirements as to carbohydrates and proteins, appropriate for labor division, which happens in relatively fixed proportions between hunting foragers and those which collect water with sugar [45]. Workers of *P. striata* were seen at the carbohydrate source in a very small frequency. This activity was included in the behavioral act of taking water in from the cotton wool. *P. striata* preferred to capture other insects to provide protein intake.

This research shows the profile of social organization of *P. striata*. We see that many behavioral acts are common for species of the subfamily Ponerinae. Although there is a narrow dimorphism in castes of *P. striata*, there is a great difference of division of labour between them. The age is a factor that controls the performance of tasks in workers.

References

[1] E. O. Wilson, *The Insect Societies*, Belknap Press, Cambridge, Mass, USA, 1971.

[2] E. O. Wilson, *Sociobiology The New Synthesis*, Belknap Press, Cambridge, Mass, USA, 1975.

[3] M. Andersson, “The evolution of eusociality,” *Annual Review of Ecology and Systematics*, vol. 15, pp. 165–189, 1984.

[4] B. Hölldobler and E. O. Wilson, *The Ants*, Belknap Press, Cambridge, Mass, USA, 1990.

[5] H. D. Sudd, “Ants: foragim, nesting, brood behavior and polyethism,” in *Social Insects*, H. R. Hermann, Ed., vol. 4, pp. 107–155, Academic Press, New York, NY, USA, 1982.

[6] E. O. Wilson, “The social biology of ants,” *Annual Review of Entomology*, vol. 8, pp. 345–368, 1963.

[7] J. H. Sudd and N. R. Franks, *The Behavioural Ecology of Ants*, Chapman and Hall, New York, NY, USA, 1987.

[8] A. B. Sendova-Franks and N. R. Franks, “Self-assembly, self-organization and division of labour,” *Philosophical Transactions of the Royal Society B*, vol. 354, no. 1388, pp. 1395–1405, 1999.

[9] B. Bolton, *A New General Catalogue of the Ants of the World*, Harvard University, Cambridge, Mass, USA, 1995.

[10] A. L. Wild, “The genus *Pachycondyla* (Hymenoptera: Formicidae) in Paraguay,” *Boletin del Museo Nacional de Historia Natural del Paraguay*, vol. 14, pp. 1–18, 2002.

[11] Fr. Smith, *Catalogue of the Hymenopterous Insects in the Collection of the British Museum*, Part 6, British Museum, London, UK, 1858.

[12] B. Bolton, *Synopsis and Classification of Formicidae*, vol. 71 of *Memoirs of the American Entomological Institute*, American Entomological Institute, 2003.

[13] W. W. Kempf, “As formigas do gênero Pachycondyla Fr. Smith no Brasil (Hymenoptera: Formicinae),” *Revista Brasileira de Entomologia*, vol. 10, pp. 189–204, 1961.

[14] W. W. Kempf, “Catalogo abreviado das formigas da região neotropical (Hymenoptera: Formicidae),” *Studia Entomologica*, vol. 5, pp. 3–344, 1972.

[15] W. W. Kempf and K. Lenko, “Levantamento da formicifauna no litoral norte e ilhas adjacentes do Estado de São Paulo, Brasil.I. subfamilias dorylinae, Ponerinae e Pseudomyrmicinae (Hymenoptera: Formicidae),” *Studia Entomologica*, vol. 19, pp. 45–66, 1976.

[16] J. Altmann, “Observational study of behavior: sampling methods,” *Behaviour*, vol. 49, no. 3-4, pp. 227–267, 1974.

[17] R. M. Fagen and R. Goldman, “Behavioural catalogue analysis methods,” *Animal Behaviour*, vol. 25, no. 2, pp. 261–274, 1977.

[18] C. J. Krebs, *Ecological Methodology*, Benjamin Cummings, Redwood City, Calif, USA, 2nd edition, 1999.

[19] M. Pérez-Bautista, J. P. Lachaud, and D. Fresneau, “La division del trabajo em la hormiga primitiva *Neoponera villosa* (Hymenoptera: Formicidae),” *Folia Entomológica Mexicana*, vol. 65, pp. 119–130, 1985.

[20] D. Fresneau and P. Dupuy, “A study of polyethism in a ponerine ant: *Neoponera apicalis* (Hymenoptera, Formicidae),” *Animal Behaviour*, vol. 36, no. 5, pp. 1398–1399, 1988.

[21] P. Jaisson, D. Fresneau, and R. W. Taylor, “Social organization in some primitive australian ants. I. *Nothomyrmecia macrops* Clark,” *Insectes Sociaux*, vol. 3, no. 4, pp. 425–438, 1992.

[22] W. F. Antonialli-Junior and E. Giannotti, “Division of labor in *Ectatomma edentatum* (Hymenoptera, Formicidae),” *Sociobiology*, vol. 39, no. 1, pp. 37–63, 2002.

[23] W. F. Antonialli, V. C. Tofolo, and E. Giannotti, “Population dynamics of *Ectatomma planidens* (Hymenoptera: Formicidae) under laboratory conditions,” *Sociobiology*, vol. 50, no. 3, pp. 1005–1013, 2007.

[24] J. Korb and J. Heinze, “Multilevel selection and social evolution of insect societies,” *Naturwissenschaften*, vol. 91, no. 6, pp. 291–304, 2004.

[25] S. Turillazzi, “The stenogastrinae,” in *The Social Biology of Wasps*, K. G. Ross and R. W. Matthews, Eds., pp. 47–98, Cornell University, Ithaca, NY, USA, 1991.

[26] E. Francescato, A. Massolo, M. Landi, L. Gerace, R. Hashim, and S. Turillazzi, “Colony membership, division of labor, and genetic relatedness among females of colonies of *Eustenogaster fraterna* (Hymenoptera, Vespidae, Stenogastrinae),” *Journal of Insect Behavior*, vol. 15, no. 2, pp. 153–170, 2002.

[27] M. F. Sledge, C. Peeters, and M. R. Crewe, “Reproductive division of labour without dominance interactions in the queenless ponerine ant *Pachycondyla (Ophthalmopone) berthoudi*,” *Insectes Sociaux*, vol. 48, no. 1, pp. 67–73, 2001.

[28] A. Henriques and P. R. S. Moutinho, “Algumas observações sobre a organização social de *Pachyconyla crassinoda Latreille*,1802 (Hymenoptera: Formicidae: Ponerinae),” *Revista Brasileira de Entomologica*, vol. 38, pp. 605–611, 1994.

[29] P. S. Oliveira and B. Hölldobler, "Agonistic interactions and reproductives dominance in *Pachycondyla obscuricornis* (Hymenoptera: Formicidae)," *Psyche*, vol. 98, pp. 215–225, 1991.

[30] B. Gobin, J. Heinze, M. Strätz, and F. Roces, "The energetic cost of reproductive conflicts in the ant *Pachycondyla obscuricornis*," *Journal of Insect Physiology*, vol. 49, no. 8, pp. 747–758, 2003.

[31] A. C. S. Chagas and V. O. Vasconcelos, "Comparação da freqüência da atividade forrageira da formiga *Pachycondyla obscuricornis* (Emery, 1890) (Hymenoptera: Formicidae) no verão e no inverno, em condições de campo," *Revista Brasileira de Zoociências*, vol. 4, p. 109, 2002.

[32] T. Monnin and C. Peeters, "Dominance hierarchy and reproductive conflicts among subordinates in a monogynous queenless ant," *Behavioral Ecology*, vol. 10, no. 3, pp. 323–332, 1999.

[33] P. S. Oliveira and B. Hölldobler, "Dominance orders in the ponerine ant *Pachycondyla apicalis* (Hymenoptera, Formicidae)," *Behavioral Ecology and Sociobiology*, vol. 27, no. 6, pp. 385–393, 1990.

[34] W. T. Tay and R. H. Crozier, "Nestmate interactions and egg-laying behaviour in the queenless ponerine ant *Rhytidoponera* sp. 12," *Insectes Sociaux*, vol. 47, no. 2, pp. 133–140, 2000.

[35] K. Kolmer and J. Heinze, "Rank orders and division of labour among unrelated cofounding ant queens," *Proceedings of the Royal Society B*, vol. 267, no. 1454, pp. 1729–1734, 2000.

[36] A. S. Vieira, W. D. Fernandes, and W. F. Antonialli-Junior, "Temporal polyethism, life expectancy, and entropy of workers of the ant *Ectatomma vizottoi* almeida, 1987 (Formicidae: Ectatomminae)," *Acta Ethologica*, vol. 13, no. 1, pp. 23–31, 2010.

[37] C. P. Peeters and R. M. Crewe, "Male biology in the queenless *Ophthalmopone berthoudi* (Formicidae: Ponerinae)," *Psyche*, vol. 93, pp. 227–283, 1986.

[38] C. Peeters, "Morphologically "primitive" ants; comparative review of social characters, and the importance of queen-worker dimorphism," in *The Evolution of Social Behavior in Insects and Arachnids*, J. Choe and B. Crespi, Eds., pp. 372–391, Cambridge University Press, Cambridge, UK, 1997.

[39] F. N. S. Medeiros and P. S. Oliveira, "Season-dependent foraging patterns case study of a neotropical Forest-dwelling ant (*Pachycondyla striata Ponerinae*)," in *Food Exploitation by Social Insects: Ecological, Behavioral, and Theoretical Approaches*, S. Jarau and M. Hrncir, Eds., chapter 4, pp. 81–95, CRC Press, 2009.

[40] V. U. Maschwitz, B. Hölldobler, and M. Möglich, "Tandelaufen als rekrutierungsverhalten bei *Brothroponera tesserinoda* forel (Formicidae: Ponerinae)," *Zei Tschrift Für Tierpsychologie*, vol. 35, pp. 113–123, 1974.

[41] N. Kaptein, J. Billen, and B. Gobin, "Larval begging for food enhances reproductive options in the ponerine ant *Gnamptogenys striatula*," *Animal Behaviour*, vol. 69, no. 2, pp. 263–299, 2005.

[42] S. C. Pratt, "Ecology and behavior of *Gnamptogenys horni* (Formicidae: Ponerinae)," *Insectes Sociaux*, vol. 41, no. 3, pp. 255–262, 1994.

[43] C. S. Pratt, F. N. Carlin, and P. Calabi, "Division of labor in *Ponera pennsylvannica* (Formicidae: Ponerinae)," *Insectes Sociaux*, vol. 41, no. 1, pp. 43–61, 1994.

[44] J. F. A. Traniello and A. K. Jayasuriya, "The biology of the primitive ant *Aneuretus simoni* (Emery) (Formicidae: Aneuretinae) II. the social ethogram and division of labor," *Insectes Sociaux*, vol. 32, no. 4, pp. 375–388, 1985.

[45] C. Agbogba and P. E. Howse, "Division of labor between foraging workers of the ponerine ant *Pachycondila caffraria* (Smith) (Hymenoptera: Formicidae)," *Insectes Sociaux*, vol. 39, pp. 455–458, 1992.

[46] D. L. Cassill, S. Brown, and D. Swick, "Polyphasic wake/sleep episodes in the fire ant, *Solenopsis invicta*," *Journal of Insect Behavior*, vol. 22, no. 4, pp. 313–323, 2009.

[47] T. B. Miguel and K. Del-Claro, "Polietismo etário e repertório comportamental de *Ectatomma opaciventre* roger, 1861 (Formicidae: Ponerinae)," *Revista Brasileira de Zoociências*, vol. 7, pp. 293–310, 2005.

[48] R. C. S. Brito, *Divisão De Trabalho: Aspectos Comportamentais Da Regulação Social Do Cuidado à Prole Em* Pachycondyla crassinoda *Latreille, 1802 (Hymenoptera: Formicidae: Ponerinae)*, thesis, USP-Univesidade de São Paulo, 1999.

[49] A. Champalbert and J. P. Lachaud, "Existence of a sensitive period during the ontogenesis of social behaviour in a primitive ant," *Animal Behaviour*, vol. 39, no. 5, pp. 850–859, 1990.

[50] M. H. Villet, "Social organization of *Platythyrea lamellosa* (Roger) (Hymenoptera: Formicidae): II division of labour," *Suid-Afrikaanse Tydskrif vir Plantkunde*, vol. 25, pp. 254–259, 1990.

[51] C. Agbogba, "Absence of temporal polyethism in the ponerine ant *Pachycondyla caffraria* (Smith) (Hymenoptera: Formicidae): early specialization of the foragers," *Behavioural Processes*, vol. 32, no. 1, pp. 47–52, 1994.

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 785424, 7 pages
doi:10.1155/2012/785424

Research Article

Evaluation of the Toxicity of *Virola sebifera* Crude Extracts, Fractions and Isolated Compounds on the Nest of Leaf-Cutting Ants

Keylla Utherdyany Bicalho,[1] Ana Paula Terezan,[1] Denise Cristina Martins,[1] Taís Garcia Freitas,[2] João Batista Fernandes,[1] Maria Fátima das Graças Fernandes da Silva,[1] Paulo Cezar Vieira,[1] Fernando Carlos Pagnocca,[2] and Odair Côrrea Bueno[2]

[1] *Departamento de Química, Universidade Federal de São Carlos, CP 13565-905 São Carlos, SP, Brazil*
[2] *Centro de Estudos de Insetos Sociais, Universidade Estadual Paulista, Campus Rio Claro, CP 199, 13506-900 Rio Claro, SP, Brazil*

Correspondence should be addressed to João Batista Fernandes, djbf@power.ufscar.br

Received 30 April 2011; Accepted 5 June 2011

Academic Editor: Jacques H. C. Delabie

The phytochemical study of *Virola sebifera* leaves led to the isolation of three lignans: (+)-sesamin, (−)-hinokinin, and (−)-kusunokinin and three flavonoids: quercetin-3-*O*-α-L-rhamnoside, quercetin-3-*O*-β-D-glucoside, and quercetin-3-methoxy-7-*O*-β-D-glucoside by using techniques as high-speed counter-current chromatography and high-performance liquid chromatography. The crude extracts, fractions, and isolated compounds were evaluated for their insecticidal and fungicidal potential against *Atta sexdens rubropilosa* and its symbiotic fungus *Leucoagaricus gongylophorus*. The bioassay results showed a high insecticidal activity for the methanol crude extract of the leaves of *V. sebifera* and its *n*-hexane, dichloromethane and ethyl acetate fractions. The fungicidal bioassay revealed high toxicity of the lignans against *L. gongylophorus*.

1. Introduction

Virola sebifera is one of the most widely spread Myristicaceae species through Brazil [1, 2]. Although it has been mainly known by its hallucinogenic effects [3, 4], this species is also employed, in folk medicine, as antiulcer and in treatment of rheumatism [5, 6]. Previous phytochemical investigations revealed a high diversity of secondary metabolites, where were found 12 lignans [5, 7–10], 23 neolignans [2, 6, 8, 11, 12], one dimeric neolignan [8], 5 polyketides [6, 13, 14], and two alkaloids [3].

Leaf-cutting ants (Hymenoptera), dominant herbivores in the tropics, are considered a serious pest for agriculture, especially when they attack cultivated plants [15]. Control of this pest is still challenging and mostly made by using synthetic insecticides that have often temporary effects and affect nontarget species [16].

They cut high amounts of vegetal matter to feed its symbiotic fungus, *Leucoagaricus gongylophorus* that produce enzymes which are necessary to metabolize polysaccharides to mono and disaccharides, which supplies the major part of the energy needs of adult workers [17]. This relationship between the leaf-cutting ants and its symbiotic fungus is essential to their survival.

Due to the difficulty in controlling this pest, an intense search for alternative methods have been made and may involve both the search for insecticides compounds, or chemical fungicides that inhibit the symbiotic fungus growth. In the present work was evaluated the toxicity of crude extract, fractions, and isolated compounds against *Atta sexdens rubropilosa* and its symbiotic fungus *L. gongylophorus*.

2. Experimental

2.1. General Procedures. The high-speed counter-current chromatography (HSCCC) system employed in the present work was a P. C. Inc. (Potomac, MD, USA) instrument equipped with a quadruple multilayer coil of 1.68 mm

Table 1: *A. sexdens rubropilosa* workers mortality (%) and survival median (Md) when fed with diet containing crude extracts (2000 $\mu g \cdot mL^{-1}$) from *V. sebifera*.

Crude extracts	Days										Md
	1	2	3	6	8	10	14	17	21	25	
Control	2	8	14	22	36	36	42	52	62	72	17[a]
Dichloromethane leaves (**I**)	0	10	18	40	64	92	98	100	100	100	7.5[b]
Methanol leaves (**II**)	0	2	4	20	38	60	70	70	76	78	10[a]
Ethanol branches (**III**)	2	10	14	32	42	48	58	64	64	66	11[a]

[a]Control or no significant and [b]significant difference according to long-rank test ($P <$ 0.05).

Table 2: *A. sexdens rubropilosa* workers mortality (%) and survival median (Md) when fed with diet containing the fractions (1000 $\mu g \cdot mL^{-1}$) of the methanol crude extract of leaves of *V. sebifera*.

Fractions	Days										Md
	1	2	3	6	8	10	14	17	21	25	
Control	0	0	2	6	8	14	18	30	42	62	23[a]
n-Hexane (**IV**)	0	8	18	36	54	72	82	88	92	94	8[b]
Dichloromethane (**V**)	2	12	20	60	82	92	94	94	94	94	5[b]
Ethyl acetate (**VI**)	0	0	4	14	36	40	60	64	82	92	12[b]
Hydroalcoholic (**VII**)	2	3	10	14	26	32	46	50	62	76	17[b]

[a]Control or no significant and [b]significant difference according to long-rank test ($P <$ 0.05).

I.D. polytetrafluoroethylene (PTFE) tubing and had a total capacity of 443 mL. The β value varied from 0.50 at the internal terminal to 0.85 at the external terminal, and the revolution radius was 10 cm ($\beta = r/R$, where r is the distance from the coil to the holder and R the revolution radius or the distance between the holder axis and the central shaft). The loop volume of the sample injection was 5 mL, and the revolution speed of the apparatus was regulated with a speed controller in the range between 0 and 1000 rpm. The flow rate was controlled with an FMI-50 QD SSY, BS/BS (Fluid Metering, New York, USA) constant flow pump. The fractions were obtained by an automated fraction collector DC-1200 (Eyela, Sunnyvale, CA, USA).

High-performance liquid chromatography (HPLC) analyses were performed using Shimadzu pump LC-6AV and a SPD 6AV UV detector set at 254 nm. HPLC grade solvents were obtained from Tedia, and H_2O was purified in a Milli-Q system.

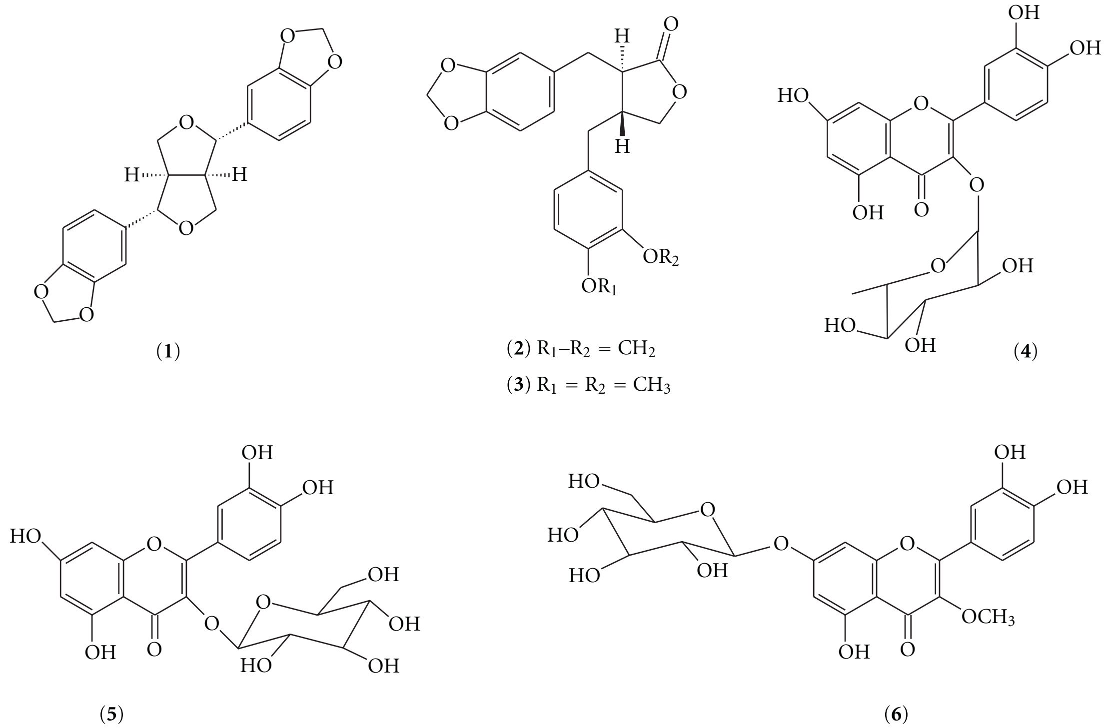
LC-UV-electrospray ionization (ESI) MS/MS data were obtained using an Alliance 2695 liquid chromatography equipped with a Waters (Milliford, MA, USA) PDA2996 photodiode array detection (DAD) system; mass spectral data were acquired in negative ion mode on a triple quadrupole Micromass Quattro LC spectrometer (Manchester, U.K.), equipped with a Z-Spray API ion source and a megaflow electrospray probe.

The ^1H NMR, ^{13}C NMR, and 2D correlations spectra were obtained using Bruker DRX-400 spectrometer, with $CDCl_3$ and DMSO-*d6*.

2.2. Plant Material. *V. sebifera* was collected at the cerrado reserve of Canchim Farm, São Carlos, São Paulo state, Brazil and identified by Dra. Maria Helena Antunes de Oliveira e Souza from the Botanic Department of Federal University of São Carlos, where can be found the voucher specimens.

2.3. Extraction and Isolation of Compounds. The extracts were prepared from leaves and branch. The leaves air-dried powered (362 g) of *V. sebifera* were subsequently extracted with dichloromethane (**I**) and methanol (**II**), and the branches air-dried powered (407 g) were extracted with ethanol (**III**). The crude methanol extract (**II**) was submitted to a liquid-liquid partition with *n*-hexane (**IV**), dichloromethane (**V**), ethyl acetate (**VI**), remaining, the hydroalcoholic phase (**VII**). The dichloromethane fraction was purified through high-speed counter-current chromatography (HSCCC) obtaining three lignans (**1**–**3**), and the ethyl acetate fraction was purified through exclusion chromatography using Sephadex LH-20 as stationary phase and high-performance liquid chromatography (HPLC) obtaining three flavonoids (**4**–**6**). The compounds were identified using NMR and MS techniques.

2.4. Fungicidal Bioassay. The experiments with the symbiotic fungus *L. gongylophorus* were conducted in Bioassays Natural Products Laboratory, Federal University of São Carlos (UFSCar). The fungus *L. gongylophorus* (Singer) Möller (syn *Rozites gongylophorus*) was isolated from an *A. sexdens rubropilosa* laboratory nest and maintained in laboratory in a culture medium composed of malt extract (20 $g \cdot L^{-1}$), bacto-peptone (5 $g \cdot L^{-1}$), yeast extract (2 $g \cdot L^{-1}$), and agar (20 $g \cdot L^{-1}$) [19]. The samples submitted for assay with the symbiotic fungus were incorporated into the culture medium and followed by the addition of distilled water. Then, in each tube were added 10 mL of culture medium with sample or only culture medium. All the material was autoclaved under the conditions 120 C and 1.0 atm. for 20 minutes. After the sterilization of the material, culture media were poured in Petri plates (80 × 15 mm) inside the laminar flow



(**1**)

(**2**) R_1–R_2 = CH_2

(**3**) R_1 = R_2 = CH_3

(**4**)

(**5**)

(**6**)

Figure 1: Chemical structures of the isolated compounds from *V. sebifera*.

cabinet, previously sterilized for 30 minutes by ultraviolet light. After solidification of the culture medium, each Petri plate was inoculated with a disc of agar (8 mm) at the center position, previously colonized by the symbiotic fungus *L. gongylophorus*. After the incubation period of 30 days at 25 C, calculations were performed in the areas of mycelial growth of the symbiotic fungus in each sample.

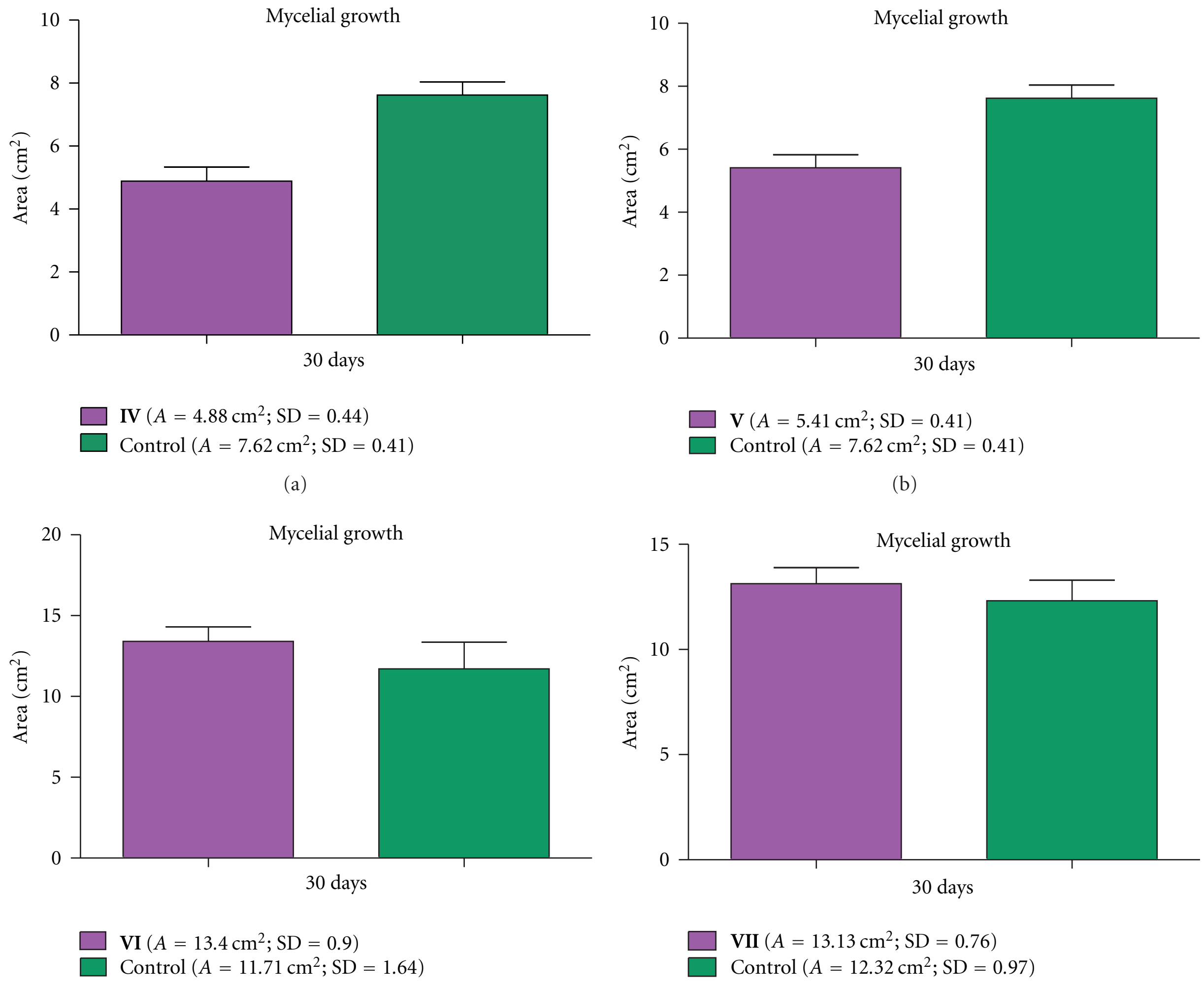
2.5. Leaf-Cutting Ant Insecticide Bioassay. The *A. sexdens rubropilosa* workers used in the assays were randomly removed from laboratory nests. They had a body mass of 20–25 mg. Before the assays, the nests were supplied daily with leaves of *Eucalyptus* sp., oat seed and occasionally with leaves of other plants such as *Hibiscus* sp., *Ligustrum* sp., or rose petals. Fifty ants were removed from the nests and put into five Petri dishes (ten ants each) for each treatment. During the assay, the ants were maintained on an artificial diet prepared with glucose ($50.0\,g{\cdot}L^{-1}$), bacto peptone ($10.0\,g{\cdot}L^{-1}$), yeast extract ($1.0\,g{\cdot}L^{-1}$), and agar ($15.0\,g{\cdot}L^{-1}$) in distilled water (100 mL) [20]. The diets (0.4-0.5 g per dish) with the addition of compounds (experiment) or without it (control) were offered daily in a small plastic cap. The control was prepared with the diet and the solvent. To ensure that undetectable remaining amounts of the solvent did not affect the ants, a comparison was made with another set of dishes in which water was used instead of solvent. As expected, the same survival rates were obtained with both systems (data not shown). The compounds were poured into the hot diet immediately after it was autoclaved. The final concentration of the extracts added to the diet was $2000\,\mu g{\cdot}mL^{-1}$, of the fractions were $1000\,\mu g{\cdot}mL^{-1}$, and of the compounds were 200 or $400\,\mu g{\cdot}mL^{-1}$. During the assays, the material was maintained in an incubator at the temperature 25 (± 1) C and relative humidity ranging between 70 and 80%. The maximum length of observation was 25 days, and the number of dead ants was registered daily.

Percentage survival was plotted as a function of time in a survival curve which was then used to calculate the median survival time (*S*50, the time at which 50% of the ants in each experiment remained alive). The *S*50 was calculated and survival curves were compared using the nonparametric log-rank test at the 95% significant level [21].

3. Results and Discussion

The compounds isolated from the dichloromethane fraction of the methanol crude extract of the leaves of *V. sebifera* were the lignans (+)-sesamin (**1**), (−)-hinokinin (**2**), and (−)-kusunokinin (**3**) (Figure 1). These compounds were identified by the comparison of NMR spectral data with those described in the literature [7, 22–24]. The compounds isolated from the ethyl acetate were the flavonoids quercetin-3-*O*-*α*-L-rhamnoside (**4**, synonyms: quecetrin or quecitrin), quercetin-3-*O*-*β*-D-glucoside (**5**), and quercetin-3-methoxy-7-*O*-*β*-D-glucoside (**6**) (Figure 1). These flavonoids were also identified by the comparison of NMR spectral data with those described in the literature [25–27].

The *V. Sebifera* crude extracts (**I**, **II,** and **III**) were evaluated by their insecticidal potential, and only the methanol crude extract of the leaves (**II**) presented insecticidal activity



(a) (b)

(c) (d)

Figure 2: Effect of the fractions **IV** (600 μg$\cdot$mL^{-1}), **V** (600 μg$\cdot$mL^{-1}), **VI** (600 μg$\cdot$mL^{-1}), and **VII** (600 μg$\cdot$mL^{-1}) on the mycelial growth of the symbiotic fungus *L. gongylophorus*.

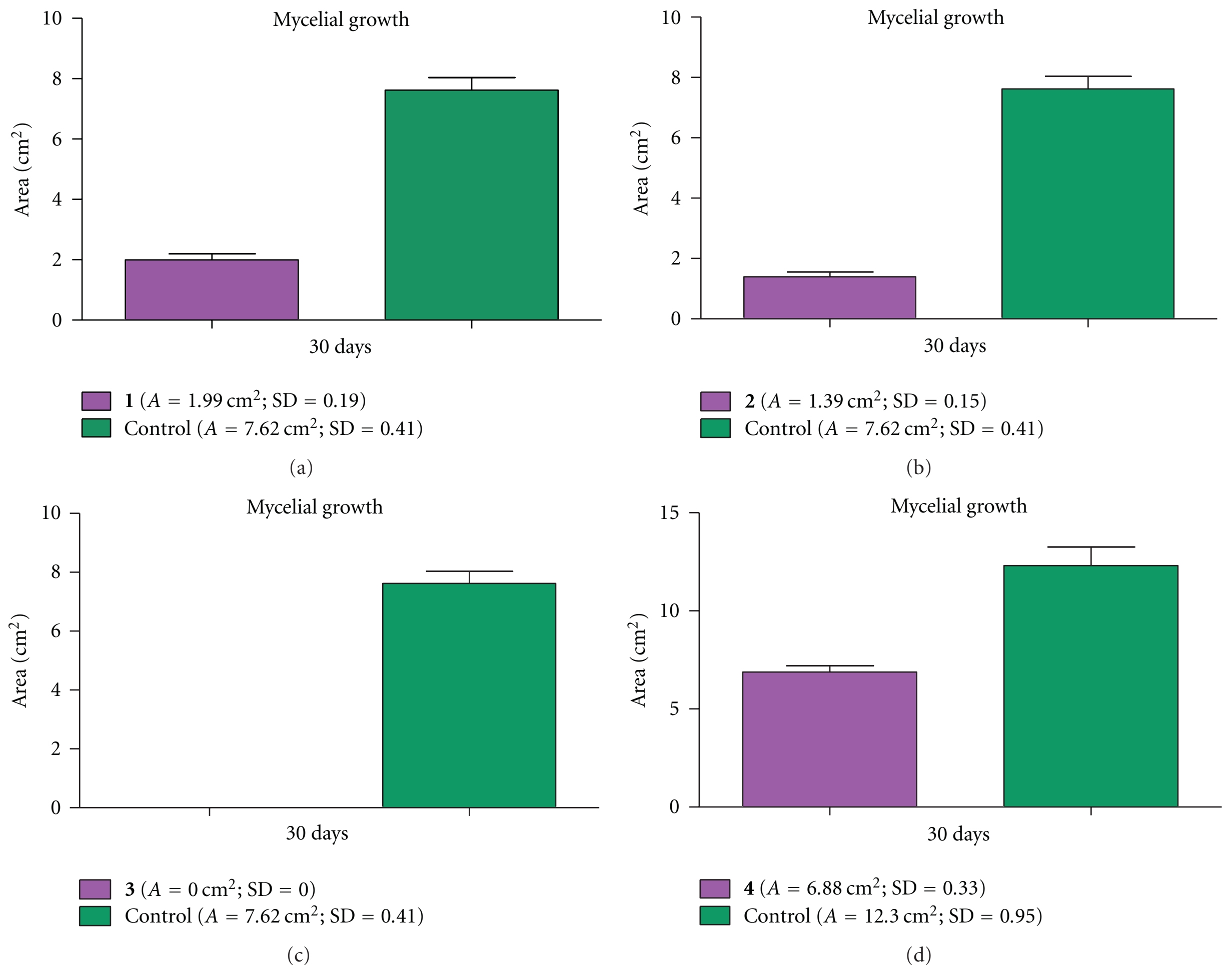
on *A. sexdens rubropilosa* (Table 1), and it was chosen for the beginning of the fractionation studies. In this treatment, the mortality of ants reached 100% at the 17th day while the control with the pure diet did not exceed 72% of mortality at the end of the 25 days of experiment.

The *n*-hexane (**IV**), dichloromethane (**V**), ethyl acetate (**VI**), and hydroalcoholic (**VII**) fractions from partition of methanol extract **II** were tested in ants (*A. sexdens rubropilosa*) ingestion bioassay (Table 2). All the fractions presented statistic difference in comparison with control; however, *n*-hexane, dichloromethane, and ethyl acetate fractions showed high cumulative mortality, 94%, 94%, and 92% of dead ants on the 25th day of experiment, respectively. The *n*-hexane and dichloromethane fractions showed the highest insecticidal activity in a short time, presenting 82% and 94% of mortality in only 12 days of experiment.

In the *in vivo* fungicidal bioassay of these fractions, the *n*-hexane and dichloromethane fractions showed 36% and 29% of inhibitory activity on symbiotic fungus; respectively, while the ethyl acetate and hydroalcoholic fractions promoted the mycelial growth of the fungus in 14% and 7%, respectively (Figure 2).

All the six compounds **1**–**6** were evaluated as their insecticidal potential against *A. sexdens rubropilosa* workers by an ingestion bioassay (Table 3). Although the compounds **2**, **3**, **5**, and **6** presented statistic difference in comparison with control, only the lignan **3** resulted in higher cumulative mortality, 90%, than the control with pure diet. These results indicate that none of the others substances were toxic to the ants workers, and only the lignan (−)-kusunokinin (**3**) was considered biologically active as an insecticide.

In contrast with the weak activity presented by most of the compounds tested, the three lignans showed a high fungicidal potential against the symbiotic fungus *L. gongylophorus*. The lignans (+)-sesamin (**1**), (−)-hinokinin (**2**), and (−)-kusunokinin (**3**) inhibited the mycelial growth in 74%, 72%, and 100%, respectively (Figures 3 and 4). In previous studies [18] were already evaluated the fungicidal



(a) (b) (c) (d)

FIGURE 3: Effect of the compounds (+)-sesamin (**1**) (100 μg·mL^{-1}), (−)-hinokinin (**2**) (100 μg·mL^{-1}), (−)-kusunokinin (**3**) (120 μg·mL^{-1}), and quercetin-3-*O*-α-L-rhamnoside (**4**) (100 μg·mL^{-1}) [18] on the mycelial growth of the symbiotic fungus *L. gongylophorus*.

TABLE 3: *A. sexdens rubropilosa* workers mortality (%) and survival median (Md) when fed with diet containing the compounds **1–4** (400 μg·mL^{-1}) and **5**, **6** (200 μg·mL^{-1}).

Fractions	Days										Md
	1	2	3	6	8	10	14	17	21	25	
Control	0	0	0	6	10	10	24	44	78	84	18.5^a
(+)-sesamin (**1**)	0	2	2	4	4	6	16	44	56	62	19^a
(−)-hinokinin (**2**)	0	2	4	4	6	10	18	22	42	64	23^b
(−)-kusunokinin (**3**)	2	6	6	18	22	24	34	70	82	90	16^b
Quercetin-3-*O*-α-L-rhamnoside (**4**)	0	2	4	10	12	20	34	42	58	74	19^a
Quercetin-3-*O*-β-D-glucoside (**5**)	0	0	2	2	4	14	26	36	40	60	25^b
Quercetin-3-methoxy-7-*O*-β-D-glucoside (**6**)	0	2	2	6	8	14	24	30	48	54	23^b

^{a}Control or no significant and ^{b}significant difference according to long-rank test ($P <$ 0.05).

potentials for furofuran and dibenzylbutyrolactone lignans such as (+)-sesamin and (−)-kusunokinin, respectively. For (+)-sesamin was confirmed its high toxicity against the fungus *L. gongylophorus*, but the results were quite different for (−)-kusunokinin. The actual bioassay uses a different methodology than that used initially, and the fact that the lignan (−)-hinokinin, another dibenzylbutyrolactone lignan, also showed toxicity against the fungus validates the results of this bioassay.

The flavonoids quercetin-3-*O*-β-D-glucoside (**5**) and quercetin-3-methoxy-7-*O*-β-D-glucoside (**6**) were not tested in this bioassay, and the flavonoid quercetin-3-*O*-α-L-rhamnoside (**4**) showed weak inhibition of fungal growth, only 44% [28].

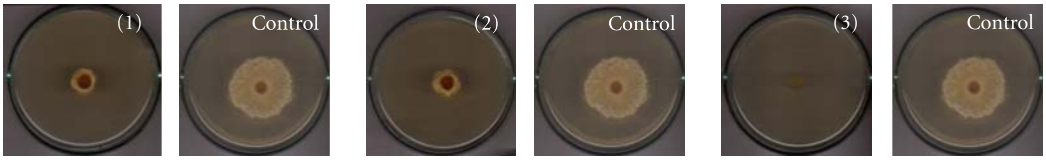


Figure 4: Images of the symbiotic fungus in the presence of the lignans (+)-sesamin (**1**), (−)-hinokinin (**2**), and (−)-kusunokinin (**3**) after 30 days of inoculations and the respective controls.

4. Conclusions

The results observed in the ingestion bioassay with ants workers for the methanol crude extract of the leaves of *V. sebifera* and the *n*-hexane, dichloromethane, and ethyl acetate fractions suggest the use of this plant to control nests of *A. sexdens rubropilosa*. Besides, the high fungicidal potentials of the lignans reveal a rich source for new fungicides.

Acknowledgments

The authors would like to thank Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPQ), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Instituto Nacional de Ciência e Tecnologia de Controle Biorracional de Insetos Pragas, and Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) for the financial support and scholarships (CNPq).

References

[1] W. A. Rodrigues, "Revisão taxonômica das espécies de *Virola* Aublet (Myristicaceae) do Brasil," *Acta Amazonica*, vol. 10, pp. 1–123, 1980.

[2] C. T. Rizzini and W. B. Mors, *Botânica econômica Brasileira*, Epu, Edusp, São Paulo, Brazil, 1976.

[3] K. Kawanishi, Y. Uhara, and Y. Hashimoto, "Alkaloids from the hallucinogenic plant *Virola sebifera*," *Phytochemistry*, vol. 24, no. 6, pp. 1373–1375, 1985.

[4] C. Denny, M. E. Zacharias, K. L. Kohn, M. A. Foglio, and J. E. Carvalho, "Atividade antiproliferativa dos extratos e da fração orgânica obtidos das folhas de *Virola sebifera* Aubl. (Myristicaceae)," *Revista Brasileira de Farmacognosia*, vol. 17, pp. 598–603, 2007.

[5] J. C. V. Martínez, M. I. J. Aldana, and L. E. S. Cuca, "Dibenzylbutane lignans from *Virola sebifera* leaves," *Phytochemistry*, vol. 50, no. 5, pp. 883–886, 1999.

[6] L. M. X. Lopes, M. Yoshida, and O. R. Gottlieb, "1,11-diarylundecan-1-one and 4-aryltetralone neolignans from *Virola sebifera*," *Phytochemistry*, vol. 21, no. 3, pp. 751–755, 1982.

[7] L. M. X. Lopes, M. Yoshida, and O. R. Gottlieb, "Dibenzylbutyrolactone lignans from *Virola sebifera*," *Phytochemistry*, vol. 22, no. 6, pp. 1516–1518, 1983.

[8] L. M. X. Lopes, M. Yoshida, and O. R. Gottlieb, "Further lignoids from *Virola sebifera*," *Phytochemistry*, vol. 23, no. 11, pp. 2647–2652, 1984.

[9] J. C. V. Martinez, L. E. S. Cuca, and P. M. Martinez, "Lignano furofuránicos em corteza de *Virola sebifera* (Aublet)," *Revista Colombiana de Química*, vol. 14, pp. 117–125, 1985.

[10] R. V. R. Rotz, L. E. S. Cuca, and J. C. V. Martinez, "Linanos em hojas de *Virola sebifera*," *Revista Colombiana de Quimica*, vol. 16, pp. 51–55, 1987.

[11] L. M. X. Lopes, M. Yoshida, and O. R. Gottlieb, "Aryltetralone and arylindanone neolignans from *Virola sebifera*," *Phytochemistry*, vol. 23, no. 9, pp. 2021–2024, 1984.

[12] K. R. Rezende and M. J. Kato, "Dibenzylbutane and aryltetralone lignans from seeds of *Virola sebifera*," *Phytochemistry*, vol. 61, no. 4, pp. 427–432, 2002.

[13] M. J. Kato, L. M. X. Lopes, H. F. Paulino Fo, M. Yoshida, and O. R. Gottlieb, "Acylresorcinols from *Virola sebifera* and Virola elongata," *Phytochemistry*, vol. 24, no. 3, pp. 533–536, 1985.

[14] C. Denny, M. E. Zacharias, A. L. T. G. Ruiz et al., "Antiproliferative properties of polyketides isolated from *Virola sebifera* leaves," *Phytotherapy Research*, vol. 22, no. 1, pp. 127–130, 2008.

[15] C. G. S. Marinho, T. M. C. Della Lucia, and M. C. Picanço, "Fatores que dificultam o controle das formigas cortadeiras," *Bahia Agrícola*, vol. 7, pp. 18–21, 2006.

[16] J. B. Fernandes, V. David, P. H. Facchini, M. F. G. F. Silva, E. Rodrigues Filho, and P. C. Vieira, "Extrações de óleos de sementes de citros e suas atividades sobre a formiga cortadeira *Atta sexdens* e seu fungo simbionte," *Quimica Nova*, vol. 25, pp. 1091–1095, 2002.

[17] A. Silva, M. Bacci Jr., C. Gomes de Siqueira, O. Correa Bueno, F. C. Pagnocca, and M. J. Aparecida Hebling, "Survival of *Atta sexdens* workers on different food sources," *Journal of Insect Physiology*, vol. 49, no. 4, pp. 307–313, 2003.

[18] F. C. Pagnocca, S. B. Ribeiro, V. L. V. Torkomian et al., "Toxicity of lignans to symbiotic fungus of leaf-cutting ants," *Journal of Chemical Ecology*, vol. 22, no. 7, pp. 1325–1330, 1996.

[19] C. H. Miyashira, D. G. Tanigushi, A. M. Gugliotta, and D. Y. A. C. Santos, "Comparison of radial growth rate of the mutualistic fungus of *Atta sexdens rubropilosa* Forel in two culture media," *Brazilian Journal of Microbiology*, vol. 41, no. 2, pp. 506–511, 2010.

[20] O. C. Bueno, M. S. C. Morini, F. C. Pagnocca, M. J. A. Hebling, and O. A. Silva, "Sobrevivência de operárias de *Atta sexdens* rubropilosa Forel (Hymenoptera: Formicidae) isoladas do formigueiro e alimentadas com dietas artificiais," *Anais da Sociedade Entomologica do Brasil*, vol. 26, pp. 107–113, 1997.

[21] R. Elandt-Johnson and N. L. Johnson, *Survival Models and Data Analysis*, John Wiley & Sons, New York, NY, USA, 1980.

[22] X. Wang, Y. Lin, Y. Geng, F. Li, and D. Wang, "Preparative separation and purification of sesamin and sesamolin from sesame seeds by high-speed counter-current chromatography," *Cereal Chemistry*, vol. 86, no. 1, pp. 23–25, 2009.

[23] D. Enders and M. Milovanovic, "Asymmetric synthesis of (+)-hinokinin, (+)-dehydrocubebin and cubebin dimethyl ether, a new lignin from *Phyllanthus niruri*," *Zeitschrift für Naturforschung*, vol. 62B, pp. 117–120, 2007.

[24] G. B. Messiano, L. Vieira, M. B. Machado, L. M. X. Lopes, S. A. De Bortoli, and J. Zukerman-Schpector, "Evaluation of insecticidal activity of diterpenes and lignans from *Aristolochia malmeana* against *Anticarsia gemmatalis*," *Journal of Agricultural and Food Chemistry*, vol. 56, no. 8, pp. 2655–2659, 2008.

[25] P. M. L. Santos, J. Schripsema, and R. M. Kuster, "Flavonoídes *O*-glicosilados de *Croton campestris* St. Hill. (Euphorbiaceae)," *Revista Brasileira de Farmacognosia*, vol. 15, pp. 321–325, 2005.

[26] B. Bennini, A. J. Chulia, M. Kaouadji, and F. Thomasson, "Flavonoid glycosides from *Erica cinerea*," *Phytochemistry*, vol. 31, no. 7, pp. 2483–2486, 1992.

[27] L. Krenn, A. Miron, E. Pemp, U. Petr, and B. Kopp, "Flavonoids from *Achillea nobilis* L," *Zeitschrift für Naturforschung C*, vol. 58, no. 1-2, pp. 11–16, 2003.

[28] L. Nebo, A. P. Terezan, S. P. Cardoso et al., "Activity of extracts and fractions from *Anacardium humile* in the nest of leafcutting ants," in *Proceedings of the 1st American Meeting of Chemical Ecology*, p. 141, Colonia del Sacramento, Uruguai, 2010.

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 780713, 7 pages
doi:10.1155/2012/780713

Research Article

Leafcutter Ant Nests Inhibit Low-Intensity Fire Spread in the Understory of Transitional Forests at the Amazon's Forest-Savanna Boundary

Karine S. Carvalho,[1] Ane Alencar,[2] Jennifer Balch,[3, 4, 5] and Paulo Moutinho[2]

[1] *Departamento de Ciências Biológicas, Universidade Estadual do Sudoeste da Bahia, Avenida José Moreira Sobrinho, 45206-190 Jequié, BA, Brazil*
[2] *Instituto de Pesquisa Ambiental da Amazônia, Avenida Nazaré 669, 66035-170 Belém, PA, Brazil*
[3] *Woods Hole Research Center, 149 Woods Hole Road, Falmouth, MA 02450, USA*
[4] *National Center for Ecological Analysis and Synthesis, 735 State Street, Santa Barbara, CA 93101, USA*
[5] *Department of Geography, The Pennsylvania State University, 302 Walker Building, University Park, PA 16802, USA*

Correspondence should be addressed to Karine S. Carvalho, ksczool@yahoo.com.br

Received 11 March 2011; Accepted 13 June 2011

Academic Editor: Jonathan D. Majer

Leaf-cutter ants (*Atta* spp.) remove leaf litter and woody debris—potential fuels—in and around their nests and foraging trails. We conducted single and three annual experimental fires to determine the effects of this leaf-cutter ant activity on the behavior of low-intensity, slow-moving fires. In a transitional forest, where the southern Amazon forest meets the Brazilian savanna, we tested whether leaf-cutter ant nests and trails (i) inhibit fire spread due to a lack of fuels, and (ii), thereby, reduce the total burned area during these experimental low-intensity fires, particularly at forest edges where leaf-cutter ant abundance was higher. Fine-medium fuel mass increased with an increase in distance from ant nest, and the mean area of bare soil was greater on nests than on the forest floor. Between 60 to 90 percent of the unburned area was within 30 m of ant nests, and burned area significantly increased with increasing distance to ant nests. In addition, the number of ant nests declined with increasing distance from the forest edge, and, with exception of the first experimental fire, burned area also increased with increasing distance from the edge. The present study provides new insight to fire ecology in Amazon environments.

1. Introduction

Leaf-cutter ants (*Atta* spp.) are considered conspicuous herbivores in the neotropics [1, 2]. Their role in the ecosystem, however, goes well beyond their herbivory because their construction and maintenance of nests causes diverse impacts to soil [3, 4] with consequences for recruitment dynamics, [5–9] nutrient access [10, 11], and growth of nearby vegetation [12].

Impacts caused by leaf-cutter ants, or bioperturbation, are associated with their behavior of cultivating symbiotic fungus in subterranean chambers linked through a network of tunnels [13–15]. In order to build these chambers, worker ants remove soil to depths up to 7 m [16] and deposit it on the soil surface, forming a mound, a characteristic heap of soil [15, 17, 18].

During ant nest excavation and expansion, the leaf litter and nearby seedlings are buried or removed, which effectively leaves the mound completely bare. Moreover, the worker ants remove debris near the nest (and along foraging trails) as part of their maintenance activities and thereby leave the nest area free of small plants and debris [7, 19, 20].

Therefore, leaf-cutter ants are considered resilient to fire because they (1) consume leaf biomass, often 12–17% of annual production of a tropical forest [1, 21–23], which is potential fuel; (2) construct subterranean nests out of non-flammable materials, for example, soil; (3) clear trails to bare mineral soil, which are effectively firebreaks for low-intensity fires. Moreover, leaf-cutting ants regulate the temperature of the fungus garden by opening or closing entrances to the nest or by modifying the culture's location inside the nest during different times of the year [2, 24]. These combined effects may allow leaf-cutter ants to avoid immediate fire damage. However, the longer-term consequences of fire, for example, habitat modification, food availability, and so forth, are not tested or discussed in this study.

Leaf cutter ants are more abundant in disturbed habitats [25–28] with degraded edges [22, 29–31]. These habitats are dominated by pioneers which have less defenses against herbivory [25, 26, 32, 33]. Based on that assumption, we propose to address the following questions: can leaf-cutter ants inhibit fire and effectively protect nearby vegetation in a forest that has experienced this type of disturbance? And if the answer is yes, is this protection more effective at the forest edge? In order to respond to these questions, we hypothesize that leaf-cutter ant trails and nest building (i) blocks fire spread by removing potential fuels and therefore (ii) reduces the total burned area, especially at the forest edge, where they are more abundant.

2. Methods

2.1. Study Site. The study was conducted in seasonally dry forests of the southern Amazon basin on Tanguro Ranch, Mato Grosso, Brazil (13 04 35.39 S, 52 23 08.85 W). The forest biome is at the Cerrado-Amazônia ecotone, and is described as the dry forests of Mato Grosso [34]. In this region, a severe dry season occurs between May and September, while the rainy season occurs between October and April. Annual mean temperature is 23.5 C with annual precipitation between 1800 to 2000 mm [35].

This study is part of the "Savannization" project created in 2004 by the Amazon Environmental Research Institute (IPAM) and the Woods Hole Research Center (WHRC), with the objective of evaluating the effects of repeated understory wildfires on the susceptibility of forests to future fires. In the context of this greater project, we worked within a 150 ha experimental block divided into three 50 ha treatments, defined as: plot (a) unburned control; plot (b) once-burned; and plot (c) thrice-burned. The scale at which wildfires occur in the Amazon required a large-scale ecosystem approach, which makes adequate experimental replication challenging [36]. A necessary limitation of this experiment is that we treat sampling within the 50 ha treatment plots as independent, which we acknowledge as a form of pseudoreplication that is often associated with experimental fires [37]. Moreover, conducting the experimental burns required that the burned plots be adjacent, and therefore treatment was not randomly assigned to each 50 ha block.

Three annual experimental burns were conducted in August or September (2004–6), near the end of the dry season, when many escaped wildfires typically occur (see [35] for a complete description of the site, experimental design, and fire behavior). During all burns, mean daily temperature ranged between 24 to 29 C, and relative humidity ranged between 51 to 57% (measured at the meteorological station). Wind speed was low in the understory (<0.5 m/s) and had little noticeable effect on fire behavior during all years. Fires were set with kerosene drip torches; a total of 10 km of fire lines were set per plot during three to four consecutive days between 9 : 00 h and 16 : 00 h. During all years, fires were extinguished at night and were relit on subsequent days. Combining both burn plots, initial mean flame height and fire spread rate (FSR; ± SE) were 31 (± 1) cm and 0.21 (± 0.01) m/min, demonstrating that these experimental fires were low-intensity and slow-moving. It is worth noting that fire intensity and spread significantly declined during the second and third burn [35]. Compared with the first burn in 2004, mean flame heights declined by 10 cm in subsequent burns, and the burned area declined by half in the third fire [35].

2.2. Measurement of Fire Inhibition of Ant Nests and Trails. In order to test the effect of ant nests on fire spread, two measurements were taken: (i) quantification of the amount of fine and small-medium woody fuels (defined here as leaves and twigs with diameter 5 cm) which dry faster than large woody debris on the forest floor on and near ant nest mounds and soil, and (ii) calculation of the total area of bare soil created by nests and trails.

Measurement of fuels was conducted between August and September 2005, within several weeks before the experimental fires of that year. For this part of the study, only the experimental burn plots were used (plots (b) and (c)), and all mature, inventoried *Atta* ant nests within the limits of these two plots were utilized (plot (b) = 11 nests and plot (c) = 4 nests).

Maximum height of small twigs was measured within a 40 cm diameter metal ring with increasing distance from each ant nest. Six rings were distributed along a 15 m transect, starting from the nest center (0 m) and extending 3, 6, 9, 12, and 15 m from the nest. After measuring fuel height, all the leaf litter fuels within the 40 cm diameter ring were collected and dried in an oven at 50 C for 48 hours.

To quantify the amount of bare soil associated with ant nests, a wooden frame (100 × 20 cm) was thrown in the nest center and in the nest extremes point. The area within the frame of covered and bare soil was noted. In addition, the length and width of the foraging trails of six nests were measured to calculate the average total area of bare soil associated with a single nest and thereby infer the total forest floor area that was inflammable due to an absence of fuels.

2.3. Relationship between Nest Abundance and Unburned Areas. In order to determine whether ant nests reduce the forest burned area, the annual burn plot (plot (c)) was selected because it was the only one that permitted comparisons between years (2004, 2005, and 2006) and was appropriate for the time period of the present study.

The location of the existing ant nests in the experimental area was registered with an inventory conducted in February of 2005. This inventory used the existing 31 transects (N-S trails which were cut every 50 m in July 2004) in the 150 ha area (each transect was 1 km in length and 40 m in width, totaling a "scanned" area of 116 ha). All of the present ant nests of *Atta* species that were seen within these transects were registered, mapped, and classified.

Nests were classified as active (when ants responded to the stimulus provided by a stick introduced into a nest opening) or inactive (when there was no response to this stimulus or no observed signs of ant activity). Only nests with active colonies were used because of the cleaning and maintenance activities by worker ants for the upkeep of trails and nest mounds.

Nests were also classified as mature (nest mound 15 m^2) or immature (nest without one big mound, with dispersed small mounds). The species of *Atta* that were registered were: *A. cephalotes*, *A. laevigata* and *A. sexdens*, with this last species being the most common (80% of active colonies). The average area covered by mature nests was 40 m^2 (± 15.7), with an estimated volume of removed soil of 6.9 m^3 (± 3.2).

2.4. Statistical Analyses. The effect of ant nests on the quantity of combustible material was evaluated using regressions with distance from nest as the independent variable and the fuel parameters (height of small woody debris and weight of leaf litter) as dependent variables. The distance from nest was defined as the distance to the edge of the mound.

In order to test the relationship between nest presence and unburned vegetation, the cumulative percentage of unburned area was calculated at 5 m intervals from each active ant nest. It was then possible to conduct linear regressions using distance from nest as an independent variable and unburned area (log-transformed, base 10) as a dependent variable. Linear regressions were used to test the effects of distance from forest edge on nest number and unburned area.

3. Results

3.1. Nests as Inhibitors of Fire Spread. The average height of small woody debris on nests was 4.1 cm (± 2.1). However, on the forest floor, the values were highly variable. In general, fuel height increased with increasing distance from the nest (Figure 1).

Leaf litter mass also increases with distance from nest (Figure 1). The least amount of leaf litter was documented on top of nest mounds (33.8 ± 136.1 g), and the greatest amount on the forest floor 15 m from ant nests (55.1 ± 12.1 g).

The average area of uncovered soil on top of ant nests was 1.58 (± 0.2) m^2, which was significantly greater when compared to that near or around ant nests (0.41 ± 0.2 m^2; $t = -9,116$; $P = 0,000$; $N = 15$).

The area of uncovered soil on top of mounds and foraging trails averaged 19 m^2 per nest. Considering the number of nests with active colonies (269) inventoried in the 150 ha block, it can be inferred that 0.53 ha (or 0.35%) would be under the protection of ants nests, if in fact all the colonies had reached maturity.

3.2. Relationship between Nest Abundance and Unburned Areas. Between 60 to 90% of the area that was unburned during the experimental understory fires occurred within approximately 30 m of leaf-cutter ant nests and declined with increasing distance from nests (Figure 2).

The number of nests diminished with increasing distance from the edge (Figure 3). Also it was noted that, with the

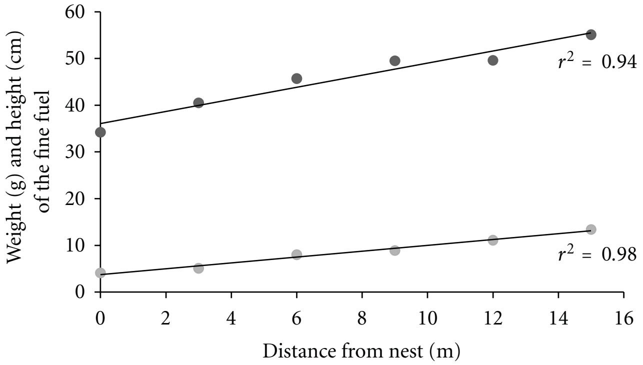
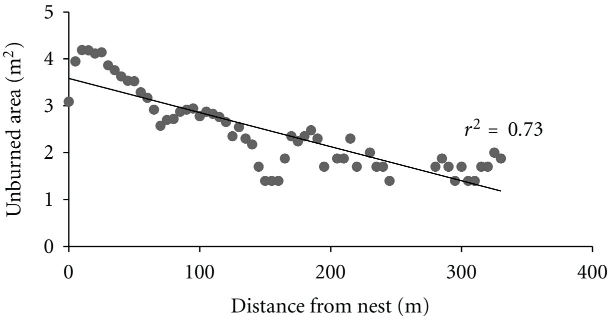
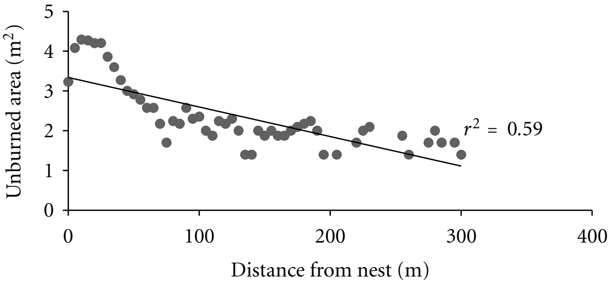


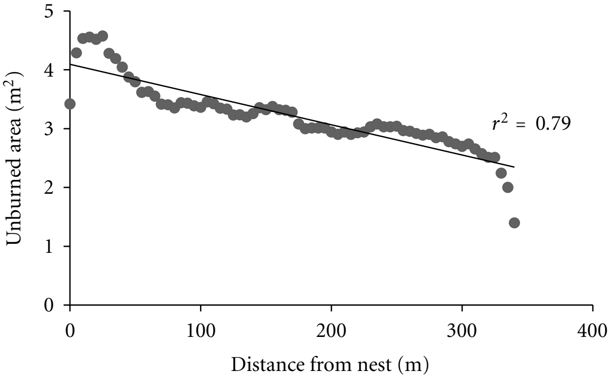
FIGURE 1: Litter mass (g) and height (cm) of small woody debris (5 cm) as a function of distance from leaf-cutter ant nests in a forest at the Amazon-Cerrado transition. Black circles: litter mass; gray circles: height of small woody debris, $N = 6$.



(a) 2004



(b) 2005



(c) 2006

FIGURE 2: Relationship between unburned area and distance to nests in the 50 ha thrice-burned plot in a transitional forest near the Amazon-Cerrado boundary, $N = 200$.

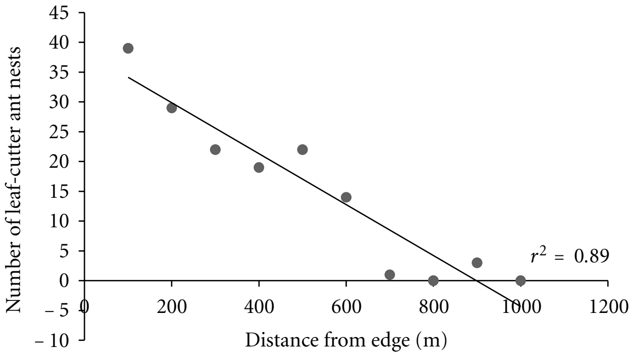


Figure 3: Number of leaf-cutter ant nests in relation to distance from the edge of a transitional forest at the Amazon-Cerrado boundary, $N = 10$.

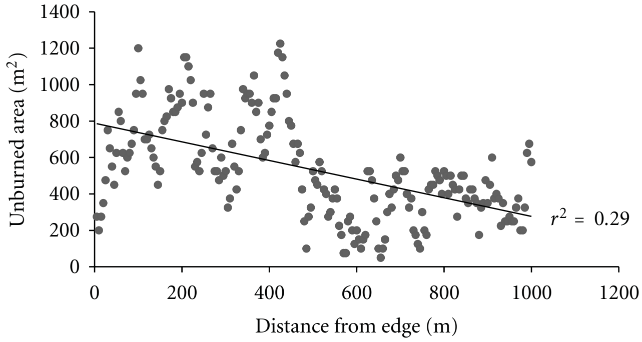
exception of the first experimental fire in 2004, there was more unburned area at the edge that in the forest interior (Figure 4).

4. Discussion

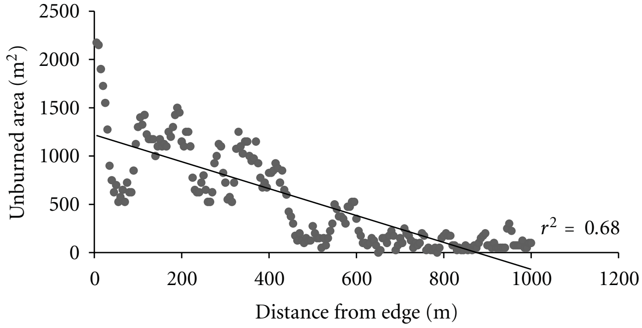
The reduction in spread of low-intensity fires (small flame heights 30 cm) and thereby burned area, is associated with the presence of ant nests. Although this study primarily demonstrates a correlation, the shortage of leaf litter and small-medium woody debris (combustible material), provoked by leaf-cutter ant bioperturbation, likely provides a mechanism whereby fire spread of low-intensity fires is diminished. In this transitional forest, fuel quantity can be more important in determining fire intensity and spread than relative humidity and other microclimate variables, which control fire behavior during the dry season of a typical humid Amazon forest [38–41]. In fact, fuel mass determined fire behavior in this transitional forest at the Amazon-Cerrado boundary, where a slight decline in fuels after two annual burns limited fire intensity and spread rates [35].

The capacity of leaf-cutter ants to diminish available surface fuels at a fine scale can be extended to the landscape scale where ant nest density is high, as is the case at forest edges [22, 29–31]. The most important result of this study is the documentation that ant nests and trails can function as effective firebreaks at forest edges, which have been traditionally known to be vulnerable to fire entry and spread [42–44]. Edge formation causes alterations in microclimate—such as a decline in humidity and increase in temperature and wind speed—all of which promote fuel drying and fire spread [45]. Further, edge formation dries out adjacent forest fragments and increases available surface fuels, as much as from leaf and branch fall due to plants that are subjected to increased wind exposure [46, 47], as from the forest damage caused by timber removal in these regions [44, 48].

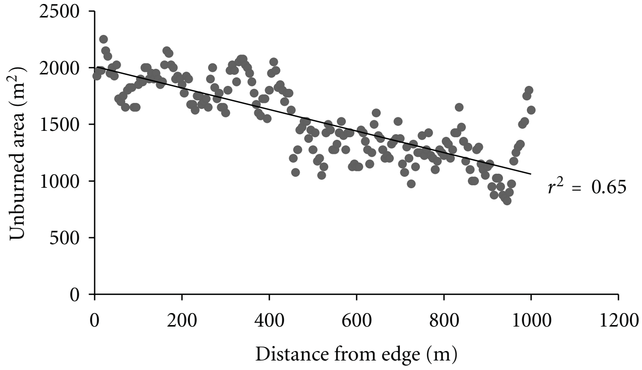
Given this context, populations of leaf-cutter ants may increase, as invertebrate herbivores are repeatedly observed more in edges than forest interiors [22, 29, 30]. Ant nest abundance in these edge areas must be related, in part, to the founding queens' choice [49], which could be driven by their attraction to sunny areas when in nuptial flight.



(a) 2004



(b) 2005



(c) 2006

Figure 4: Relationship between unburned area and edge distance in the 50 ha annual burn plot in a transitional forest at the Amazon-Cerrado boundary, $N = 4$.

Beyond the founding queen's dispersal choice, the majority of ant nests in border areas also could be explained by greater colony survival rates in these locations. Leaf-cutter ants require a certain quantity of solar radiation to reach their mounds, and, because of this, they may establish better in locations without shade [14, 32].

Leaf-cutter ant nests occupy large areas, and their populations have a high turnover rate [21, 50]. This means that, beyond the area free of debris that is potentially important in protecting against fire, these deep nests represent frequent and intense disturbance covering large areas in the forest, beyond even what is visible. Fire-induced mortality rate of plants from these mimicked understory fires, calculated for this transitional forest, was the lowest documented for Amazon forests [35]. A possible explanation for this low mortality was the lowered flammability related to a lack of fuel mass during a third annual experimental burn [35], which limited ignition of larger woody debris or standing dead wood. The degree of flammability depends on the rate of accumulation of fuels and production of litterfall [51] which, in the study area, was substantially lower than in other Amazon forests [35].

The reduction in fuels close to leaf-cutter ant nests could also be influenced by other factors, such as the selectivity of these ants to nest in areas with low leaf litter and woody debris. However, even if other factors contribute to lowered forest flammability and attenuate the damaging effects of fire, the contribution of ant nests in protecting nearby vegetation from low-intensity fires cannot be ignored. This study demonstrates that the behavior of these leaf-cutter ants diminishes the volume of fuels in the environment, by creating, establishing, and maintaining their conspicuous nests in the surface soil of a transitional forest at the Amazon-Cerrado boundary.

This study provides new insights into fire ecology from Amazon studies because the nest effects are off-setting, so that edge areas with lots of nests may not be more susceptible to low-intensity fire than interior plots, as had previous been thought.

Further study should investigate how effective ant nests and trails are at inhibiting more intense or faster fires, such as those observed during more severe droughts. *Atta* is a neotropical genus, and does not have an equivalent organism in well-studied fire-prone ecosystems in Old World systems, as South Africa or Australia; future study may also reveal if there are analog behaviors in Old World invertebrate species. It can be hypothesized from this work that increasing fire frequency, associated with an expanding agricultural frontier, will select for *Atta* species over wood-building taxa, due to their fire-proof construction materials and firebreak trails. This selection may leave lasting effects on arthropod community structure and composition. Given the inherent fire-protection that *Atta* provides, this provides an incentive for farmers and ranchers to avoid using insecticides at agriculture-forest edges. Further study should document the abundance and distribution of *Atta* colonies in burned-over forests through time and their influence on fire behavior of more intense, repeated fires.

Acknowledgments

The authors are grateful to the Woods Hole Research Center and Instituto de Pesquisa Ambiental da Amazônia (IPAM) for institutional support. Special thanks are due to Grupo Amaggi, who invited this research to be conducted on their farm and provided infrastructure support. The authors especially thank IPAM staff Darlisson Nunes, Osvaldo Portela, Raimundo Mota Quintino, Roberto Baena, Joelson Carvalho Serrão, Aderlan Pedroso, and Adriano Portela for assistance during fieldwork. Special acknowledgment is due to Paul Lefebvre for map elaboration and Daniel Nepstad for his contribution to the overall study. Eric Davidson provided helpful comments on earlier versions of the paper. Financial support came from the Programa de Bolsas de Estudo para a Conservação da Amazônia of Instituto Internacional de Educação no Brasil (BECA- IEB) and Fundação de Amparo a Pesquisa do Estado da Bahia (FAPESB). Financial support for the project at large was provided by the David and Lucile Packard Foundation, NASA LBA-ECO program, and NSF Biocomplexity in the Environment and Ecosystems programs.

References

[1] J. M. Cherret, "History of the leaf-cutting ant problem," in *Fire Ants and Leaf-Cutting Ants: Biology and Management*, C. S. Lofgren and R. K. Vander Meer, Eds., pp. 10–17, Westview Press, Boulder, Colo, USA, 1986.

[2] J. M. Cherret, "Leaf-cutting ants, biogeographical studies," in *Ecosystem of the World 14 b, Tropical Rain Forest Ecosystem*, H. Lieth and M. Werger, Eds., pp. 437–486, Elsevier, Amsterdam, The Netherlands, 1989.

[3] P. Moutinho, D. C. Nepstad, and E. A. Davidson, "Influence of leaf-cutting ant nests on secondary forest growth and soil properties in Amazonia," *Ecology*, vol. 84, no. 5, pp. 1265–1276, 2003.

[4] L. V. Verchot, P. R. Moutinho, and E. A. Davidson, "Leaf-cutting ant (*Atta sexdens*) and nutrient cycling: deep soil inorganic nitrogen stocks, mineralization, and nitrification in Eastern Amazonia," *Soil Biology and Biochemistry*, vol. 35, no. 9, pp. 1219–1222, 2003.

[5] M. Garrettson, J. F. Stetzel, B. S. Halpern, D. J. Hearn, B. T. Lucey, and M. J. Mckone, "Diversity and abundance of understorey plants on active and abandoned nests of leaf-cutting ants (*Atta cephalotes*) in a Costa Rican rain forest," *Journal of Tropical Ecology*, vol. 14, no. 1, pp. 17–26, 1998.

[6] A. G. Farji-Brener and L. Ghermandi, "Influence of nests of leaf-cutting ants plant species diversity in road verges of northern Patagonia," *Journal of Vegetation Science*, vol. 11, no. 3, pp. 453–460, 2000.

[7] A. G. Farji-Brener and A. E. Illes, "Do leaf-cutting ant nests make 'bottom-up' gaps in neotropical rain forests?: a critical review of the evidence," *Ecology Letters*, vol. 3, no. 3, pp. 219–227, 2000.

[8] A. G. Farji-Brener, "The effect of abandoned leaf-cutting ant nests on plant assemblage composition in a tropical rainforest of Costa Rica," *Ecoscience*, vol. 12, no. 4, pp. 554–560, 2005.

[9] M. M. Corrêa, P. S. D. Silva, R. Wirth, M. Tabarelli, and I. R. Leal, "How leaf-cutting ants impact forests: drastic nest effects on light environment and plant assemblages," *Oecologia*, vol. 162, no. 1, pp. 103–115, 2010.

[10] L. D. S. L. Sternberg, M. C. Pinzon, M. Z. Moreira, P. Moutinho, E. I. Rojas, and E. A. Herre, "Plants use macronutrients accumulated in leaf-cutting ant nests," *Proceedings of the Royal Society B*, vol. 274, no. 1608, pp. 315–321, 2007.

[11] L. Sousa-Souto, J. H. Schoereder, and C. E. G. R. Schaefer, "Leaf-cutting ants, seasonal burning and nutrient distribution in Cerrado vegetation," *Austral Ecology*, vol. 32, no. 7, pp. 758–765, 2007.

[12] K. S. Carvalho, *Influências dos ninhos de saúva (Formicidae: Attini) na nutrição, crescimento e proteção da vegetação contra o fogo, em uma floresta de transição Amazônia-Cerrado*, Ph.D. dissertation, Museu Paraense Emílio Goldi, Belém, Brazil, 2009.

[13] F. A. M. Mariconni, *As Saúvas*, Universidade de São Paulo, São Paulo, Brazil, Agronômica Ceres edition, 1970.

[14] N. A. Weber, *Gardening Ants: The Attines*, American Philosophical Society, Philadelphia, Pa, USA, 1972.

[15] B. Holldobler and E. O. Wilson, *The Ants*, Harvard University Press, Cambridge, Mass, USA, 1990.

[16] A. A. Moreira, L. C. Forti, M. A. C. Boaretto, A. P. P. Andrade, J. F. S. Lopes, and V. M. Ramos, "External and inter-nal structure of *Atta* bisphaerica Forel (Hymenoptera: Formicidae) nests," *Journal of Applied Entomology*, vol. 128, no. 3, pp. 204–211, 2004.

[17] M. Autuori, "Contribuição para o conhecimento da saúva," *Arquivos do Instituto Biológico*, vol. 18, pp. 39–70, 1947.

[18] E. Amante, "Nota prévia sobre a estrutura do ninho de uma nova formiga saúva (*Atta* sp.) (Hymenoptera: Formicidae)," *Biológico*, vol. 30, pp. 96–97, 1964.

[19] A. Alvarado, C. Berish, and F. Peralta, "Leaf-cutter ant (*Atta cephalotes*) Influence on the morphology of andepts in Costa Rica," *Soil Science Society America Journal*, vol. 45, pp. 790–794, 1981.

[20] A. G. Farji-Brener and J. Silva, "Leaf cutting ants and soil fertility in a well-drained savanna in western Venezuela," *Biotropica*, vol. 27, pp. 250–253, 1995.

[21] R. Wirth, H. Herz, R. J. Ryel, W. Beyschlag, and B. Holldobler, *Herbivory of Leaf-Cutting Ants: A Case Study on* Atta *colombica in the Tropical Rainforest of Panama*, Springer, Berlin, Germany, 2003.

[22] P. Urbas, M. V. Araújo Jr., I. R. Leal, and R. Wirth, "Cutting more from cut forests: edge effects on foraging and herbivory of leaf-cutting ants in Brazil," *Biotropica*, vol. 39, no. 4, pp. 489–495, 2007.

[23] N. A. Costa, L. H. Vasconcelos, H. M. E. Vieira-Neto, and M. E. Bruna, "Do herbivores exert top-down effects in Neotropical savannas? Estimates of biomass consumption by leaf-cutter ants," *Journal of Vegetation Science*, vol. 19, no. 6, pp. 849–854, 2008.

[24] J. Navarro and K. Jaffé, "On the adaptive value of nest features in the grass-cutting ant *Acromyrmex landolti*," *Biotropica*, vol. 17, pp. 347–348, 1985.

[25] H. G. Fowler, "Distribution patterns of Paraguayan leaf-cutting ants (*Atta* and *Acromyrmex*) (Formicidae: Attini)," *Studies Neotropical Fauna and Environment*, vol. 18, pp. 121–138, 1983.

[26] H. L. Vasconcelos and J. M. Cherrett, "Changes in leaf-cutting ant populations (Formicidae: Attini) after the clearing of mature forest in Brazilian Amazonia," *Studies on Neotropical Fauna and Environment*, vol. 30, no. 2, pp. 107–113, 1995.

[27] M. Rao, "Variation in leaf-cutter ant (*Atta* sp.) densities in forest isolates: the potential role of predation," *Journal of Tropical Ecology*, vol. 16, no. 2, pp. 209–225, 2000.

[28] B. A. Santos, C. A. Peres, M. A. Oliveira, A. Grillo, C. P. Alves-Costa, and M. Tabarelli, "Drastic erosion in functional attributes of tree assemblages in Atlantic forest fragments of northeastern Brazil," *Biological Conservation*, vol. 141, no. 1, pp. 249–260, 2008.

[29] V. S. Barbosa, I. R. Leal, L. Iannuzzi, and J. Almeida-Cortez, "Distribution pattern of herbivorous insects in a remnant of Brazilian Atlantic forest," *Neotropical Entomology*, vol. 34, no. 5, pp. 701–711, 2005.

[30] R. Wirth, S. T. Meyer, W. R. Almeida, M. V. Araujo Jr., V. S. Barbosa, and I. R. Leal, "Increasing densities of leaf-cutting ants (*Atta* spp.) with proximity to the edge in a Brazilian Atlantic forest," *Journal of Tropical Ecology*, vol. 23, no. 4, pp. 501–505, 2007.

[31] S. T. Meyer, I. R. Leal, and R. Wirth, "Persisting Hyper-abundance of Leaf-cutting Ants (*Atta* spp.) at the edge of an old atlantic forest fragment," *Biotropica*, vol. 41, no. 6, pp. 711–716, 2009.

[32] K. Jaffe and E. Vilela, "On nest densities of the leaf-cutting ant *Atta cephalotes* in tropical primary forest," *Biotropica*, vol. 21, no. 3, pp. 234–236, 1989.

[33] A. G. Farji-Brener, "Why are leaf-cutting ants more common in early secondary forests than in old-growth tropical forests? An evaluation of the palatable forage hypothesis," *Oikos*, vol. 92, no. 1, pp. 169–177, 2001.

[34] D. Oren, *Portfolio de Áreas Importantes para a Conservação da Biodiversidade Brasileira: uma Análise por Ecorregião*, The Nature Conservancy, Brasília, Brazil, 2005.

[35] J. R. K. Balch, D. C. Nepstad, P. M. Brando et al., "Negative fire feedback in a transitional forest of southeastern Amazonia," *Global Change Biology*, vol. 14, no. 10, pp. 2276–2287, 2008.

[36] L. Oksanen, "Logic of experiments in ecology: is pseudoreplication a pseudoissue?" *Oikos*, vol. 94, no. 1, pp. 27–38, 2001.

[37] P. Van Mantgem, M. Schwartz, and M. Keifer, "Monitoring fire effects for managed burns and wildfires: coming to terms with pseudoreplication," *Natural Areas Journal*, vol. 21, no. 3, pp. 266–273, 2001.

[38] D. Nepstad, P. Lefebvre, U. L. Da Silva et al., "Amazon drought and its implications for forest flammability and tree growth: a basin-wide analysis," *Global Change Biology*, vol. 10, no. 5, pp. 704–717, 2004.

[39] D. Ray, D. Nepstad, and P. Moutinho, "Micrometeorological and canopy controls of fire susceptibility in a forested Amazon landscape," *Ecological Applications*, vol. 15, no. 5, pp. 1664–1678, 2005.

[40] G. M. Blate, "Modest trade-offs between timber management and fire susceptibility of a Bolivian semi-deciduous forest," *Ecological Applications*, vol. 15, no. 5, pp. 1649–1663, 2005.

[41] A. Alencar, D. Nepstad, and M. Del Carmen Vera Diaz, "Forest understory fire in the Brazilian Amazon in ENSO and non-ENSO years: area burned and committed carbon emissions," *Earth Interactions*, vol. 10, no. 6, pp. 1–17, 2006.

[42] M. A. Cochrane and M. D. Schulze, "Fire as a recurrent event in tropical forests of the eastern Amazon: effects on forest structure, biomass, and species composition," *Biotropica*, vol. 31, no. 1, pp. 2–16, 1999.

[43] M. A. Cochrane, A. Alencar, M. D. Schulze et al., "Positive feedbacks in the fire dynamic of closed canopy tropical forests," *Science*, vol. 284, no. 5421, pp. 1832–1835, 1999.

[44] D. C. Nepstad, A. Veríssimo, A. Alencar et al., "Large-scale impoverishment of amazonian forests by logging and fire," *Nature*, vol. 398, no. 6727, pp. 505–508, 1999.

[45] V. Kapos, "Effects of isolation on the water status of forest patches in the Brazilian Amazon," *Journal of Tropical Ecology*, vol. 5, no. 2, pp. 173–185, 1989.

[46] W. F. Laurance, L. V. Ferreira, J. M. Rankin-De Merona, S. G. Laurance, R. W. Hutchings, and T. E. Lovejoy, "Effects of forest fragmentation on recruitment patterns in Amazonian tree communities," *Conservation Biology*, vol. 12, no. 2, pp. 460–464, 1998.

[47] H. L. Vasconcelos and F. J. Luizão, "Litter production and litter nutrient concentrations in a fragmented amazonian landscape," *Ecological Applications*, vol. 14, no. 3, pp. 884–892, 2004.

[48] C. Uhl and J. B. Kauffman, "Deforestation effects on fire susceptibility and the potential response of tree species to fire in the rain forest of the eastern Amazon," *Ecology*, vol. 71, pp. 437–449, 1990.

[49] H. L. Vasconcelos, E. H. M. Vieira-Neto, F. M. Mundim, and E. M. Bruna, "Roads alter the colonization dynamics of a keystone herbivore in neotropical savannas," *Biotropica*, vol. 38, no. 5, pp. 661–665, 2006.

[50] I. Perfecto and J. Vandermeer, "Distribution and turnover rate of a population of *Atta cephalotes* in a tropical rain forest in Costa Rica," *Biotropica*, vol. 25, no. 3, pp. 316–321, 1993.

[51] D. Nepstad, P. Moutinho, M. B. Dias-Filho et al., "The effects of partial throughfall exclusion on canopy processes, aboveground prodution, and biogeochemistry of the Amazon forest," *Journal of Geophysical Research*, vol. 107, pp. 1–18, 2002.

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 694910, 11 pages
doi:10.1155/2012/694910

Review Article

Chemical Recruitment for Foraging in Ants (Formicidae) and Termites (Isoptera): A Revealing Comparison

Klaus Jaffe, Solange Issa, and Cristina Sainz-Borgo

Departamento de Biología de Organismos, Universidad Simón Bolívar, Caracas 1080, Venezuela

Correspondence should be addressed to Klaus Jaffe, kjaffe@usb.ve

Received 29 April 2011; Revised 30 May 2011; Accepted 31 May 2011

Academic Editor: Jacques H. C. Delabie

All termites secrete trail pheromones from their sternal gland, whereas ants use a variety of glands for this purpose. This and the diversity of chemical compounds that serve as trail pheromones among ants, and the uniformity of chemicals among termite trails, suggest a different evolutionary historical dynamics for the development of chemical mass recruitment in both taxa. Termites in addition show pheromonal parsimony. This suggest a single evolutionary origin of pheromone trails in Isoptera, whereas chemical mass recruitment among Formicidae seems to have evolved many times and in different ways. Despite these very different evolutionary histories, both taxa evolved chemical recruitment systems involving attractants and orientation signals, and at least two divergent decision making system for recruitment. This evolutionary analogy suggests that chemical mass recruitment is constraint by fundamental physical dynamic laws. Artificial intelligence including "mass intelligence" and "ant intelligence", emulates mass recruitment in interacting virtual agents in search of optimal solutions. This approach, however, has copied only the "Democratic" recruitment dynamics with a single compound pheromone. Ant and termite evolution shows more sophisticated recruitment dynamics which, if understood properly, will improve our understanding of nature and applications of artificial "swarm intelligence".

1. Introduction

One of the great advantages of society is the use of large numbers of individuals to perform tasks that a lonely individual is unable to perform [2, 3]. One of the most studied group task in social insects is recruitment for food retrieval, after an individual discovers a food source that is much larger than what it can handle on its own. Some of the communication signals modulating this recruitment are based on auditory or visual signals, but the most important communication signal used in recruitment, in the great majority of ant and termite species, is chemical. In recruitment to food, these signals are at least of two different kinds as first detailed for ants [4] : one used to orient workers to the food source, that is trail pheromones; another to attract workers to the trail and thus to the food source, that is attractants for food recruitment. Some species use chemicals for only one of these signals and signal the other function by means of tactile or acoustic signals. An illustrative intermediate recruitment system is called "Tandem Running" [5], where the scout physically carries a nestmate to the food source. In tandem calling [6], the recruiting workers lead nestmates to the newly discovered food source by physically guiding them to the source, sometimes using chemical trails to help orientate to the food. Other species lay chemical trails that fulfill both functions, requiring different chemicals for attracting and orienting ants [7, 8]. These intermediate stages in the evolution of chemical mass recruitment, starting from individual foraging, allow us to suggest phylogenies for recruitment systems illuminating the possible evolutionary history of chemical mass recruitment. Such comparisons suggest that the evolution of chemical recruitment seems to have happened several times, at least in ants [9].

Termites seem also to use both type of chemicals, attractants and orientation signals, in their foraging trails [10, 11], although the details of the chemical communication system used by termites are less well known than in ants.

As both, ants and termites, are terrestrial and arboreal, and that both use chemical mass recruitment, we can compare the different chemical recruitment systems known among ants and among termite in order to extract some general rules.

2. Methods

We explored the existing literature collected by Pherobase [1] for publications on trail pheromones for ants and Isoptera and by Bordereau and Pasteels [12] for additional data on Isoptera. Pherobase, among many other things, reports for Isoptera and for Formicidae all publications mentioning chemicals that had been related to trail pheromones by the author of the publication. Pherobase provides, if available, the exact molecular structure of the chemical and the link to the reference where the trail pheromone was published, grouped by taxonomic or by chemical criteria. Thus, for more details of all references indicated in the Tables, the reader should consult Pherobase for ants and Isoptera, and Bordereau and Pasteels for Isoptera.

3. Results

3.1. Ants. Reports of the chemical nature of the communication signal used for recruitment in ants revealed an interesting pattern of chemical compounds. The summary of available data for ants is presented in Table 1. This table shows that, in many cases, the various compounds produced by a single species are very similar as they constitute small variants of a common chemical skeleton, as is the case for *Monomorium pharaonis*. We suggest that this might be due to the fact that in the biochemical process leading to the synthesis of one or a few active compounds, other chemicals are produced in the process. Indirect evidence for this suggestion comes from other insects where it was shown that synthesizing pure chemicals in pheromone secreting glands is very difficult, if not impossible [13]. In other cases, an adaptive purposeful chemical diversity seems to be present, as chemicals from completely different biochemical pathways are produced as a substrate for the chemical recruitment signal. This is the case for the *Atta* and *Acromyrmex* species and *Daceton armigerum*. In these cases, as shown in Table 1, some compounds have high carbon numbers and low volatility, and others have high volatility, appropriate for the fulfillment of different communication functions such as orientation and attraction.

The chemical survey presented in Table 1 reveals that the pattern of chemical compounds related to trail pheromones in ants correlates with what we know about the decision making behavior used during chemical mass recruitment to food [14]. We know that ants use either one of two decision making systems regulating chemical mass recruitment. The "Democratic" mass recruitment was described in detail for *Solenopsis invicta* [15] and the "Autocratic" system first described for *Atta cephalotes* [16]. The main difference is that in the Democratic system, all workers eventually perform all tasks as in *Solenopsis*; in the Autocratic system, workers specialize either in scouting or in food retrieval [17], as in *Atta*. The Democratic recruitment system is adapted for fast recruitment towards ephemeral food sources. Here all workers participating in the recruitment process have the same responsibility and add a fixed amount of recruitment pheromone to the trail. The more trail pheromone, the stronger the signal, the more workers are recruited. This leads to an increase in the workforce allowing engaging the maximum worker strength in the shortest possible time, so as to collect a scarce recourse (a recently discovered dead cockroach for example) before a competitor does.

The Autocratic recruitment system is adapted for the simultaneous exploitation of a diversity of durable food sources. Here workers specialize in chemical communication or in food retrieval. Communication specialists then visit different food sources and signal the palatability, quality, or quantity of a food source with varying levels of chemical concentrations. Thus, a very good food source will trigger trail laying with plenty of an attractive chemical, whereas food sources of low quality will be signaled with low amounts of this chemical laid on the trail. This system allows for the fine tuning of sophisticated recruitment activity such as described for several *Atta* species, where one group of workers recruit nestmates to the tree canopy where they cut large leaves at their base, so that they fall whole to the ground. There, another group of workers is recruited to each of the leaves that accumulate on the ground, where the workers cut the leave in smaller pieces and transport these pieces to intermediate sites, from where another group of workers transport the leaf fragments to the nest [18].

In both cases, the trail needs to be marked with a chemical that will orient workers towards the food source. If the food source is ephemeral in its existence, an efficient chemical mark does not need to last long. As soon as the food has been collected, the chemical evaporates and the trail disappears. For the simultaneous exploitation of several food sources, however, several longer lasting chemical signals could be very useful, as the source could be revisited fast after spots of inactivity due to rain, heat, cold, or other daily rhythmic patterns. Yet a long lasting chemical signal is not appropriate if it has to work also as an attractant, as any changes in the required workforce will take a long time to achieve if the long lasting chemical need, to evaporate first. Therefore in this later case, highly volatile chemicals, together with some of low volatility, are required to modulate recruitment. Species using chemicals to only attract or orient ants need only one—or a few—chemical compounds to perform this function, whereas species using chemical trails for both, attraction and orientation of nestmates, have to produce a range of chemicals for these two purposes.

As Table 1 shows, most ant species seem to use a few compounds as trail pheromone. Only 14 out of 57 species (25%) seem to use more than 3 chemicals, and only 10% of the species listed use six or more compounds. The use of a few compounds corresponds well to Tandem Calling or even to a Democratic recruitment system. In contrast, species such as the leaf cutting and fungus growing ants *Atta*, *Trachymyrmex*, and *Acromyrmex* secrete over six different chemicals on their trails. Other species using the Democratic system, such as *Solenopsis*, seem to produce much simpler trail pheromones from the standpoint of chemical diversity of compounds. The trail pheromone composition of

Table 1: Chemical compounds reported in trail pheromones of ants. All data were extracted from Pherobase [1].

Myrmicinae
Acromyrmex octospinosus
Cross JH 1982. J. Chem. Ecol. 8 : 1119
me-4me-pyrrole-2-carboxylate
2me5me-3-ethylpyrazine
3me5me-2-ethylpyrazine
Acromyrmex subterraneus subterraneus
Do Nascimento RR 1994. J. Chem. Ecol. 20 : 1719
me-4me-pyrrole-2-carboxylate
Aphaenogaster albisetosus
Hölldobler B 1995 J. Insect Physiol. 41 : 739
4Sme-7-3Kt
4Rme-7-3Kt
Aphaenogaster cockerelli
Hölldobler B 1995. J. Insect Physiol. 41 : 739
1R-phenylethanol
4Sme-7-3Kt
Aphaenogaster rudis
Attygalle AB 1998b Naturwissenschaften 85 : 38
anabasine
anabaseine
2,3-bipyridyl
isopentyl-2-phenylethylamine
Atta bisphaerica
De Oliveira JS 1990 An. Soc. Entomol. Brasil 19 : 145
me-4me-pyrrole-2-carboxylate
2me5me-3-ethylpyrazine
2-phenylacetic acid
bornylene
8OH
Atta cephalotes
Evershed RP 1983 Insect Biochem. 13 : 469
me-4me-pyrrole-2-carboxylate
2me5me-3-ethylpyrazine
2Ald
Riley RG 1974b J. Insect Physiol. 20 : 651
me-4me-pyrrole-2-carboxylate
Atta laevigata
De Oliveira JS 1990 An. Soc. Entomol. Brasil 19 : 145
me-4me-pyrrole-2-carboxylate
2-phenylacetic acid
bornylene
8OH
Atta sexdens
Robinson SW 1978 Bull. Entomol. Res. 68 : 159
me-4me-pyrrole-2-carboxylate
Atta sexdens rubropilosa
Evershed RP 1983 Insect Biochem. 13 : 469
me-4me-pyrrole-2-carboxylate
2me5me-3-ethylpyrazine
2Ald
Cross JH 1979 J. Chem. Ecol. 5 : 187
2me5me-3-ethylpyrazine
methyl phenylacetate
ethyl phenylacetate
me-4me-pyrrole-2-carboxylate
Atta sexdens sexdens
Billen J 1992 Ethol. Ecol. Evol. 4 : 197
2me5me-3-ethylpyrazine
me-4me-pyrrole-2-carboxylate
Evershed RP 1983 Insect Biochem. 13 : 469
me-4me-pyrrole-2-carboxylate
2me5me-3-ethylpyrazine
2Ald
Atta texana
Tumlinson JH 1972b J. Insect Physiol. 18 : 809
me-4me-pyrrole-2-carboxylate
Sonnet PE 1972 J. Agric. Food Chem. 20 : 1191
me-4me-pyrrole-2-carboxylate
Crematogaster castanea
Morgan ED 2004 Chemoecology 14 : 119
R-dodecan-2-ol
Daceton armigerum
Morgan ED 1992 J. Chem. Ecol. 18 : 2161
2me5me-pyrazine
2me3me5me-pyrazine
2me5me-3-ethylpyrazine
delta9-23Hy
23Hy
delta9-25Hy
Eutetramorium mocquerysi
Tentschert J 2000 Naturwissenschaften 87 : 377
2me3me-5-2-methylpropylpyrazine
Manica rubida
Attygalle AB 1986a Physiol. Entomol. 11 : 125
2me5me-3-ethylpyrazine
Mayriella overbecki
Kohl E 2000 Naturwissenschaften 87 : 320
me-2-hydroxy-6me-benzoate
Messor bouvieri
Jackson BD 1989a Experientia 45 : 487
anabasine
2me5me-3-ethylpyrazine
Messor capensis
Brand JM 1993 J. Chem. Ecol. 19 : 1315
anabasine
anabaseine

Table 1: Continued.

Myrmicinae
Messor ebeninus
Coll M 1987 Z. Naturforsch. C 42 : 1027
anabasine
Metapone madagascarica
Hölldobler B 2002 Chemoecology 12 : 147
me-pyrrole-2-carboxylate
Metapone madagascarica
Hölldobler B 2002 Chemoecology 12 : 147
me-pyrrole-2-carboxylate
Monomorium pharaonis Linnaeus
Edwards JP 1978 Ann. Appl. Biol. 89 : 395
3-butyl-5me-octahydroindolizine
Ritter FJ 1977b Crop Prot. Agents : 195
monomorine I
Ritter FJ 1977a Tetrahedron Lett. 30 : 2617
faranal
Ritter FJ 1975b Uni. Dijon : 99
monomorine I
monomorine II
monomorine III
monomorine IV
monomorine V
Pheidole pallidula
Ali MF 1988c Physiol. Entomol. 13 : 257
2me5me-3-ethylpyrazine
Pogonomyrmex barbatus
Liu Y 2002 Fenxi Huaxue 47 : 369
2me3me5me-pyrazine
2me5me-3-ethylpyrazine
2me5me-pyrazine
Hölldobler B 2001 J. Insect Physiol. 47 : 369
2me5me-pyrazine
2me3me5me-pyrazine
2me5me-3-ethylpyrazine
Pogonomyrmex maricopa
Hölldobler B 2001 J. Insect Physiol. 47 : 369
2me5me-pyrazine
2me3me5me-pyrazine
2me5me-3-ethylpyrazine
Pogonomyrmex occidentalis
Hölldobler B 2001 J. Insect Physiol. 47 : 369
2me5me-pyrazine
2me3me5me-pyrazine
Pogonomyrmex rugosus
Hölldobler B 2001 J. Insect Physiol. 47 : 369
2me5me-pyrazine
2me3me5me-pyrazine
2me5me-3-ethylpyrazine
Solenopsis invicta
Van der Meer RK 1983 Fla. Entomol. 66 : 39
Z,E-alpha-farnesene
E,E-alpha-farnesene
Z,E-alpha-homofarnesene
Z,Z-alpha-homofarnesene
17Hy
Z,Z,Z-allofarnesene
Williams HJ 1981b Experientia 37 : 1159
Z,Z,Z-allofarnesene
Van der Meer RK 1981 Tetrahedron Lett. 22 : 1651
Z,E-alpha-farnesene
E,E-alpha-farnesene
Z,E-alpha-homofarnesene
Z,Z-alpha-homofarnesene
Tetramorium caespitum
Attygalle AB 1984J. Chem. Ecol. 10 : 1453
2me5me-pyrazine
2me5me-3-ethylpyrazine
Attygalle AB 1983b Naturwissenschaften 70 : 364
2me5me-pyrazine
2me5me-3-ethylpyrazine
Tetramorium impurum
Morgan ED 1990 J. Chem. Ecol. 16 : 349
me-2-hydroxy-6me-benzoate
Morgan ED 1987 Naturwissenschaften 74 : 596
me-2-hydroxy-6me-benzoate
Tetramorium meridionale Emery
Jackson BD 1990c Naturwissenschaften 77 : 294
2me-pyrazine
2me5me-pyrazine
2me3me5me-pyrazine
2me5me-3-ethylpyrazine
Formicinae
Camponotus atriceps
Haak U 1996 Chemoecology 7 : 85
6-butyl-tetrahydro-3me5me-pyran-2Kt
nerolic acid
Camponotus balzani
Kohl E 2003 Chemoecology 13 : 113
8-hydroxy-3me5me7me-isochromanone
Camponotus castaneus
Kohl E 2003 Chemoecology 13 : 113
6-butyl-tetrahydro-3me5me-pyran-2Kt
Camponotus floridanus
Haak U 1996 Chemoecology 7 : 85
6-butyl-tetrahydro-3me5me-pyran-2Kt
nerolic acid
Camponotus herculeanus
Bestmann HJ 1999 Chem. Eur. J. 5 : 2984
2Sme4Rme5S-5-hexanolide
Payne TL 1975 Ann. Entomol. Soc. Am. 68 : 385

Table 1: Continued.

Formicinae
me-2-hydroxy-6me-benzoate
mellein
Hölldobler B 1965 Z. vergl. Physiol. 50 : 551
me-2-hydroxy-6me-benzoate
mellein
10me-12Acid
Camponotus inaequalis
Bestmann HJ 1997 Angew. Chem. 36 : 395
3,4-dihydro-8-hydroxy-3me5me7me-isocoumarin
Camponotus ligniperda
Bestmann HJ 1999 Chem. Eur. J. 5 : 2984
2Sme4Rme5S-5-hexanolide
Bestmann HJ 1999 Chem. Eur. J. 5 : 2984
2Sme4Rme5S-5-hexanolide
Camponotus rufipes
Uebler E 1995 Naturwissenschaften 82 : 523
mellein
Camponotus sericeiventris
Kohl E 2003 Chemoecology 13 : 113
8-hydroxy-3me5me7me-isochromanone
Camponotus silvicola
Uebler E 1995 Naturwissenschaften 82 : 523
8-hydroxy-3me5me7me-isochromanone
Camponotus socius
Kohl E 2001 Chemoecology 11 : 67
2Sme4Rme5S-5-hexanolide
2,3-dihydro-3,5-dihydroxy-6me-pyran-4Kt
Bestmann HJ 1999 Chem. Eur. J. 5 : 2984
2Sme4Rme5S-5-hexanolide
Formica rufa
Bestmann HJ 1992 Angew. Chem. 31 : 795
R-mellein
Lasius fuliginosus
Kern F 1997 J. Chem. Ecol.23 : 779
mellein
2,3-dihydro-3,5-dihydroxy-6me-pyran-4Kt
Akino T 1996 Jap. J. Appl. Entomol. Zool.40 : 233
caproic acid
enanthic acid
caprylic acid
pelargonic acid
caprinic acid
lauric acid
Huwyler S 1975 J. Insect Physiol. 21 : 779
caproic acid
enanthic acid
caprylic acid
pelargonic acid
caprinic acid
lauric acid
Formicinae
Lasius niger
Bestmann HJ 1992 Angew. Chem.31 : 795
3,4-dihydro-8-hydroxy-3me5me7me-isocoumarin
Linepithema humile
Greenberg L 2000 J. Econ. Entomol. 93 : 119
Cordova YL 1998 Eur. J. Entomol.95 : 501
sulcatone
sulcatol
13-2Kt
Z9-16Ald
Van Vorhis Key SE 1982 J. Chem. Ecol. 8 : 3
Z9-16Ald
Cavill GWK 1979 Experientia 35 : 989
Z9-16Ald
Dolichoderinae
Dolichoderus thoracicus
Attygalle AB 1998a Naturwissenschaften 85 : 275
Z9-18Ald
Z9-16Ald
Tapinoma simrothi
Simon T 1991 Insectes Soc. 38 : 17
iridodial
iridomyrmecin
Ectatomminae
Ectatomma ruidum
Bestmann HJ 1995 Naturwissenschaften 82 : 334
geranylgeraniol acetate
geranylgeraniol
Gnamptogenys striatula
Blatrix R 2002 J. Chem. Ecol. 28 : 2557
4-methylgeraniol
bishomogeraniol
E2,4S6-3me4me7me-octadienyl decanoate
E2,4S6-3me4me7me-octadienyl dodecanoate
Ponerinae
Leptogenys diminuta
Kern F 1993 Naturwissenschaften 80 : 424
3R4Sme-heptan-3-ol
Attygalle AB 1991b Naturwissenschaften 78 : 90
isogeraniol
Attygalle AB 1988c Naturwissenschaften 75 : 315
3R4Sme-heptan-3-ol
isogeraniol
Leptogenys peuqueti
Janssen E 1997b Naturwissenschaften 84 : 122
1-ethyl-4me-heptyl acetate
1-isopropyl-4me-heptyl acetate
1-propyl-4me-heptyl acetate
4me-dodecan-7-ol
3me9me-dodecan-6-ol

Table 1: Continued.

Ponerinae
1-pentyl-4me-heptyl acetate
4me-tridecan-7-ol
4me10me-tridecan-7-ol
4me-tetradecan-7-ol
3me-hexyl-4me-heptyl acetate
3me-hexyl-octyl acetate
heptyloctyl acetate
4me-hexadecan-7-ol
3me-hexyl-decyl acetate
Megaponera foetens
Janssen E 1995 J. Chem. Ecol. 21 : 1947
dimethyluracil
actinidine
Longhurst C 1979 J. Chem. Ecol. 5 : 703
1me2me-disulfane
1me3me-trisulfane
benzyl methyl sulfane
Longhurst C 1979 J. Chem. Ecol. 5 : 703
11Hy
13Hy
Pachycondyla tarsata
Janssen E 1999 Chemoecology 9 : 9
17-9Kt
Rhytidoponera metallica
Meinwald J 1983Naturwissenschaften 70 : 46
isogeraniol
3-hydroxybenzaldehyde
Aenictinae (dorylinae)
Aenictus sp
Oldham NJ 1994, Experientia 50 : 763
methyl anthranilate
methyl nicotinate

Solenopsis invicta recalls the case of *Monomorium pharaonis* discussed above. Although over 5 different chemicals can be recognized in Table 1, all these chemicals have the same chemical skeleton. Thus, the Autocratic chemical recruitment system could be associated to a more advanced chemical signaling. The case of the hunting and recruiting foragers of *Daceton armigerum* [19] that use a multitude of recruitment strategies is interesting. Table 1 shows that its trail pheromone has many chemical compounds, hinting to a sophisticated diverse chemical communication system.

Many ant species in the subfamily Myrmicinae with large colonies and a sophisticated social structure, use carboxylates and pyrazines to lay their pheromone trail. These are semivolatile compounds. The Myrmicinae, *Atta*, and *Acromyrmex*, for example, need to constantly recruit many workers to supply big colonies with a great quantity of leaves which they use as a substrate to grow their fungus. In contrast, ants with less developed societies living in smaller colonies, such as species of the subfamily Ponerinae, use alcohols and acetate, which are more volatile and thus might serve as chemical attractants to trigger foraging to collect ephemeral food sources. Ponerinae individuals feed opportunistically on dispersed food items. This requires quick recruitment of workers, and, as a consequence, the compounds of the pheromone trail are more volatile and less permanent in time, compared to the carboxylates of the leaf cutter ants. In some species of Ponerinae, chemical trails also regulate nest moving [20].

The Formicinae ants are mostly predators but differ from Ponerinae by their greater social complexity, larger colonies, and more diverse worker castes or polymorphism. The trail pheromones of Formicinae species use a mix of compounds that are more complex than that of Ponerinae, probably due to a more elaborate recruitment system. Table 1 reflects this showing among Formicinae, compounds with elevated molecular weights, such as mullein, in addition to compound of low molecular weight and probably low volatility. Formicinae trail pheromone chemistry seems to be closer to the Myrmicinae than the Ponerinae. This suggests trails with both short-term attractant and long-term orientation function. In the case of Dolichoderinae species, the information is scarcer. In the Argentine ant, *Linepithema humile*, a tramp species with supercolonies of hundreds of thousands of workers, the trail pheromone has short-chain volatile aldehydes, suggesting a foraging strategy with fast short term bouts of recruitment. The continuous reinforcement of a trail made with short lasting volatiles can last long if it is reinforced by hundreds of workers.

3.2. Termites. Termite species also show diverse ecological life types. We know species that live and feed in the same piece of wood, and species that have their nest separated from their food source [21]. But even the "one-piece" life type species possess trail pheromones which they use to recruit workers for defense or nest moving. Termites of "one-piece" life type do not require orientation systems a priori. Secretions of their sternal gland are considered to function in the recruitment of nestmates to source disturbance within the nest. These termites might also use trail following pheromones to colonize new food sources to where they move their nest [22, 23]. Most termites forage on relatively durable food sources containing cellulose. In addition, most termite species forage on several food sources simultaneously, suggesting a recruitment system closer to the above described Autocratic chemical recruitment system, which seem to be the case in the only termite species where this has been explored so far [24]. Table 2 presents what we know about the chemicals used in trail pheromones by termites. The available data shows that pheromone trails among each termite species are constructed with one or a few compounds among a total of 8 chemicals. For the families where chemical trail pheromones have been reported, the Rhinotermitidae, Termitidae, and Kalotermitidae seem to use mainly neocembrene and a dodecatrienol; *Nasutitermes corniger* uses in addition to these two compounds trinervitatriene; whereas Mastotermitidae and Termopsidae use a trimethylundecadienol for trail following. That is, all trail pheromones in Isoptera are synthesized from a much

Table 2: Chemical compounds reported from trail pheromones of termites. All data were extracted from Pherobase [1], and from Bordereau and Pasteels [12].

Mastotermitidae
Mastotermes darwiniensis
Sillam-Dussès, D. et al. 2007. J Chem. Ecol 33 : 1960–1977
(*E*)-2,6,10-trimethyl-5,9-undecadien-1-ol
Termopsidae
Porotermitinae
Porotermes adamsoni
Sillam-Dussès, D. et al. 2007. J Chem. Ecol 33 : 1960–1977
(*E*)-2,6,10-trimethyl-5,9-undecadien-1-ol
Stolotermitinae
Stolotermes victoriensis
Sillam-Dussès, D. et al. 2007. J Chem. Ecol 33 : 1960–1977
(*E*)-2,6,10-trimethyl-5,9-undecadien-1-ol
Termopsinae
Zootermopsis angusticollis
Greenberg SL 1986 Int. J. Insect Morphol. Embryol. 15 : 283
Heneicosano
Tricosane
Bordereau C. et al. 2010 Biol J Linn Soc 100 : 519–530
4,6-dimethyldodecanal
Zootermopsis nevadensis
Karlson P. et al. 1968 J. Insect Physiol. 14 : 1763
n-Hexanoic acid
Caproic acid
Bordereau, C. et al. 2010 Biol J Linn Soc 100 : 519–530
4,6-Dimethyldodecanal
Kalotermitidae
Cryptotermes brevis
Sillam-Dussès D. et al. 2009 Chemoecology19 : 103–108
(*Z*)-dodec-3-en-1-ol
Cryptotermes darlingtonae
Sillam-Dussès D. et al. 2009 Chemoecology 19 : 103–108
(*Z*)-dodec-3-en-1-ol
Cryptotermes pallidus
Sillam-Dussès D. et al. 2009 Chemoecology 19 : 103–108
(*Z*)-dodec-3-en-1-ol
Incisitermes tabogae
Sillam-Dussès D. et al. 2009 Chemoecology 19 : 103–108
(*Z*)-dodec-3-en-1-ol
Kalotermes flavicollis
Klochkov and Zhuzhikov 1990. Advances in life science. Birkhäuser, Basel, pp 41–43
Nonanol
Decanol
Undecanol
dodecanol

Table 2: Continued.

Kalotermitidae
Sillam-Dussès D. et al. 2009 Chemoecology 19 : 103–108
(*Z*)-dodec-3-en-1-ol
Neotermes holmgreni
Sillam-Dussès D. et al. 2009 Chemoecology 19 : 103–108
(*Z*)-dodec-3-en-1-ol
Postelectrotermes howa
Sillam-Dussès et al. 2009 Chemoecology 19 : 103–108
(Z)-dodec-3-en-1-ol
Procryptotermes falcifer
Sillam-Dussès D. et al. 2009 Chemoecology 19 : 103–108
(*Z*)-dodec-3-en-1-ol
Procryptotermes leewardensis
Sillam-Dussès D. et al. 2009 Chemoecology 19 : 103–108
(*Z*)-dodec-3-en-1-ol
Rhinotermitidae
Prorhinotermitinae
Prorhinotermes canalifrons
Sillam-Dussès D. et al. 2005 Chemoecology 15 : 1–6
Neocembrene A
Prorhinotermes simplex
Sillam-Dussès D. et al. 2005 Chemoecology 15 : 1–6
Neocembrene
Sillam-Dussès D. et al. 2009 J. Insect Physiol 55 : 751-757
Neocembrene A
(*Z,Z,E*)-dodeca-3,6,8-trien-1-ol
Coptotermitinae
Coptotermes formosanus
Tokoro M. et al. 1994 J. Chem. Ecol. 20 : 199
(*Z,E,E*)-dodeca-3,6,8-trien-1-ol
Coptotermes gestroi
Arab A. et al. 2004 Sociobiology 43 : 377
(*Z,Z,E*)-dodeca-3,6,8-trien-1-ol
Sillam-Dussès D. et al. 2006 Proceedings XV IUSSI. Washington 100-101
(*Z,Z,E*)-dodeca-3,6,8-trien-1-ol
Heterotermitinae
Heterotermes tenuis
Arab A. et al. 2004 Sociobiology 43 : 377
(*Z,Z,E*)-dodeca-3,6,8-trien-1-ol
Sillam-Dussès D. et al. 2006 Proceedings XV IUSSI. Washington 100-101
(*Z,Z,E*)-dodeca-3,6,8-trien-1-ol
Reticulitermes flavipes
Howard R. et al. 1976 J. Chem. Ecol. 2 : 147
(*Z,Z,E*)-dodeca-3,6,8-trien-1-ol
Matsumura F. et al. 1968 Nature 219 : 963
(*Z,Z,E*)-dodeca-3,6,8-trien-1-ol

Table 2: Continued.

Rhinotermitidae
Reticulitermes hesperus
Zhong CM 1979 Sci. Silvae Sin. 15 : 15
Z3-4-phenyl-4OH
Reticulitermes lucifugus grassei
Wobst B. et al. 1999 J. Chem. Ecol. 25 : 1305
(*Z*,*Z*,*E*)-dodeca-3,6,8-trien-1-ol
Reticulitermes santonensis
Wobst B. et al. 1999 J. Chem. Ecol. 25 : 1305
(*Z*,*Z*,*E*)-dodeca-3,6,8-trien-1-ol
Laduguie N. et al. 1994 J. Insect Physiol. 40 : 781
(*Z*,*Z*,*E*)-dodeca-3,6,8-trien-1-ol
Reticulitermes speratus
Tokoro M. et al. 1990 J. Chem. Ecol. 16 : 2549
(*Z*,*Z*,*E*)-dodeca-3,6,8-trien-1-ol
Yamaoka R. et al. 1987 J. Chromatogr. 399 : 259
(*Z*,*Z*,*E*)-dodeca-3,6,8-trien-1-ol
Reticulitermes tibialis
Bernklau EJ 2005 J. Econ. Entomol. 98 : 476
CO2
Zhong CM 1979 Sci. Silvae Sin. 15 : 15
Z3-4-phenyl-4OH
Howard R. et al. 1976 J. Chem. Ecol. 2 : 147
(*Z*,*Z*,*E*)-dodeca-3,6,8-trien-1-ol
Reticulitermes virginicus
Howard R. et al. 1976 J. Chem. Ecol. 2 : 147
(*Z*,*Z*,*E*)-dodeca-3,6,8-trien-1-ol
Tai A. et al. 1969 J. Org. Chem. 34 : 2180
(*Z*,*Z*,*E*)-dodeca-3,6,8-trien-1-ol
Matsumura F. et al. 1968 Nature 219 : 963
(*Z*,*Z*,*E*)-dodeca-3,6,8-trien-1-ol
Rhinotermitinae
Rhinotermes marginalis
Sillam-Dussès D. et al. 2006 Proc. XV Congress IUSSI, Washington, DC, 100–101
(*Z*,*Z*,*E*)-dodeca-3,6,8-trien-1-ol
Schedorhinotermes lamanianus
Sillam-Dussès D. et al. 2006 Proc. XV Congress IUSSI, Washington, DC, 100–101
(*Z*,*Z*,*E*)-dodeca-3,6,8-trien-1-ol

Termitidae
Macrotermitinae
Ancistrotermes pakistanicus
Robert A. et al. 2004 Naturwissenschaften 91 : 34–39
(*Z*,*Z*)-dodeca-3,6-dien-1-ol
Macrotermes annandalei
Peppuy A. et al. 2001 Insectes Soc. 48 : 245
(*Z*)-dodec-3-en-l-ol
Peppuy A. et al. 2001 J. Insect Physiol. 47 : 445
(*Z*)-dodec-3-en-l-ol
Macrotermes barneyi
Peppuy A. et al. 2001 Insectes Soc. 48 : 245
(*Z*)-dodec-3-en-l-ol
Macrotermes bellicosus
Peppuy A. et al. 2001 Insectes Soc. 48 : 245
(*Z*)-dodec-3-en-l-ol
Macrotermes subhyalinus
Peppuy A. et al. 2001 Insectes Soc. 48 : 245
(*Z*)-dodec-3-en-1-ol
Odontotermes formosanus
Deng XJ. et al. 2002 Acta Entomol. Sin. 45 : 739
(*Z*,*Z*)-dodeca-3-6-dien-1-ol
Du TY 1982 Acta Entomol. Sin. 25 : 172
(*Z*,*Z*)-dodeca-3-6-dien-1-ol
Odontotermes hainanensis
Peppuy A. et al. 2001 Insectes Soc. 48 : 245
(*Z*)-dodec-3-en-1-ol
Odontotermes maesodensis
Peppuy A. et al. 2001 Insectes Soc. 48 : 245
(*Z*)-dodec-3-en-1-ol
Pseudacanthotermes militaris
Bordereau C. et al. 1993 Actes Coll. Insectes Soc. 17 : 2177
(*Z*,*Z*,*E*)-dodeca-3,6,8-trienol-1-ol
Pseudacanthotermes spiniger
Bordereau C. et al. 1991 J. Chem. Ecol. 17 : 2177
(*Z*,*Z*,*E*)-dodeca-3,6,8-trienol-1-ol
Termitinae
Cubitermes sp.
Sillam-Dussès D. et al. 2006 Proc. IUSSI, Washington, DC, 100–101
(*Z*,*Z*,*E*)-dodeca-3,6,8-trien-1-ol
Drepanotermes perniger
Sillam-Dussès D. et al. 2006 Proc. IUSSI, Washington, DC, 100–101
(*Z*,*Z*,*E*)-dodeca-3,6,8-trien-1-ol
Termes hispaniolae
Sillam-Dussès D. et al. 2006 Proc. IUSSI, Washington, DC, 100–101
(*Z*,*Z*,*E*)-dodeca-3,6,8-trien-1-ol
Amitermes evuncifer
Kotoklo E. et al. 2010 Sociobiology 55 : 1-10
Dodecatrienol
Neocembrene A
Syntermitinae
Cornitermes bequaerti
Sillam-Dussès D. et al. 2006 Proc. IUSSI, Washington, DC, 100–101
(*Z*,*Z*,*E*)-dodeca-3,6,8-trien-1-ol

Table 2: Continued.

Termitidae
Cornitermes cumulans
Sillam-Dussès D. et al. 2006 Proc. IUSSI, Washington, DC, 100–101
(*Z*,*Z*,*E*)-dodeca-3,6,8-trien-1-ol
Cornitermes snyderi
Sillam-Dussès D. et al. 2006 Proc. IUSSI, Washington, DC, 100–101
(*Z*,*Z*,*E*)-dodeca-3,6,8-trien-1-ol
Syntermes grandis
Sillam-Dussès D. et al. 2006 Proc. IUSSI, Washington, DC, 100–101
(*Z*,*Z*,*E*)-dodeca-3,6,8-trien-1-ol
Nasutitermitinae
Constrictotermes cyphergaster
Sillam-Dussès D. et al. 2010 Biol. J. Linnean Soc. 99 : 20
Dodecatrienol
Neocembrene-A
Nasutitermes corniger
Sillam-Dussès D. et al. 2010 Biol. J. Linnean Soc. 99 : 20
Dodecatrienol
Neocembrene-A
Trinervitatriene
Nasutitermes diabolus
Sillam-Dussès D. et al. 2010 Biol. J. Linnean Soc. 99 : 20
Dodecatrienol
Neocembrene-A
Nasutitermes ephratae
Sillam-Dussès D. et al. 2010 Biol. J. Linnean Soc. 99 : 20
Dodecatrienol
Neocembrene-A
Nasutitermes exitiosus
Sillam-Dussès D. et al. 2010 Biol. J. Linnean Soc. 99 : 20
Dodecatrienol
Neocembrene-A
Birch AJ 1972 J. Chem. Soc. 1 : 2653
Neocembrene-A
Nasutitermes graveolus
Moore P 1966 Nature 211 : 746–747
Neocembrene-A
Birch A. et al. 1972 J Chem Soc Perkin Trans 1 : 2653–2658
Neocembrene-A
Nasutitermes guayanae
Sillam-Dussès D. et al. 2010 Biol. J. Linnean Soc. 99 : 20
Dodecatrienol
Neocembrene-A
Nasutitermes kemneri
Sillam-Dussès D. et al. 2010 Biol. J. Linnean Soc. 99 : 20
Dodecatrienol
Neocembrene-A
Nasutitermes lujae
Sillam-Dussès D. et al. 2010 Biol. J. Linnean Soc. 99 : 20
Dodecatrienol
Neocembrene-A
Nasutitermes walkeri
Sillam-Dussès D. et al. 2010 Biol. J. Linnean Soc. 99 : 20
Neocembrene-A
Nasutitermes voeltzkowi
Sillam-Dussès D. et al. 2010 Biol. J. Linnean Soc. 99 : 20
Dodecatrienol
Neocembrene-A
Trinervitermes bettonianus
McDowell PG and Oloo G. 1984 J. Chem. Ecol. 10 : 835
Neocembrene-A
Trinervitermes geminatus
Sillam-Dussès D. et al. 2010 Biol. J. Linnean Soc. 99 : 20
Dodecatrienol
Neocembrene-A
Trinervitermes trinervoides
Sillam-Dussès D. et al. 2010 Biol. J. Linnean Soc. 99 : 20
Dodecatrienol
Neocembrene-A

conserved metabolic route eventually leading to a compound with the same carbon skeleton as that of a dodecatrienol, where two subfamilies have diverged somewhat from the rest in that they synthesize trimethylundecadienol instead of dodecatrienol as the rest of termite species does.

In the case of termites, volatile chemicals for modulating the recruitment of workers are most likely to be used outside the nest or outside the covered galleries. This seems natural if we take into account that most termites forage in galleries which orient workers to their food sources. Very volatile chemicals are of little use in closed environments where they cannot disperse. Long-lasting, low-volatility chemicals may be useful for trail orientation outside the nest and might form the substrate around which galleries are built [25]. Thus, other signals seem to be more appropriate here in modulating communication. Many termite species add feces, saliva, and other secretions to the trail. This explains foraging trails that are reused after several years. A different situation may occur among termites foraging on grasses or leaves in open habitats and foraging at the end of their galleries where they can display very sophisticated foraging and recruitment strategies [26]. When recruitment behavior was explored in an open setting in a Nasutitermitinae [24], the decision making systems used to modulate the recruitment dynamics conformed to the Autocratic kind described for *Atta*.

4. Discussion

This paper is based only on published reports, and many more compounds used as trail pheromones are surely to be discovered in the future. For example, it is very likely that *Atta texana* uses a larger pool of compounds as trail pheromones as that reported in Table 1, as it is unlikely to differ very much from other *Atta* species in this regard. Thus, results in the Tables are biased towards species that have drawn more attention from researchers. Another cautionary remark regards the assessment of volatility based on chemical structure alone. In general, compounds of the same kind of lower molecular weight are more volatile than the ones of higher molecular weight or longer carbon chains. Biologically relevant volatility, however, depends not only on the compound but also on the substrate on which the chemical is secreted, on its concentrations on the substrate, and on the humidity and temperature of the surrounding air. Thus, simple direct correlations between molecular weight, assumed volatility, and behavioral function of a compound should be avoided.

The work behind the literature used for this study, evidently, was not performed with our objectives in mind, but it is unlikely that methodological limitations explain the lack of more chemical compound associated with trail pheromones among termites than among ants. Despite many possible limitations of this study, the large extend of the research effort explored and the large number of species covered guarantee a minimum of robustness that makes drawing conclusion from these data reasonable.

Despite these and other limitations of this paper, we might suggest two basic trends: (1) evolutionary history of the evolution of ant and termite trails is very different, and (2) the dynamics of interacting individuals achieving a recruitment process mediated by chemicals follow basic rules.

4.1. Different Evolutionary Histories between Ants and Termites. The diversity of chemical structures among ant trail pheromones and the uniformity of chemical compounds among termite trails suggest a different evolutionary history for the development of chemical mass recruitment in both taxa. In termites, often trail pheromone compounds are synthesized also by other exocrine glands and are used as sex pheromones. This pheromonal parsimony seems to be characteristic of termites [12] and is not common among ants.

Chemical mass recruitment among ants seems to have evolved at least 8 times [9], whereas chemical mass recruitment among termites seems to be a more conservative phenomenon where all species seem to share a common ancestor that had already developed chemical recruitment. This explains also the large difference between ants and termites in the glands responsible for the secretion of the trail pheromones. Many different glands are used by different species among ants [27], whereas only the sternal gland is used by termites [12]. Another factor explaining this difference is the ecological diversity of ant species, each exploring different food source. Termites in contrast exploit more uniform ecological niches in their search for cellulose.

4.2. Basic Rules Govern the Recruitment Dynamics. The main conclusion from this study is that despite the fact that the evolutionary history of the chemical mass recruitment of ants and termites is different, a similar recruitment dynamics has evolved in both groups. This evolutionary analogy suggests that chemical mass recruitment is constraint by basic physical-dynamic laws. This would explain the convergence to chemical mass recruitment in the two evolutionary processes studied. A third convergence towards similar solution for the modulation of mass recruitment dynamics is nowadays repeated in the development of artificial intelligence, where the “mass intelligence” of ants copied in the interaction of simple virtual computer agents is in search of optimal solutions. Artificial intelligence, however, has copied only the simple recruitment dynamics named here as the Democratic system with a single compound pheromone. More sophisticated modeling could bear fruits to artificial intelligence that might echo the fruits chemical mass recruitment that has brought to social insect species evolving them.

References

[1] A. M. El-Sayed, “The pherobase: database of insect pheromones and semiochemicals,” 2008, http://www.pherobase.net.

[2] K. Jaffe, “An economic analysis of altruism: who benefits from altruistic acts?” *JASSS*, vol. 5, no. 3, 2002.

[3] K. Jaffe, “Quantifying social synergy in insect and human societies,” *Behavioral Ecology and Sociobiology*, vol. 64, no. 11, pp. 1721–1724, 2010.

[4] K. Jaffe, “Theoretical analysis of the communication system for chemical mass recruitment in ants,” *Journal of Theoretical Biology*, vol. 84, no. 4, pp. 589–609, 1980.

[5] E. O. Wilson, “Communication by tandem running in the ant genus *Cardiocondyla*,” *Psyche*, vol. 66, no. 3, pp. 29–34, 1959.

[6] M. Möeglich, U. Maschwitz, and B. Höelldobler, “Tandem calling: a new kind of signal in ant communication,” *Science*, vol. 186, no. 4168, pp. 1046–1047, 1974.

[7] K. Jaffe, C. Ramos, C. Lagalla, and L. Parra, “Orientation cues used by ants,” *Insectes Sociaux*, vol. 37, no. 2, pp. 101–115, 1990.

[8] E. D. Morgan, “Trail pheromones of ants,” *Physiological Entomology*, vol. 34, no. 1, pp. 1–17, 2009.

[9] K. Jaffe, “Negentropy and the evolution of chemical recruitment in ants,” *Journal of Theoretical Biology*, vol. 106, no. 4, pp. 587–604, 1984.

[10] G. W. Oloo and R. H. Leuthold, “The influence of food on trail-laying and recruitment behaviour in *Trinervitermes bettonianus* (Termitidae : Nasutitermitinae),” *Entomologia Experimentalis et Applicata*, vol. 26, no. 3, pp. 267–278, 1979.

[11] J. Affolter and R. H. Leuthold, “Quantitative and qualitative aspects of trail pheromones in *Macrotermes subhyalinus* (Isoptera, Termitidae),” *Insectes Sociaux*, vol. 47, no. 3, pp. 256–262, 2000.

[12] C. Bordereau and J. M. Pasteels, “Pheromones and chemical ecology of dispersal and foraging in termites,” in *Biology of Termites: A Modern Synthesis*, D. E. Bignell, Y. Roisin, and N. Lo, Eds., Springer, New York, NY, USA, 2011.

[13] B. Mirás, A. Cabrera, and K. Jaffe, "Mate selection in the moth *Neoleucinodes elegantalis*: evidence for a supernormal chemical stimulus in sexual attraction," *Animal Behaviour*, vol. 73, no. 4, pp. 727–734, 2007.

[14] K. Jaffe, Villegas G., Colmenares O. et al., "Two different decision-making systems in recruitment to food in ant societies," *Behaviour*, vol. 92, pp. 9–21, 1985.

[15] E. O. Wilson, "Chemical communication among workers of the fire ant *(Solenopsis saevissima)*," *Animal Behaviour*, vol. 10, no. 1-2, pp. 134–164, 1962.

[16] K. Jaffe and P. E. Howse, "The mass recruitment system of the leaf- cutting ant *Atta cephalotes*," *Animal Behaviour*, vol. 27, no. 3, pp. 930–939, 1979.

[17] K. Jaffe and J. L. Deneubourg, "On foraging, recruitment systems and optimum number of scouts in ants," *Insectes Sociaux*, vol. 39, no. 2, pp. 201–213, 1992.

[18] H. G. Fowler and S. W. Robinson, "Foraging by *Atta sexdens*: seasonal patterns, caste and efficiency," *Ecological Entomology*, vol. 4, pp. 239–247, 1979.

[19] Y. Mady and K. Jaffe, "On foraging behavior of the polymorphic tree dwelling ant *Daceton armigerum*," *Entomotropica*, vol. 21, pp. 117–123, 2006.

[20] B. Gobin, C. Peeters, J. Billen, and E. D. Morgan, "Interspecific trail following and commensalism between the ponerine ant *Gnamptogenys menadensis* and the formicine ant *Polyrhachis rufipes*," *Journal of Insect Behavior*, vol. 11, no. 3, pp. 361–369, 1998.

[21] P. Eggleton and I. Tayasu, "Feeding groups, lifetypes and the global ecology of termites," *Ecological Research*, vol. 16, no. 5, pp. 941–960, 2001.

[22] A. M. Stuart, "Social behavior and communication," in *Biology of Termites*, K. Krishna and F. M. Weesner, Eds., vol. 1, pp. 193–232, Academic Press, New York, NY, USA, 1969.

[23] J. F. A. Traniello and R. H. Leuthold, "Behavior and ecology of foraging in termites," in *Termites: Evolution, Sociality, Symbioses, Ecology*, T. Abe, D. E. Bignell, and M. Higashi, Eds., pp. 141–168, Kluwer Academic Publisher, Dordrecht, The Netherlands, 2000.

[24] C. Andara, S. Issa, and K. Jaffe, "Decision-making systems in recruitment to food for two nasutitermitinae," *Sociobiology*, vol. 44, no. 1, pp. 139–151, 2004.

[25] E. Bonabeau, G. Theraulaz, J. L. Deneubourg et al., "A model for the emergence of pillars, walls and royal chambers in termite nests," *Philosophical Transactions of the Royal Society B*, vol. 1375, pp. 1561–1576, 1998.

[26] D. Alfonso, *Ecología y comportamiento de Syntermes (Isoptera,Termitidae Syntermitinae) en la Gran Sabana, Estado Bolívar*, MSc Thesis in Biology, Universidad Simón Bolívar, Caracas, Venezuela, 2011.

[27] J. Billen and E. D. Morgan, "Pheromone communication in social insects: sources and secretions," in *Pheromone Communication in Social insects. Ants, Wasps, Bees, and Termites*, R. K. van der Meer et al., Ed., pp. 3–33, Westview Press, New York, NY, USA, 1998.

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 783945, 8 pages
doi:10.1155/2012/783945

Research Article

Effects of the Trophobiont Herbivore *Calloconophora pugionata* (Hemiptera) on Ant Fauna Associated with *Myrcia obovata* (Myrtaceae) in a Montane Tropical Forest

Roberth Fagundes,[1,2] Kleber Del-Claro,[1] and Sérvio Pontes Ribeiro[2]

[1] *Post-Graduate Program in Ecology and Conservation of Natural Resources, Laboratory of Behavior Ecology and Interactions, Federal University of Uberlandia, 38400-902 Uberlandia, MG, Brazil*
[2] *Post-Graduate Program in Ecology of Tropical Biomes, Laboratory of Evolutionary Ecology of Canopy Insects and Natural Succession, Department of Biodiversity, Evolution and Environment, Federal University of Ouro Preto, 35400-000 Ouro Preto, MG, Brazil*

Correspondence should be addressed to Roberth Fagundes, roberthbio@yahoo.com.br

Received 1 April 2011; Revised 22 May 2011; Accepted 24 May 2011

Academic Editor: Jacques H. C. Delabie

Many studies have investigated the mechanisms behind the structure of arboreal ant assemblages. In this study, the objective was to evaluate the effect of availability of honeydew-producing colonies of *Calloconophora pugionata* (Membracidae) on the structure of ant assemblages associated with the host plant *Myrcia obovata* (Myrtaceae) in an Atlantic forest of Minas Gerais (Brazil). Our experiment consisted in a gradual exclusion of hemipteran colonies out of the host plant crown and further record of the ant assemblage response (species richness, composition, and occurrence) to the presence and density of treehopper colonies. The hypothesis was that an increase in the number of trophobiont herbivores results in an increase in tending ant occurrence but a reduction in ant species diversity. Results corroborated our main hypothesis: membracids had a positive effect on the occurrence of ants but negative on species richness. Overall insect occurrence was also reduced with increasing in *C. pugionata* colonies, probably due to strengthening dominant ant species territory sizes and intensification of patrolling.

1. Introduction

The outstanding occurrences of large arboreal ant colonies result in the most remarkable animal biomass found in any tropical canopy [1]. Territory patrolling behaviour causes species dominance which reflects in nest sizes and intense search for food [2, 3]. The most common and rich food resource for ants is extrafloral nectaries secretion and exudates of sap-sucking herbivores, the honeydew [4–6]. These resources are predictable, highly energetic, and nutritive, leading to an increase of ant activity on the foliage [7] and ant fitness [8].

The trophobiosis is a relationship between ants and honeydew-producer insects [9]. It is a mutualistic interaction that involves consumption of honeydew by ants in return for protection of the hemipterans against natural enemies [10]. This kind of resource characterizes its consumers as indirect herbivores and provides energy necessary to achieve higher population sizes [3, 10]. However, the honeydew is a spatially limited resource, despite its importance, and consequently it may trigger interspecific competition [11].

Resource competition is one of the most important forces driving ant assemblage structure [2, 12]. In the canopy habitat, there are a small variety of resources for numerous ant species that share the same kind of preferred food, like honeydew or nectar, and canopy may be indeed one of the most competitive tropical environments [11, 13]. Studies with stable isotopes showed that many ant species frequently use honeydew and nectar as main food item, and thus these resources do shape arboreal ant community [3, 11, 14, 15].

The bottom-up effect caused by the sugar resources consumed in such interactions may lead to a cascade effect at multitrophic scales [15–17]. The resource monopolization by the dominant species may increase the interespecific competition and the encounter frequencies between competitors, reducing the forage of nondominant ant species [18, 19]. In addition, when colony nutritional demands increase beyond the offer of honeydew, predatory behaviour became more frequent, along with the protective behaviour of removing any arthropod from the foliages close to the sugar resources, thus reducing the arthropods in the host plant [20–22]. The last case may generate an indirect benefit to the host plant by reducing herbivore occurrence and thus leaf chewing damage [20].

Trophobiosis has been largely studied in lowland, close tropical rainforests; and in the Brazilian Cerrado, among a few other ecosystems [17, 18, 21, 23, 24]. Although it is a well-described mutualistic system, likely to result in similar ecological output wherever it happens, it is necessary to investigate such interactions in other habitats [23]. For instance, climatically challenging conditions, or biogeographically isolated and intensely disturbed ecosystems, would result in harsh ecological conditions, capable for altering the expected output of increasing territories and competition around honeydew producers. Namely, how resilient a large colony would be to hemipteran density variation in space or time, under extreme environments?

In the present study we evaluated the effect of variation in the presence and density of hemipterans exudates producers among tree crowns on the arboreal ant species richness and occurrence, in a secondary montane forest ecosystem. We tested the hypothesis that the availability of the *Calloconophora pugionata* Driecht colonies positively affects the feeding behaviour and diversity of ants associated with the host plant *Myrcia obovata* (O. Berg) Nied (Myrsinaceae). Further, we expected that a high density of ants around the hemipteran colonies would affect other arthropods, from plant natural enemies, such as herbivore beetles, to membracid predators, such as spiders.

2. Material and Methods

2.1. Study Sites. The field work was conducted in Itacolomi State Park (20 26 26 S, 43 30 52 W) located between the cities of Ouro Preto and Mariana, Minas Gerais State, Brazil. This ecological reserve has an area of 7,000 ha covered with a mosaic of Atlantic montane forests and Cerrado. The rainfall regime varies between 1,500 to 2,000 mm per year and temperature between 19 C and 22 C. The rainy season extends from September to February and the dry season from March to August.

2.2. Model System. The tritrophic interaction is composed by *Myrcia obovata* (O. Berg) Nied (Myrtaceae), a common Atlantic forest tree, *Calloconophora pugionata* Driecht (Membracidae), a sap-sucking insect and honeydew producer, and the associated ant species, mostly *Camponotus crassus* Mayr, 1862 (Formicidae) and *Camponotus rufipes* Fabricius, 1775 (Formicidae), two of the numerical dominant ants in these forests [25]. This system occurs mostly in tropical montane forests established in the “canga”, an ironstone outcrop areas.

The field work was carried out in October and November of 2009 (wet season). Thirty-six individuals of *M. obovata* with similar structure (number of stems, height, crown circumference) were tagged in this site. From this subsample, 20 trees were randomly marked and divided in two groups of 10 plants named according to the presence of membracid as treatment (with membracid colonies) or control (without colonies). The colonies of *C. pugionata* hosted in each experimental plant had 25.4 ± 5.3 membracids (mean ± s.d.; $n = 30$), between adults and nymphs. Trees of *M. obovata* may occur isolated or in the same patch, but with a minimal distance of five meters between each one. Control and treatment plants were randomly selected from the original population, so their crowns are not grouped but mixed in the same canopy.

2.3. Experimental Design. The experiment was set by gradual removal of the membracid colonies (one colony per tree each time), and then we evaluate how the ant assemblage responds to that (Table 1). The procedure was carried out through four periods separated by three-day interval, which simulated a reducing resource gradient. At the end of each period all individuals of one colony of *C. pugionata* were removed from each treatment plant which were then monitored again straight way for the next days. In the last period, treatment plants had all colonies removed. The control plants were not manipulated and had no trophobioses in all periods. Hence, all ten plants of each group (independent variable) were successively observed (six events per period) along the resource gradient (period then used as repeated measures). These observations were made every two days on both control and treatment trees during two weeks for each period and last for 20 minutes per plant individual, and all visiting ants were recorded. Additionally, the other arthropods specimens observed were also quantified. Every species was classified using behaviour and morphological characteristics, as trophobiont ants, nontrophobiont ants, potential *C. pugionata* predator arthropods, potential *M. obovata* herbivore arthropods. Vouchers specimens of ant species were deposited at the insect collection of the Laboratory of Evolutionary Ecology of Canopy Insects and Natural Succession at Federal University of Ouro Preto, Ouro Preto, Brazil.

2.4. Data Analysis. The mean ant species richness (number of species per tree at each observation) and the mean occurrence of ants (number of ants per species observed in each tree) were analyzed using repeated measures ANOVA models, with the experimental groups as group factor (treatment and control) and the four periods as repeated measures (resource gradient). Repeated measure ANOVA was also used to compare the relative proportion of trophobiont ant species between the treatment groups for each period. A Fisher's LSD post hoc test was used, performed as paired test.

The total ant species richness (total number of ant species observed at each period for both experimental groups) for every case was estimated using Jackniffe I with 500 repetitions. After that, the values of total estimated

Table 1: Scheme represented the sampling design of the experiment.

Groups[1]	Experiment (two months) Period 1[2] (Two weeks)	Period 2[2] (Two weeks)	Period 3[2] (Two weeks)	Period 4[2] (Two weeks)
Treatment (10 plants)	3 colonies[3]	2 colonies[3]	1 colony[3]	No colonies[3]
Control (10 plants)	No colonies[3]	No colonies[3]	No colonies[3]	No colonies[3]

[1] The same plants were monitored in all periods.

[2] Six days of observations per period.

[3] Colonies of *Calloconophora pugionata* per tree.

species richness were interpreted for the treatments with visual analyses on the overlap of the confidence intervals (95%) as indicator of difference. Additionally, the ant species composition was compared by discriminant analysis using the periods as grouping factor.

The mean occurrence of herbivores, predators, and all nonant arthropods grouped (including dipterans, cockroaches, etc.) was also analyzed using repeated measures ANOVA models as performed to ants data. Fisher's LSD test was used after ANOVA as paired test. All analyses were performed with data transformed ($X = \log_{10}X$), but graph was plotted with original data.

3. Results

We recorded a total of 1,897 ants visiting *M. obovata*, belonging to 10 species from four subfamilies, with 81.5% only at the treatment group (Tables 2 and 3). The subfamily Formicinae was the most representative group with *Camponotus* species as the numerically dominant group (89.4%). *M. obovata* was also visited by 1,125 nonant arthropods, including 62.5% in the control plants and 37.5% in the treatment plants (Table 3).

The presence and amount of *C. pugionata* colonies positively affected ant forage in the trees. In the treatment plants we observed an decrease in the ant number responding to reduced availability of honeydew sources, while nothing changed in the control (Repeated measures ANOVA: Group Period: $F(3;354) = 4.4$; $P < 0.01$; Figure 1). Besides, the ant foraging was higher in the treatment plants except for trophobiose-lack period, when the ant activity was similar for both groups (LSD: $P < 0.05$). In fact, treatment plants were mostly occupied by honeydew-feeding ants, but again only at the periods when hemipterans colonies occurred (Repeated measures ANOVA: $F(3;354) = 3.6$; $P < 0.02$; Figure 2).

The mean ant species richness per plant, that is, the number of ant species foraging at the same time on each crown, was higher in the presence of mutualistic hemipteran colonies, although the result did not change in response to colony removal (Repeated measures ANOVA by Group: $F(1;118) = 10.47$; $P < 0.01$; Figure 3). Still, mean richness was always lower in the control than in treatment plants (LSD: $P < 0.05$). In opposite, the estimated total number of ant species was higher in the control plants than in the treatment but became similar to the control plants in the last period (Figure 4).

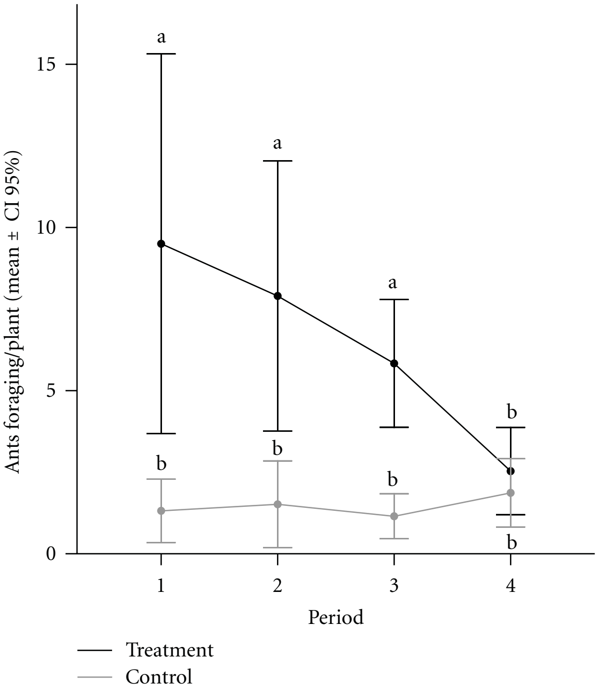


Figure 1: Positive relationship between the availability of hemipterans colonies and the amount of ants foraging on each plant (Repeated measures ANOVA: Group Period: $F(3;354) = 4.4$; $P < 0.01$). The largest amount of ants was recorded in period 1 and gradually decreases until period 4 when it became identical to values found in all phases of the control group. Different letters indicate significant differences according to post hoc test (LSD: $P < 0.05$).

The ant species composition also changed in response to trophobiont hemipteran occurrence (Discriminant analysis: Wilk's $\lambda = 0.206$; $\chi^2 = 110.47$; d.f. = 70; $P < 0.01$). Accordingly, with 75.9% of the variance explained by the first function and 8.6% by the second, the ant assemblage associated with plants hosting ant-hemipteran mutualism was significantly different from plants where hemipterans were totally removed or never existed (Figure 5). This difference was mainly associated with the massive presence of the two trophobiont ant species, *Camponotus crassus* and *C. rufipes*, when plants had colonies of *C. pugionata (C. crassus*: $F(7;72) = 5.46$; $P < 0.01$; *C. rufipes*: $F(7;72) = 3.31$; $P < 0.01$; other species did not contribute significantly for the model).

Table 2: List of ant species observed associated with *Myrcia obovata* and respective total number of occurrence.

	Total number of ants	
	Treatment	Control
Family Formicidae		
Subfamily Formicinae		
Camponotus rufipes Fabricius 1775	635	23
Camponotus crassus Mayr 1862	1315	132
Camponotus novogranadensis Mayr 1870	122	113
Camponotus fastigatus Roger 1863	22	29
Subfamily Myrmicinae		
Crematogaster sp1	0	118
Cephalotes pusillus Klug 1824	16	13
Pheidole sp1	23	19
Subfamily Pseudomyrmicinae		
Pseudomyrmex gracilis Fabricius 1804	41	35
Pseudomyrmex pallidus Smith 1855	7	10
Subfamily Ponerinae		
Gnamptogenys striatula Mayr 1884	2	0

Table 3: Total number of occurrences registered for each experimental group throughout the experiment.

	Group		
	Treatment	Control	Total
Ants	1546	351	**1897**
Herbivores	276	384	**660**
Predators	102	253	**355**
Others arthropods	44	66	**110**
Total	**1968**	**1054**	**3022**

Arthropods other than ants visiting *M. obovata* showed a positive response to decrease honeydew source gradient (Repeated measures ANOVA group periods: Non-ant arthropods: $F(3;354) = 3.62$; $P < 0.05$; Figure 6(a). The control group did not change through the periods despite low fluctuations (LSD: $P > 0.05$). A similar pattern was observed when herbivores and predators were analyzed separately (Repeated measures ANOVA group periods: Herbivores: $F(3;354) = 3.21$; $P < 0.05$; Predators: $F(3;354) = 4.66$; $P < 0.01$; Figures 6(b) and 6(c). The occurrence of every other arthropod guilds in the treatment plants was lower than that in the control plants, except at the last period when both plant groups presented the same number of foreign visitors, as expected (LSD: $P < 0.05$).

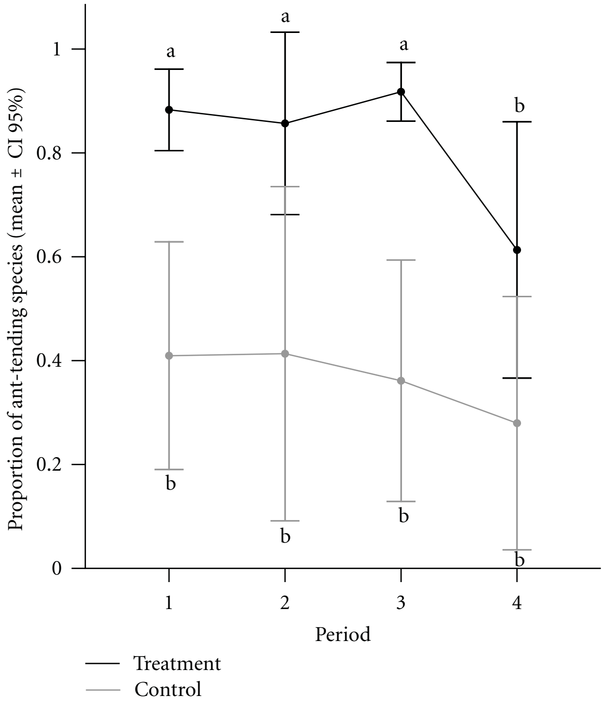


Figure 2: The ant foraging fauna on plants with trophobioses is formed mostly by exudates-feeding species (Repeated ANOVA: $F(3;354) = 3.6$; $P = 0.02$). Lines show the proportion of the occurrence of trophobiont ant species from total ants. Different letters indicate significant differences according to post hoc test (LSD: $P < 0.05$).

4. Discussion

The bottom-up effect caused by *C. pugionata* was noticeable for both tending ants as well as for the rest of the associated fauna in *M. obovata*. The availability of exudate-producing herbivore colonies positively affected the occurrence of foraging ants on the plants. There was an increase in the numerical dominance of species collecting honeydew, along with a decreasing in species richness. Still, the number of species foraging at the same time was greater in the presence of membracid, probably due to the high frequency of trophobiont species. Furthermore, we found a low occurrence of potential host plant herbivores and likely predators when colonies of mutualistic hemipterans were present. Such findings suggest the presence of mutual benefit among the

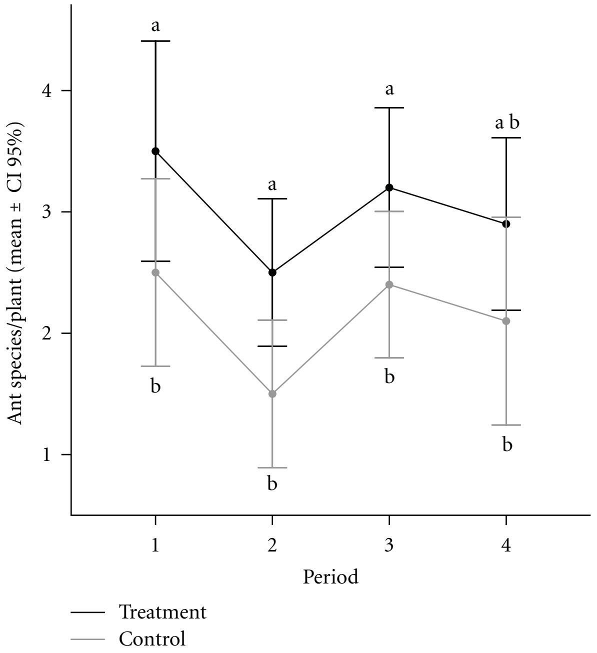


Figure 3: Plants of the treatment group presented higher mean ant richness than control group in all periods (Repeated measures ANOVA: Group: $F(1;118) = 10.47$; $P < 0.01$). Different letters indicate significant differences according to post hoc test (LSD: $P < 0.05$).

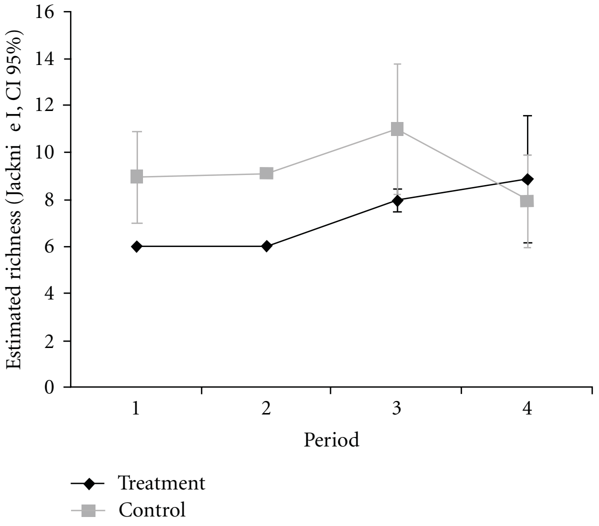


Figure 4: Estimated total richness calculated for the four periods in both groups. Treatment group shows low richness compared to control group in the three first periods.

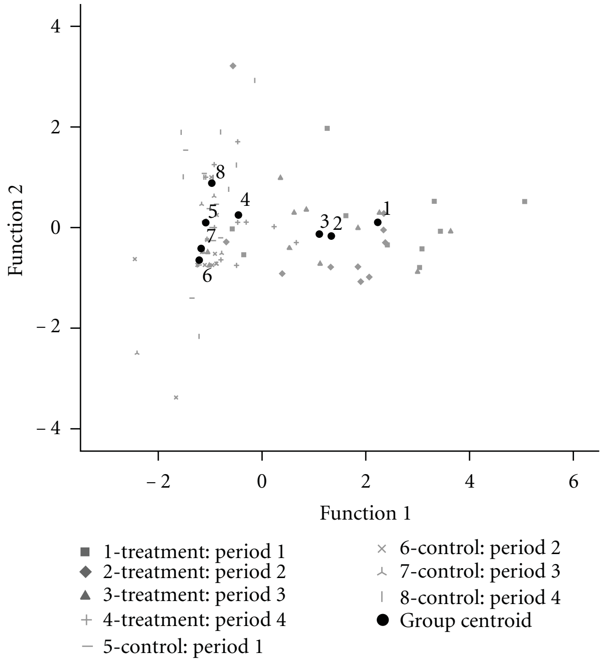


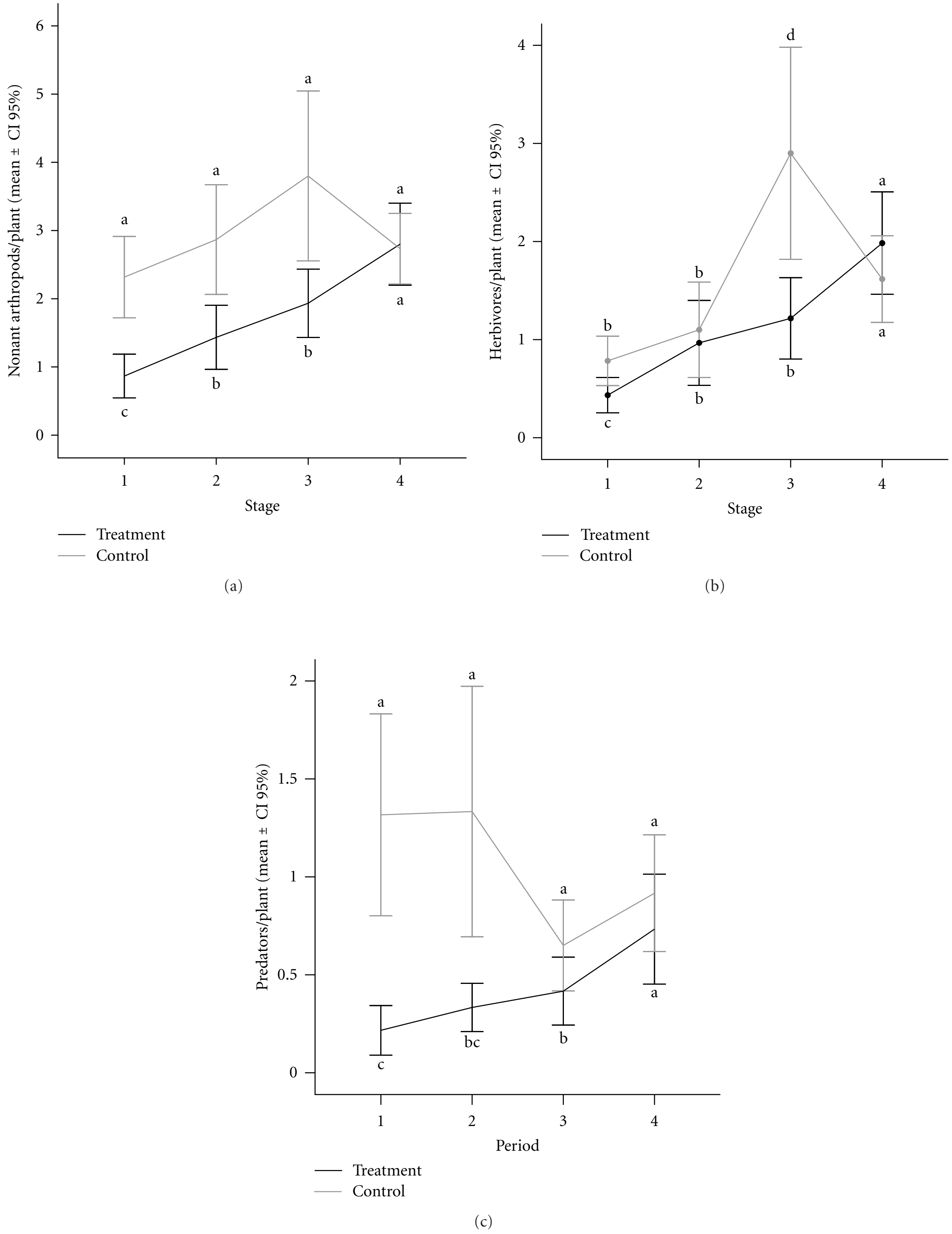
Figure 5: Discriminant analysis comparing the experimental groups (for each period of experiment) using ant species composition and relative occurrence. With 75.9% of the variance explained by the first and 8.6% by the second function, periods were discriminated in cases with trophobioses and without trophobioses by the high occurrence of the trophobiont ant species *Camponotus rufipes* and *C. crassus* in the first group (Wilk's $\lambda = 0.206$; $P < 0.01$; *C. crassus*: $F(7;72) = 5.46$; $P < 0.01$; *C. rufipes*: $F(7;72) = 3.31$; $P < 0.01$; other species did not contribute significantly for the model).

mutualism actors (e.g. [17]), or at least some compensation for the sap-sucking damage on the host plant.

The existence of an ant dominance and patrolled territory in association with hemipteran colonies or extrafloral nectaries is a pattern extensively described for various tropical habitats, although it is relatively unknown for montane forests [3, 11, 26–28]. Clearly, ecology of arboreal ants is strongly related to plant hemipteran sweet exudates, and the dominant ants are the principal consumer of this sort of trophic resource [29]. Such phenomena may even explain the formation of large mosaic type of territories in the canopies of tropical native and cultivated forests [11, 26, 27].

It is common knowledge that the number of ants foraging in the canopy is proportional to the amount of resources, as sources of nectar or exudates [11, 15, 21]. When they engage in trophobiosis, they assume a primary consumers status, and their occurrence is equal or larger than the other herbivores in its community. In the absence of sugary secretions, predation becomes the primary feeding behaviour; then the situation is reversed, and the ants assume low occurrence [6, 10, 29]. Other studies also showed that the increased aggressiveness and occurrence of ants are related to the availability of honeydew sources [4, 5, 11, 21, 30].

Blüthgen et al. [15] showed that the ant species richness in host plants with trophobiosis was lower compared with plants carrying extrafloral nectaries or with non-myrmecophilous plants. Dominant ants are considered the most aggressive species, and they are also numerous in other food sources such an extrafloral nectaries [15]. This behaviour, along with high territoriality, affects negatively the ant species richness due to the exclusion of competing species, reduction of co-occurrences, and avoiding species replacement [11, 15]. Thus, the same pattern we observed in the system *M. obovata*-*C. pugionata*-ants was similar to



(a)

(b)

(c)

Figure 6: Mean occurrence of the whole nonants arthropods (a) and for herbivores (b) and predators (c) separately, registered in the experimental groups (lines) at each period (x axis). These arthropods respond positively to decrease occurrence of ants and consequently the absence of *C. pugionata* (ANOVA: nonants arthropods: $F(3;354) = 3.62$; $P < 0.01$; Herbivores: $F(3;354) = 3.21$; $P < 0.01$; Predators: $F(3;354) = 4.66$; $P < 0.01$). Different letters indicate significant differences according to post hoc test (LSD: $P < 0.05$).

different ecosystems with other types of myrmecophily [11, 28, 31, 32].

The interaction between trophobiont herbivores and dominant ant species may alter the entire food web [9, 33–35]. This could generate benefits for the host plants and mutualistic treehoppers by killing or repelling their natural enemies [29, 30, 35]. Such protection has consequences as reducing of herbivory [17, 36] and increasing plant fitness [24, 37]. Rosumek et al. [22] and Schoereder et al. [28] reviewed the ant protective role and the importance of nectaries and trophobiont hemipterans, showing that most studies presented a negative correlation between ants and herbivores mainly when myrmecophilous resources are involved. In this interaction system, the host plant is the one taken some costs, due to the constant sap-sucking activity from the hemipterans, plus the damage caused by opportunistic phytopathologies [38]. However, such cost may be compensated by the protective action from the ants against the chewing herbivores [8, 24]. Further studies are needed to evaluate the actual damage caused by *C. pugionata* and its effects on *M. obovata* fitness.

The establishment of trophobioses can also result in an ecological cascade with further evolutionary consequences for the entire community [28]. For example, one quarter of the species and one third of the plant individuals in the Brazilian Cerrado have extrafloral nectaries and/or trophobiont hemipterans [39]. In addition, a third of the ant species that feed in the Cerrado vegetation are typically sugary exudates consumer [28, 40–42]. In one hand, the low, accessible tree crowns in the cerrado, montane forests, and rupestrian field's vegetation allow such type of investigation and a precise quantitative analysis of the actual availability of such resources. Therefore, the investigation of how relevant trophobiosis would be for other tropical ecosystems is constrained mostly by restricted canopy access to a large enough area in order to produce comparative results. The present work was developed in relatively low and also accessible canopies of a secondary montane forest. This unique situation allowed us to explore the very mechanisms of the interactions plant-hemipteran-ants in this distinct forest habitat, where its relevance and ecological strength seem similar to that previously observed in the Cerrado.

Our study provides empirical evidence of bottom-up control exerted by the sap-sucking hemiptera *C. pugionata* in their community, an effect clearly perceptible in the ant assemblage. By means of the trophobioses, the mutualistic membracids are capable of altering not only the ant species richness and occurrence but also the structure of the entire arthropod community associated with its host plant. In the tritrophic system formed by *M. obovata*, *C. pugionata,* and ants, any species seem to benefit from the interaction [17]. In conclusion, myrmecophillous resources produced by several animals and plant species can be key elements for the configuration of hierarchically structured ant assemblage, as observed coherently among different ecosystems, and then affect all the arboreal community associated [3, 11, 14, 15, 28, 40].

Acknowledgments

The authors thank Filipe L. Paixão and Pricila G. S. Bonifácio for collecting data, Jacques H. C. Delabie, Ricardo I. Campos, and Julio Fontenelle for original paper revision, the State Institute of Forestry (IEF) and the administration of Itacolomi State Park for providing permits and logistical facilities for the work. They also thank CNPq for research grant provided to K. Del-Claro and S. P. Ribeiro, and master's grant to R. Fagundes FAPEMIG funded the research. K. Del-Claro also thanks CNPq, FAPEMIG, and Capes for financial support.

References

[1] N. E. Stork and T. M. Blackburn, "Occurrence, body size and biomass of arthropods in tropical forest," *Oikos*, vol. 67, no. 3, pp. 483–489, 1993.

[2] B. Hölldobler and E. O. Wilson, *The ants*, The Belknap Press of Harvard University Press, Cambridge, Mass, USA, 1990.

[3] D. W. Davidson, S. C. Cook, R. R. Snelling, and T. H. Chua, "Explaining the abundance of ants in lowland tropical rainforest canopies," *Science*, vol. 300, no. 5621, pp. 969–972, 2003.

[4] B. L. Bentley, "Extrafloral nectaries and protection by pugnacious bodyguards," *Annual Review of Ecology, Evolution, and Systematics*, vol. 8, pp. 407–427, 1977.

[5] B. L. Bentley, "The protective function of ants visiting the extrafloral nectaries of *Bixa orellana* L (Bixaceae)," *Journal of Ecology*, vol. 65, pp. 27–38, 1977.

[6] M. J. Way, "Mutualism between ants and honeydew producing Homoptera," *Annual Review of Entomology*, vol. 8, pp. 307–344, 1963.

[7] S. Koptur, "Extrafloral nectary-mediated interactions between insects and plants," in *Insect Plant Iteractions*, E. Bernays, Ed., pp. 81–129, CSC Press, Boca Raton, Fla, USA, 1992.

[8] J. Byk and K. Del-Claro, "Ant-plant interaction in the Neotropical savanna: direct beneficial effects of extrafloral nectar on ant colony fitness," *Population Ecology*, vol. 53, no. 2, pp. 327–332, 2011.

[9] J. H. C. Delabie, "Trophobiosis between formicidae and hemiptera (sternorrhyncha and auchenorrhyncha): an overview," *Neotropical Entomology*, vol. 30, no. 4, pp. 501–516, 2001.

[10] J. Ness, K. Mooney, and L. Lach, "Ants as mutualists," in *Ant Ecology*, L. Lach, C. L. Parr, and K. L. Abbott, Eds., pp. 97–114, Oxford University Press, New York, NY, USA, 2010.

[11] N. Blüthgen, M. Verhaagh, W. Goitía, K. Jaffé, W. Morawetz, and W. Barthlott, "How plants shape the ant community in the Amazonian rainforest canopy: the key role of extrafloral nectaries and homopteran honeydew," *Oecologia*, vol. 125, no. 2, pp. 229–240, 2000.

[12] C. L. Parr and H. Gibb, "Competition and the role of dominant ants," in *Ant Ecology*, L. Lach, C. L. Parr, and K. L. Abbott, Eds., pp. 77–96, Oxford University Press, New York, NY, USA, 2010.

[13] S. P. Yanoviak and M. Kaspari, "Community structure and the habitat templet: ants in the tropical forest canopy and litter," *Oikos*, vol. 89, no. 2, pp. 256–266, 2000.

[14] N. Blüthgen, G. Gebauer, and K. Fiedler, "Disentangling a rainforest food web using stable isotopes: dietary diversity in a species-rich ant community," *Oecologia*, vol. 137, no. 3, pp. 426–435, 2003.

[15] N. Blüthgen, G. Gottsberger, and K. Fiedler, "Sugar and amino acid composition of ant-attended nectar and honeydew sources from an Australian rainforest," *Austral Ecology*, vol. 29, no. 4, pp. 418–429, 2004.

[16] K. Del-Claro and H. M. Torezan-Silingardi, "Insect-plant interactions: new pathways to a better comprehension of ecological communities in Neotropical savannas," *Neotropical Entomology*, vol. 38, no. 2, pp. 159–164, 2009.

[17] M. V. S. Moreira and K. Del-Claro, "The outcomes of an ant-treehopper association on *Solanum lycocarpum* St. Hill: Increased membracid fecundity and reduced damage by chewing herbivores," *Neotropical Entomology*, vol. 34, no. 6, pp. 881–887, 2005.

[18] N. Blüthgen, D. Mezger, and K. E. Linsenmair, "Ant-hemipteran trophobioses in a Bornean rainforest—diversity, specificity and monopolisation," *Insectes Sociaux*, vol. 53, no. 2, pp. 194–203, 2006.

[19] K. Mooney and C. V. Tillberg, "Stable Isotopes in the study of ant diets," in *Ant Ecology*, L. Lach, C. L. Parr, and K. L. Abbott, Eds., pp. 117–118, Oxford University Press, New York, NY, USA, 2010.

[20] K. Del-Claro and P. S. Oliveira, "Ant-homoptera interactions in a neotropical savanna: The honeydew-producing treehopper, *Guayaquila xiphias* (Membracidae), and its associated ant fauna on *Didymopanax vinosum* (Araliaceae)," *Biotropica*, vol. 31, no. 1, pp. 135–144, 1999.

[21] K. Del-Claro and P. S. Oliveira, "Conditional outcomes in a neotropical treehopper-ant association: temporal and species-specific effects," *Oecologia*, vol. 124, no. 2, pp. 156–165, 2000.

[22] F. B. Rosumek, F. A. O. Silveira, F. S. Neves et al., "Ants on plants: a meta-analysis of the role of ants as plant biotic defenses," *Oecologia*, vol. 160, no. 3, pp. 537–549, 2009.

[23] J. N. Thompson, "Specific hypotheses on the geographic mosaic of coevolution," *American Naturalist*, vol. 153, pp. S1–S14, 1999.

[24] K. Del-Claro, V. Berto, and W. Réu, "Herbivore deterrence by visiting ants increases fruit-set in an extrafloral nectary plant *Qualea multiflora* (Vochysiaceae) in cerrado vegetation," *Journal of Tropical Ecology*, vol. 12, pp. 887–892, 1996.

[25] N. B. Espirito-Santo, R. Fagundes, G. L. Silva et al., "A distribuição e diversidade de formigas arborícolas de florestas montanas em diferentes estágios sucessionais," *O Biológico*, vol. 69, pp. 335–338, 2007.

[26] J. E. Tobin, "A neotropical rainforest canopy, ant community: some ecological considerations," in *Ant–plant interactions*, C. R. Huxley and D. F. Cutler, Eds., pp. 536–538, Oxford University Press, New York, NY, USA, 1991.

[27] J. D. Majer, J. H. C. Delabie, and M. R. B. Smith, "Arboreal ant community patterns in Brazilian cocoa farms," *Biotropica*, vol. 26, no. 1, pp. 73–83, 1994.

[28] J. H. Schoereder, T. G. Sobrinho, M. S. Madureira, C. R. Ribas, and P. S. Oliveira, "The arboreal ant community visiting extrafloral nectaries in the Neotropical cerrado savanna," *Terrestrial Arthropods Reviews*, vol. 3, pp. 3–27, 2010.

[29] D. W. Davidson, "The role of resource imbalances in the evolutionary ecology of tropical arboreal ants," *Biological Journal of the Linnean Society*, vol. 61, no. 2, pp. 153–181, 1997.

[30] S. Koptur, "Nectar as fuel for plant protectors," in *Plant-Provided Food for Carnivorous Insects: A Protective Mutualism and Its Applications*, F. L. Wackers, P. C. J. van Rijn, and J. Bruin, Eds., pp. 75–108, Cambridge University Press, Cambridge, UK, 2005.

[31] A. DeJean, A. Akoa, C. Djietolordon, and A. Lenoir, "Mosaic ant territories in an African secondary rain forest (Hymenoptera, Formicidae)," *Sociobiology*, vol. 23, no. 3, pp. 275–292, 1994.

[32] A. Dejean and B. Corbara, "A review of mosaics of dominant ants in rainforests and plantations," in *Arthropods of Tropical Forests: Spatio-Temporal Dynamics and Resource Use in The Canopy*, Y. Basset, V. Novotny, M. E. Scott, and R. L. Kitching, Eds., pp. 341–347, Cambridge University Press, Cambridge, UK, 2003.

[33] D. K. Letourneau and P. Barbosa, "Ants, stem borers, and pubescence in *Endospermum* in Papua New Guinea," *Biotropica*, vol. 31, no. 2, pp. 295–302, 1999.

[34] G. M. Crutsinger and N. J. Sanders, "Aphid-tending ants affect secondary users in leaf shelters and rates of herbivory on *Salix hookeriana* in a coastal dune habitat," *American Midland Naturalist*, vol. 154, no. 2, pp. 296–304, 2005.

[35] D. W. Davidson and L. Patrell-Kim, "Tropical arboreal ants: why so abundant?" in *Neotropical Biodiversity and Conservation*, A. C. Gibson, Ed., pp. 127–140, Mildred E. Mathias Botanical Garden, University of California, Los Angeles, Calif, USA, 1996.

[36] K. Del-Claro, J. Byk, G. M. Yugue, and M. G. Morato, "Conservative benefits in an ant-hemipteran association in the Brazilian tropical savanna," *Sociobiology*, vol. 47, no. 2, pp. 415–421, 2006.

[37] F. J. Messina, "Plant protection as a consequence of an ant-membracid mutualism: interactions on goldenrod (*Solidago* sp.)," *Ecology*, vol. 62, no. 6, pp. 1433–1440, 1981.

[38] R. C. Buckley, "Interactions involving plants, Homoptera, and ants," *Annual review of ecology and systematics. Vol. 18*, pp. 111–135, 1987.

[39] P. S. Oliveira and H. F. Leitão-Filho, "Extrafloral nectaries: their taxonomic distribution and occurrence in the woody flora of cerrado vegetation in Southeast Brazil," *Biotropica*, vol. 19, pp. 140–148, 1987.

[40] P. S. Oliveira, V. Rico-Gray, C. Díaz-Castelazo, and C. Castillo-Guevara, "Interaction between ants, extrafloral nectaries and insect herbivores in Neotropical coastal sand dunes: Herbivore deterrence by visiting ants increases fruit set in *Opuntia stricta* (Cactaceae)," *Functional Ecology*, vol. 13, no. 5, pp. 623–630, 1999.

[41] B. C. Lopes, "Treehoppers (Homoptera, Membracidae) in southeastern Brazil: use of host plants," *Revista Brasileira de Zoologia*, vol. 12, no. 3, pp. 595–608, 1995.

[42] T. J. Guerra, F. Camarota, F. S. Castro, C. F. Schwertner, and J. Grazia, "Trophobiosis between ants and Eurystethus microlobatus Ruckes 1966 (Hemiptera: Heteroptera: Pentatomidae) a cryptic, gregarious and subsocial stinkbug," *Journal of Natural History*, vol. 45, no. 17-18, pp. 1101–1117, 2011.

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 571430, 4 pages
doi:10.1155/2012/571430

Research Article

Geographic Spread of *Gnamptogenys triangularis* (Hymenoptera: Formicidae: Ectatomminae)

Joseph A. MacGown[1] **and James K. Wetterer**[2]

[1] *Department of Entomology and Plant Pathology, Mississippi State University, MS 39762, USA*
[2] *Wilkes Honors College, Florida Atlantic University, 5353 Parkside Drive, Jupiter, FL 33458, USA*

Correspondence should be addressed to Joseph A. MacGown, jmacgown@entomology.msstate.edu

Received 3 May 2011; Accepted 25 May 2011

Academic Editor: Fernando Fernández

Gnamptogenys triangularis (Mayr), native to the forests of South and Central America, is a predatory ant that feeds on millipedes. In its native range, this species is known from Buenos Aires, Argentina (38.1 S) in the south to Costa Rica (10.4 N) in the north, with records from eight countries in South America (all except Chile, French Guiana, and Paraguay), and the two southernmost countries of Central America (Panama and Costa Rica). The first records of *G. triangularis* outside its native range came from Florida beginning in 1985 (six sites: 25.5 –30.4 N) and Alabama in 1996 (one site: 30.4 N). Here we present the first records of *G. triangularis* from Mississippi, dating from 2002–2010 (five sites: 30.5 –31.2 N). Based on its South American range, it appears that *G. triangularis* has the potential to spread to forests throughout much of the southeastern USA. There are no documented impacts of *G. triangularis,* and it seems unlikely that this species will ever become a major pest.

1. Introduction

Gnamptogenys triangularis (Mayr), native to the forests of South and Central America, is a predatory ant that feeds on millipedes [1, 2]. Kusnezov [3] wrote that in Tucuman, Argentina, *G. triangularis* occurred by streams in the subtropical cloud forest areas. In Surinam, Kempf [4] recorded *G. triangularis* from a primary forest and a "marshy wood." Lattke et al. [5] wrote that *G. triangularis* nests in trees and broken branches lying on the forest floor in wet primary and secondary forests, from sea level to elevations >1,000 m. L. R. Davis collected specimens in Harrison County, Mississippi, nesting in a rotten pine limb in leaf litter beneath grape vines (from Mississippi Entomological Museum specimen label data). Other collections of this species in Mississippi were in deciduous forests. Lattke [1] reported that *G. triangularis* colonies typically have only 80–120 workers, up to a probable maximum of 150 workers.

The first records of *G. triangularis* outside its native range came from Miami-Dade County, Florida, beginning in 1985 [6, 7]. Deyrup [8] reported *G. triangularis* from two additional counties in Florida (Broward and Escambia). MacGown and Forster [9] were the first to report this ant from Alabama (Mobile County). Here, we report the first records of *G. triangularis* from Mississippi and evaluate its potential spread based on its known native range.

2. Taxonomy and Identification

Ectatomma triangulare (*G. triangularis*) was originally described in Uruguay in 1887 [10]. Junior synonyms include *Ectatomma triangulare richteri* Forel, described in 1913 in Argentina [11] and *Ectatomma aculeaticoxae* Santschi, described from "Haute Carsevenne, French Guiana" in 1921 [12] (now Alto Rio Calçoene, Brazil) [2].

Gnamptogenys triangularis and *Gnamptogenys hartmani* (Wheeler) are the only two members of the subfamily Ectatomminae known to occur in the southeastern USA. These very distinctive ants can be recognized immediately by the deep horizontal grooves covering the entire head and body. *Gnamptogenys triangularis* workers are 5.0 mm in length and dark brown (Figure 1(a)). Females are similar in appearance to workers, but are slightly larger (5.5 mm in length) and have brownish gray colored wings (Figure 1(b)).

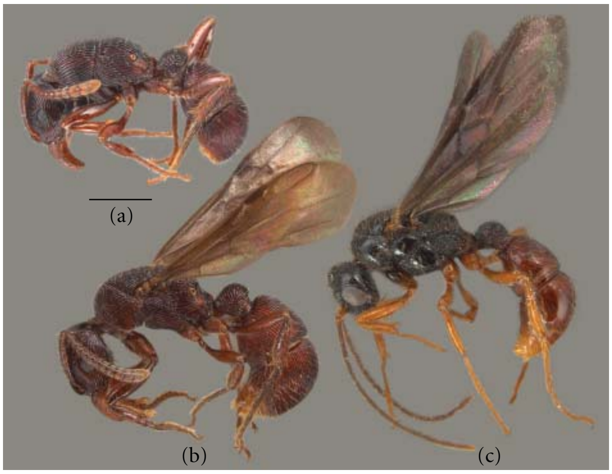


Figure 1: Profile views of *Gnamptogenys triangularis:* (a) worker, (b) alate female, and (c) alate male. Scale bar equals 1.0 mm.

Males (Figure 1(c)) are approximately the same length as females (5.5 mm), but are wasp-like in appearance and differ considerably from workers and females. The deep horizontal grooves characteristic of the genus are mostly absent except on the face and first gastral tergite. Sides of head, pronotum, much of the mesonotum, and gaster have reduced sculpture and are shiny, and the remainder of mesosoma and petiole are rugoreticulate. Males are bicolored with the head and mesosoma dark reddish black to black, petiole dark reddish brown, and gaster reddish orange. The legs, antennal scape, and first segment of funiculus are orangish red, the remainder of funiculus is gray, and the wings are dusky gray. In comparison, *Gnamptogenys hartmani* workers are 3.5–4.0 mm and pale reddish brown. Females are 5 mm and similar in appearance to workers. Males are approximately the same size as females, but horizontal grooves are greatly reduced, and overall they are shinier in appearance. The entire body is reddish brown, legs and scapes are yellowish brown, and the funiculus is dark colored.

3. Methods

Using published and unpublished records, we documented the native and exotic range of *G. triangularis.* We obtained unpublished site records from museum specimens in the collections of the Museum of Comparative Zoology (MCZ, identified by S. Cover) and the Smithsonian Institution (SI, identified by M. Smith). In addition, we used online databases with collection information on specimens by Antweb (http://www.antweb.org/) and the Global Biodiversity Information Facility (http://www.gbif.org/).

4. Results

In South and Central America, *G. triangularis* has been recorded from 12 countries (Table 1) from central Argentina to Costa Rica (Figure 2). References to this species occurring in French Guiana appear to be the type locale of *G. aculeaticoxae* (*G. triangularis*), nowin Brazil (see Section 1).

Table 1: Earliest known records for *Gnamptogenys triangularis* from South and Central America. MCZ: Museum of Comparative Zoology.

	Earliest record
Uruguay	1887 [10]
Bolivia	1893 [13]
Argentina	1898 [14]
Brazil	1898 (as *E. aculeaticoxae*) [12]
Guyana	1922 (as *G. aculeaticoxae*) [15]
Panama	1941 (as *G. aculeaticoxae*) [15]
Costa Rica	1949 (L. Garling, MCZ): La Selva
Surinam	1959 (as *G. aculeaticoxae*) [4]
Peru	1967 (W. L. Brown and W. Sherbrooke, MCZ): Tingo Maria
Colombia	1972 (M. Corn, MCZ): near Puerto Asis
Ecuador	1975 [16]
Venezuela	1982 (as *G. aculeaticoxae*) [1]

Published records of *G. triangularis* outside its native range come from Florida beginning in 1985 (four sites: 25.5 –30.4 N) and Alabama in 1996 (one site: 30.4 N).

Based on specimens in the Mississippi Entomological Museum (identified by JAM), we report records of *G. triangularis* from five sites in four Mississippi counties: Forrest Co., 10 mi S Hattiesburg at diner near Camp Shelby (one male; 31.188 N, 89.251 W; 12 Nov 2010, leg. D. C. Cross), Stone Co., DeSoto National Forest (one gyne; 30.869 N, 89.001 W; 7–13 June 2002, Malaise sample, leg. T. L. Schiefer and J. Schonewitz), Pearl River Co., White Sand (16 gynes and 32 males; 30.794 N, 89.659 W; 24 May–13 July 2002: five different weekly Malaise samples, leg. T. L. Schiefer and L. Thomas), Harrison Co., 1 mi. NE Wortham (one worker; 30.570 N, 89.129 W; 21 July–7 Aug 2006, Lindgren funnel), and Harrison Co., Wool Market (nine workers; 30.484 N, 88.963 W; 27 June 2004, leg. L. R. Davis).

A collection by L. R. Davis from Alabama represents the northernmost record in the United States: Monroe Co., Frisco City, along rt. 21; 2 miles South of jct. rt. 84, (31.453 N, 87.374 W; 4 May 2005; L. R. Davis, Jr., pers. comm.). In addition, two unpublished records from Florida on Antweb represent a new county record: Marion Co., Ocala; 5454 SW 84th St. (29.101 N, 82.210 W; 7 May 2004; leg. M. Jones, Archbold Biological Station) and Marion Co., Ocala, 6455 SW Hwy 200 (29.111 N, 82.227 W; 21 Jul 2004, leg. J. Mangold, California Academy of Sciences).

5. Discussion

Records of *G. triangularis* come from eight countries in South America (all except Chile, French Guiana, and Paraguay), and the two southernmost countries of Central America (Panama and Costa Rica) (Figure 2, Table 1). Because there are no discernable geographic barriers, it seems very likely that the native range of *G. triangularis* also extends into forest habitats in French Guiana, Paraguay, and farther

Figure 2: Map showing the known records of *Gnamptogenys triangularis*.

Table 2: Earliest known records for *Gnamptogenys triangularis* from the USA. +: no previously published records. LRD: L. R. Davis collection. MEM: Mississippi Entomological Museum.

	Earliest record
Florida	1985 [7]
Alabama	1996 (L. R. Davis, LRD): Mobile [9]
+Mississippi	2002 (T. L. Schiefer and L. Thomas, MEM): White Sand

north in Central America, but has not yet been recorded in these areas due to its rarity.

In its exotic range, *G. triangularis* is now known from four counties in Florida (six sites: 25.5 –30.4 N), two in Alabama, and four in Mississippi (five sites: 30.5 –31.2 N) (Figure 2, Table 2). Based on its South American range, extending to 38.1 S, it is possible that *G. triangularis* could spread to forests throughout much of the southeastern USA, perhaps as far north as Richmond, Virginia (37.5 N) and Lexington, Kentucky (38.0 N).

Many of the Mississippi records are based on specimens collected in Malaise traps. These traps and other flight interception traps may be useful methods for monitoring the movements of exotic species, especially alate males and females.

In both its native and exotic ranges, *G. triangularis* inhabits forests and preys on millipedes [2, 3, 8]. There are no known impacts of *G. triangularis*, even though if this species was having a localized impact on millipede populations, it seems unlikely that this would have been detected. Nonetheless, it seems unlikely that this species will ever become a major pest.

Acknowledgments

Thanks are due to Terry Schiefer, David Cross, and Lloyd Davis for collecting specimens and donating them to the Mississippi Entomological Museum. This research was supported by Mississippi Agricultural and Forestry Experiment Station State Project MIS-311080 and the USDA-ARS Areawide Management of Imported Fire Ant Project (Richard L. Brown, Principal Investigator). This paper is approved for publication as Journal Article no. J12004 of the Mississippi Agricultural and Forestry Experiment Station, Mississippi State University.

References

[1] J. E. Lattke, “Revision del genero *Gnamptogenys en Venezuela*,” *Acta Terromoria*, vol. 2, pp. 1–47, 1990.

[2] J. E. Lattke, “Revision of the ant genus *Gnamptogenys* in the New World (Hymenoptera: Formicidae),” *Journal of Hymenoptera Research*, vol. 4, pp. 137–193, 1995.

[3] N. Kusnezov, “Lista de las hormigas de Tucumán con descripción de dos nuevos géneros (Hymenoptera, Formicidae),” *Acta Zoológica Lilloana*, vol. 13, pp. 327–339, 1953.

[4] W. W. Kempf, “A survey of the ants of the soil fauna in Surinam (Hymenoptera: Formicidae),” *Studia Entomologica*, vol. 4, pp. 481–524, 1961.

[5] J. E. Lattke, F. Fernández, T. M. Arias-Penna, E. E. Palacio, W. Mackay, and E. Mackay, “Género *Gnamptogenys* Roger,” in *Sistemática, Biogeografía y Conservación de las Hormigas Cazadoras de Colombia*, pp. 66–100, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá D. C., Colombia, 2008.

[6] M. Deyrup, C. Johnson, G. C. Wheeler, and J. Wheeler, “A preliminary list of the ants of Florida,” *Florida Entomologist*, vol. 72, pp. 91–101, 1989.

[7] M. Deyrup, L. Davis, and S. Cover, “Exotic ants in Florida,” *Transactions of the American Entomological Society*, vol. 126, no. 3-4, pp. 293–326, 2000.

[8] M. Deyrup, “An updated list of Florida ants (Hymenoptera: Formicidae),” *Florida Entomologist*, vol. 86, no. 1, pp. 43–48, 2003.

[9] J. A. MacGown and J. A. Forster, “A preliminary list of the ants (Hymenoptera: Formicidae) of Alabama,” *Entomological News*, vol. 116, no. 2, pp. 61–74, 2005.

[10] G. Mayr, “Südamerikanische formiciden,” *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien*, vol. 37, pp. 511–632, 1887.

[11] A. Forel, “Fourmis d’Argentine, du Brésil, du Guatémala & de Cuba. Reçues de MM. Bruch, Prof. v. Ihering, Mlle Baez, M. Peper et M. Rovereto,” *Bulletin de la Société Vaudoise des Sciences Naturelles*, vol. 49, pp. 203–250, 1913.

[12] F. Santschi, “Ponerinae, Dorylinae et quelques autres formicides néotropiques,” *Bulletin de la Société Vaudoise des Sciences Naturelles*, vol. 54, pp. 81–103, 1921.

[13] C. Emery, “Studi sulle formiche della fauna neotropica. VI-XVI,” *Bullettino della Società Entomologica Italiana*, vol. 26, pp. 137–241, 1894.

[14] C. Emery, “Studi sulle formiche della fauna Neotropica,” *Bollettino della Societa Entomologica Italiana*, vol. 37, pp. 107–194, 1906.

[15] W. L. Brown Jr., “Contributions toward a reclassification of the Formicidae. II. Tribe Ectatommini (Hymenoptera),” *Bulletin of the Museum of Comparative Zoology*, vol. 118, pp. 175–362, 1958.

[16] J. E. Lattke, F. Fernandéz, and E. E. Palacio, “Una nueva especie de *Gnamptogenys* (Hymenoptera: Formicidae) y comentarios sobre las especies del génereo en Colombia y Ecuador,” *Iheringia. Série Zoologia*, vol. 94, pp. 341–349, 2004.

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 426719, 4 pages
doi:10.1155/2012/426719

Research Article

Nest Digging by Leaf-Cutting Ants: Effect of Group Size and Functional Structures

Roberto da Silva Camargo, Ricardo Toshio Fujihara, and Luiz Carlos Forti

Laboratório de Insetos Sociais-Praga, Departamento de Produção Vegetal, Faculdade de Ciências Agronômicas, UNESP, P.O. Box 237, 18603-970 Botucatu, SP, Brazil

Correspondence should be addressed to Roberto da Silva Camargo, camargobotucatu@yahoo.com.br

Received 27 April 2011; Revised 25 May 2011; Accepted 6 June 2011

Academic Editor: Fernando Fernández

Leaf-cutting ant workers dig underground chambers, for housing their symbiotic fungus, interconnected by a vast quantity of tunnels whose function is to permit the entrance of food (leaves), gaseous exchanges, and movement of workers, offspring, and the queen. Digging is a task executed by a group of workers, but little is known about the group effect and group-constructed functional structures. Thus, we analyzed the structures formed by worker groups (5, 10, 20, and 40 individuals) of the leaf-cutting ant, *Atta sexdens rubropilosa*, for 2 days of excavation. The digging arena was the same for the 4 groups, with each group corresponding to a different density. Our results verified a pattern of tunneling by the workers, but no chamber was constructed. The group effect is well known, since the 40-worker group dug significantly more than the groups of 5, 10, and 20. These groups did not differ statistically from each other. Analysis of load/worker verified that workers of the smallest group carried the greatest load. Our paper demonstrates the group effect on the digging of nests, namely, that excavation is proportional to group size, but without emergence of a functional structure such as a chamber.

1. Introduction

Medium-sized leaf-cutting ant workers are responsible for digging new functional structures within the nest including chambers and tunnels [1]. These workers respond well to the stimulus to dig even when isolated or in small groups. During digging the workers must be involved in coordinated activity and respond actively to regions excavated by other ants. After the initial construction process is established, nestmates must be recruited to the location of the activity. This recruitment of nest companions is governed by a positive feedback mechanism by means of communication between the initial excavators and the recruits. The signal utilized for the recruitment is probably stridulatorial communication [2], which runs through the substrate (soil) to recruit nestmates to the point of activity. When the density increases, this signal ceases, as does its function.

Concomitant with the growth of the structure, we would find a negative feedback coordinating the activity, in other words, conducting the workers to finalize the task of digging. The workers may perceive this via chemical cues (pheromones), metabolic products of the workers (CO_2) [3, 4], or by the encounter rate among them [5]. The touches among these workers are a product of momentary density in the area of activity, that is, a monitoring of the task [5].

This hypothesis is based on the allocation of tasks without centralized control, in which the individuals respond to simple local cues (signals). This rate of signals depends on group characteristics such as their size and density [5]. Thus, the functional structures emerge from the activity of the ants, ceasing with the enlargement of the required structures, whether they be tunnels or chambers.

It is known that among leaf-cutting ants, when small groups of workers are formed (2 to 8) for digging, they do not increase the number of tunnels and instead deepen those already excavated, demonstrating social organization and coordination of work [1]. These indications constitute strong evidence of a nest construction system, although this has not yet been demonstrated experimentally.

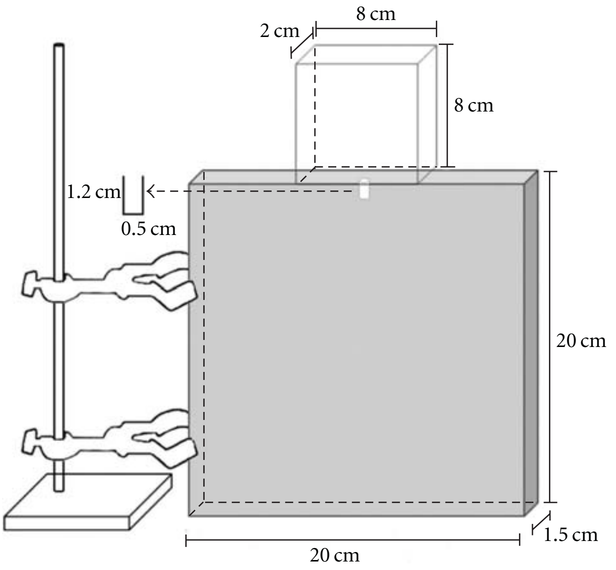


Figure 1: Experimental setup: the workers were allocated into a box with a *pregiven* tunnel to incite digging. The workers continued to dig for 48 hours.

In the present work we analyzed the structures formed by groups of workers (5, 10, 20 and 40 individuals) of the leaf-cutting ant, *Atta sexdens rubropilosa*, for 2 days of digging. The size of the excavation arena was the same for the 4 groups, with each group corresponding to a different density. The excavation arena was disposed vertically, permitting visualization of the digging in a uniform environment. Thus, it was possible to study the group effect on the nest digging by small groups of workers.

2. Material and Methods

2.1. Selection of Workers. Twenty-five workers from the field were collected in adult nests during nest digging. These were isolated, labeled, and transported to the laboratory. The following aspects were measured: head width, body mass, and load mass (soil pellet). This enabled patterning of the size of the ants that effectively do the digging in a natural situation.

In the laboratory, workers were selected according to their size class (head width from 1.2 to 1.6 mm) in midsized colonies (3 years) maintained in the Laboratory of Insect Pests—FCA/UNESP—Botucatu, São Paulo State, Brazil.

2.2. Excavation Boxes. The fifteen glass boxes utilized had dimensions of 20 cm in length and height, and 1.5 cm in thickness. These were filled with soil collected at a depth of 60 cm and sieved (soil density = 1.6 g/cm^3 [6]; water content: 5.4%). A small tunnel, constructed manually (artificially) in this apparatus, was 1.2 cm in length and 0.5 cm in width.

Above this apparatus was placed a small glass box (8 × 8 × 2 cm) into which was transferred a colony for conducting the experiment (Figure 1).

2.3. Rate of Digging and Structures Formed. We analyzed the structures formed by groups of generalist workers (5, 10, 20, and 40 individuals) of the leaf-cutting ant, *Atta sexdens rubropilosa*, for 2 days of digging.

The workers stayed in the digging box for 48 hours, with the excavated soil being removed every 12 hours. The soil volume dug out by the workers in the 12-hour period was collected and dried in an oven for 24 hours at 80 C.

After the 48-hour digging period, liquid plaster was added to obtain the exact dimensions of the architecture of these constructions. After the plaster had dried, these structures and the soil were removed and carefully analyzed.

The structures were analyzed by measuring the area excavated by the workers on two planes; the structures were photographed and their area calculated in mm^2 via the program Image J from the National Institutes of Health, USA., http://rsb.info.nih.gov/ij/. These measures were correlated with the number of workers involved in the excavation, thereby providing a ratio between the number of structures formed and the number of workers.

The volume of these structures was calculated by their weight, with the volume in g, converted to mL.

2.4. Statistical Analyses. A linear regression was applied to correlate the mass of workers with their load in the field, to enable selection of the size class appropriate for digging. The head widths of field workers were compared with those of laboratory workers by the test of Mann-Whitney ($\alpha = 0.05$). The data for the area and volume of excavated soil were submitted to analysis of variance (ANOVA; $\alpha = 0.05$), with subsequent paired comparison by the methods of Student-Newman-Keuls and Dunn.

3. Results

3.1. Selection of Workers. The workers from the field presented a linear relationship between their body mass (0.004 ± 0.002 g) and the mass of soil pellets (0.017 ± 0.01 g) deposited outside the nest ("best-fit" linear equation, $x = 0.00125 + (0.173 \quad y)$, $R = 0.849$, ($t = 7.702$, $P < 0.001$)) (Figure 2). In their pellets these workers carry on average 4-times their body mass (ratio = soil pellet mass/worker mass, mean = 4.05; standard deviation = 1.66, $N = 25$). These pellets are transported frontally to the exterior of the nest by the mandibles, without projecting all the load mass behind the body, as they do when collecting vegetal matter. This must be the manner by which they fabricate such pellets. The pellets are formed by the behavioral act of "biting" the soil matrix with the mandibles; in other words, the workers remove the soil fragments and aggregate them with the aid of their metathoracic legs. After the soil pellet is formed, it is taken to the exterior of the nest, but is carried frontally, between the mandibles. In unpublished data on leaf-cutting ant queens, we observed that when one of the tibiae of the metathoracic legs is mutilated or cut, these queens become slower and dig more slowly than normal ones. This is due to an inefficiency in aggregating soil to form the soil pellets.

TABLE 1: Digging rate (g), area excavated (mm^2), and volume of soil excavated (cm^3) by groups of workers (5, 10, 20, and 40), as a function of elapsed time.

Group size	Volume of soil (g)					Load/worker ratio	Trips	Area	Volume
	12	24	36	48	total				
5	3.0	1.5	0.0	0.0	4.5	0.90	53	828.5 ± 436	7.36 ± 4.1
10	4.5	1.1	0.0	0.0	5.6	0.56	33	1066.0 ± 464.64	7.37 ± 3.5
20	9.8	0.3	0.0	0.0	10.1	0.50	30	1176.5 ± 461.01	11.40 ± 4.5
40	21.6	1.7	1.1	2.4	26.9	0.67	40	4530.4 ± 1863.67	36.33 ± 12.7

Load/worker ratio = total soil volume/number of workers in the group; trips = (load/worker ratio)/0.017 (average mass of soil pellets).

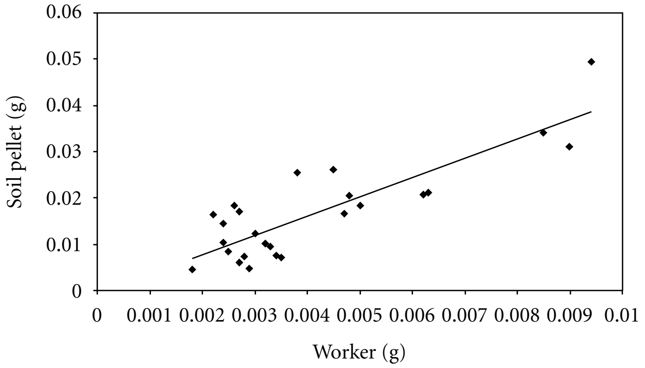


FIGURE 2: Ratio between mass of workers and their soil load in a natural situation. Linear regression was applied with the "best-fit" linear equation ($x = 0.00125 + (0.173 \quad y)$, $R = 0.849$, ($t = 7.702$, d.f. $= 24$, $P < 0.001$)).

In addition to mass, the head width was measured in both field and laboratory workers. The field workers presented a head width of 1.5 ± 0.3 mm while those of the laboratory did not differ significantly at 1.4 ± 0.5 mm ($U = 568.500$, $P = 0.174$). Thus, it may be stated that workers from the field and laboratory were similar, belonging to the same class size, which we can denominate the generalists ([7], on head width from 1.2 to 1.6 mm).

3.2. Digging Rate and Structures Formed. The highest digging rate occurred in the first 12 hours after the release of the workers, and decreased over time (Table 1). There was a significant difference among the times (Kruskal-Wallis test, $H = 10.727$, d.f. $= 3$, $P < 0.05$) while the posttest (Student-Newman-Keuls) determined that the volume of soil excavated in 12 hours differed significantly from the other evaluation periods.

We calculated that each worker transported from 0.50 to 0.90 g of soil throughout the experiment, within each group. The trips were calculated according to the average volume of soil that each worker transported per trip (0.017 g), resulting in 30 to 53 trips during the experiment (Table 1).

In relation to the structures formed by groups, we verified a specific tunneling pattern by the workers (Figure 3). The area excavated by the groups presented a significant difference (Kruskal-Wallis test, $H = 34.697$, d.f. $= 3$, $P < 0.001$) while the posttest (Student-Newman-Keuls) determined that the 40-worker group dug significantly more than the groups of 5, 10, and 20. These groups did not differ significantly from each other.

The volume of structures created by the workers, determined by the plaster molds, differed significantly among the groups (Kruskal-Wallis test, $H = 36.359$, d.f. $= 3$, $P < 0.001$), while the posttest (Dunn) showed that the 40-worker group dug significantly more than the 5-, 10-, and 20-worker groups. There was no significant difference among these groups.

4. Discussion

The results obtained by the present study verified that the workers dug tunnels, but no chamber to house them (Figure 3). The emergence of a functional structure, such as a chamber, is only possible in leaf-cutting ants when the worker group is larger and symbiotic fungus is present as a stimulus for its construction. Fröhle and Roces [8] verified the emergence of functional structures, including chambers, in larger groups (750, 1500, 2500 workers), with diverse volumes of fungus. These workers were apt to enlarge a fungus chamber to house a greater fungus volume, independent of the number of ants.

A higher digging rate was observed at the beginning of the experiment, followed by a reduction as time elapsed (Table 1), as already observed in other species [4, 8, 9]. According to Buhl et al. [9], this decrease in activity at the end of the digging dynamic can be explained by two possible mechanisms: the first corresponds to a reduction in activity by means of a perception of specific signals from individuals such as the concentration of CO_2 [10] or the rate of encounters among ants [11]. The second relies on the propagation properties of the recruitment, leading to a stopping activity according to the determinate density of ants [12].

The volume of excavated soil varies directly with the number of ants in the group (Table 1); however, almost all of the ants were observed to dig. Nevertheless, it is known that in small groups the workers dig more than those in larger groups, as explained by Fröhle and Roces [8]. This is due to the population density; in other words, the smaller the group, the more possibilities the workers will have to dig and all are recruited with opportunities to execute their task.

In summary, our study demonstrates the group effect on the digging of nests, namely, that digging is proportional to group size, but without emergence of a functional structure such as a chamber.

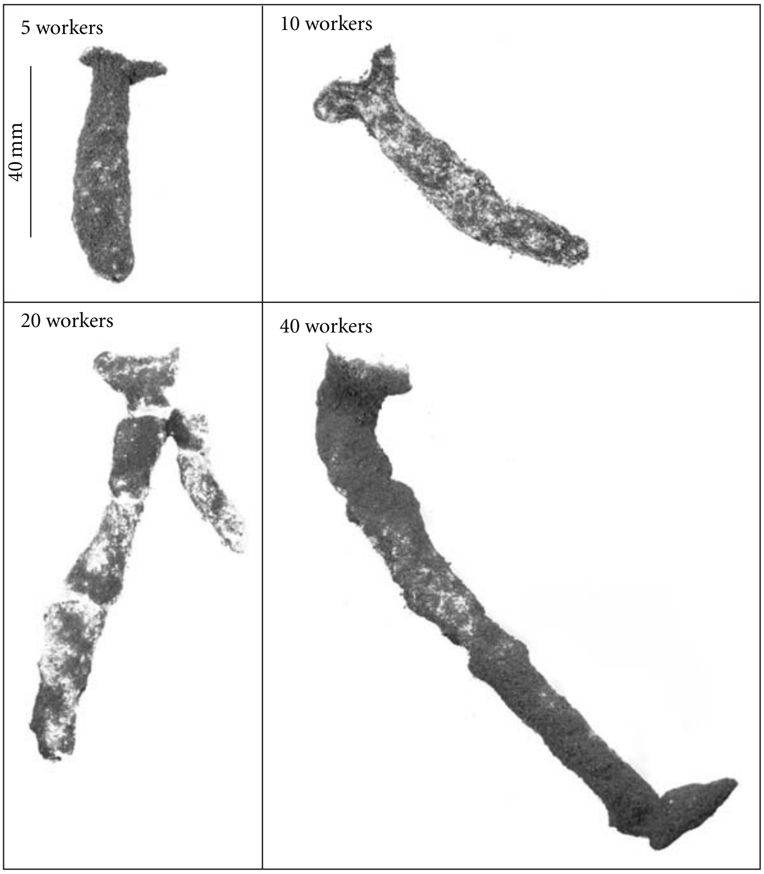


FIGURE 3: Structures produced by groups of *Atta sexdens rubropilosa* workers, in groups of 5, 10, 20, and 40, throughout 48 hours.

Acknowledgment

The authors would like to thank "Fundação de Amparo à Pesquisa do Estado de São Paulo" (FAPESP) for the postdoctoral scholarship to the first author (2007/04010-0) and for a research aid (2007/07091-0).

References

[1] M. M. P. Rodrigues and F. L. Ribeiro, "Organização da escavação em obreiras de *Atta sexdens rubropilosa*: Atração por túneis iniciados," in *I Encontro Paulista de Etologia*, p. 242, São Paulo, Brazil, 1983.

[2] H. Markl, "Stridulation in leaf-cutting ants," *Science*, vol. 149, no. 3690, pp. 1392–1393, 1965.

[3] P. P. Hangartner, "Carbon dioxide, a releaser for digging behavior in *Solenopsis geminata* (Hymenoptera: Formicidae)," *Psyche*, vol. 76, no. 1, pp. 58–67, 1969.

[4] P. Rasse and J. L. Deneubourg, "Dynamics of nest excavation and nest size regulation of *Lasius niger* (Hymenoptera: Formicidae)," *Journal of Insect Behavior*, vol. 14, no. 4, pp. 433–449, 2001.

[5] D. M. Gordon and N. J. Mehdiabadi, "Encounter rate and task allocation in harvester ants," *Behavioral Ecology and Sociobiology*, vol. 45, no. 5, pp. 370–377, 1999.

[6] C. Stein and G. F. Xavier, "Does substrate density affect the nest depth of female *Atta sexdens rubropilosa* (Forel, 1908) (*Hymenoptera, formicidae*)," *Brazilian Journal of Medical and Biological Research*, vol. 17, pp. 297–300, 1984.

[7] E. O. Wilson, "Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: Atta)—I: the overall pattern in *A. sexdens*," *Behavioral Ecology and Sociobiology*, vol. 7, no. 2, pp. 143–156, 1980.

[8] K. Fröhle and F. Roces, "Underground agriculture: the control of nest size in fungus-growing ants," in *From Insect Nest to Human Architecture*, G. Theraulaz, R. Solé, and P. Kuntz, Eds., pp. 95–104, Venice, Italy, 2009.

[9] J. Buhl, J. Gautrais, J. L. Deneubourg, and G. Theraulaz, "Nest excavation in ants: group size effects on the size and structure of tunneling networks," *Naturwissenschaften*, vol. 91, no. 12, pp. 602–606, 2004.

[10] M. D. Cox and G. B. Blanchard, "Gaseous templates in ant nests," *Journal of Theoretical Biology*, vol. 204, no. 2, pp. 223–238, 2000.

[11] D. M. Gordon, R. E. Paul, and K. Thorpe, "What is the function of encounter patterns in ant colonies?" *Animal Behaviour*, vol. 45, no. 6, pp. 1083–1100, 1993.

[12] J. L. Deneubourg and N. R. Franks, "Collective control without explicit coding: the case of communal nest excavation," *Journal of Insect Behavior*, vol. 8, no. 4, pp. 417–432, 1995.

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 491592, 6 pages
doi:10.1155/2012/491592

Research Article

Plant Killing by Mutualistic Ants Increases the Density of Host Species Seedlings in the Dry Forest of Costa Rica

Sabrina Amador-Vargas[1, 2]

[1] *Escuela de Biología, Universidad de Costa Rica, San Pedro, Costa Rica*
[2] *Integrative Biology, University of Texas at Austin, 1 University Station C0930, Austin, TX 78712, USA*

Correspondence should be addressed to Sabrina Amador-Vargas, samadorv@gmail.com

Received 1 April 2011; Accepted 7 June 2011

Academic Editor: Jonathan D. Majer

Some species of plant-mutualistic ants kill the vegetation growing in the vicinities of their host plant, creating an area of bare ground (clearing). The reduced competition in the clearing may facilitate the establishment of host species sprouts (clones and seedlings), which in turn benefits the ants with additional food and shelter ("sprout-establishment hypothesis"). To test this hypothesis, the density and origin of *Acacia collinsii* sprouts growing inside clearings and in the vicinities of acacia plants without clearings were compared. Also, to assess the pruning selectivity of acacia ants (*Pseudomyrmex spinicola*), seedlings were transplanted into clearings. The reaction of ants towards unrewarding acacia seedlings (without food and shelter) was also tested. The density of acacia sprouts growing inside clearings was almost twice that in the vicinities of host plants without clearings, and sprouts were inhabited by nestmates of the colony that made the clearing. Clones and seedlings were found in similar proportions in the clearings, and ants did not kill unrewarding acacia seedlings or seedlings unrelated to their host. The benefit reported here for the ants could be in conflict with the host plant, especially when the plant has rhizomal reproduction.

1. Introduction

In obligatory ant-plant mutualisms, the ants obtain food and shelter from their host, and, in exchange, they defend the plant against herbivores [1, 2]. In addition to attacking insect or vertebrate herbivores, some ants (henceforth, resident ants) also kill plants in the vicinity of their host tree by biting or poisoning [1, 3–10], functioning as allelopathic agents [4]. By killing neighboring plants, the ants leave an area of bare ground around the host plant (henceforth, "clearing"; Figure 1).

Two main functions have been attributed to the clearings: (1) isolating the colony and (2) reducing competition for the host plant. The isolation that the clearings provide to the host tree may also prevent invasions from other ants by reducing or eliminating access venues to the colony that other invasive ants might use to enter the tree. Davidson et al. [11] noted that most ant species that kill nearby vegetation defend themselves by stinging and are unable to defend themselves against ants that are chemically defended (i.e., ants that are stingless and use chemical sprays). Empirical data showed contradictory results: *Triplaris* trees inhabited by *Pseudomyrmex* ants that were artificially connected to neighboring vegetation had more invading ants than isolated ones, but connected trees of *Cordia nodosa* associated with *Allomerus* ants did not have more invasions [11]. Also, *Crematogaster* ants living in nonwaxy species of *Macaranga* trees pruned more intensively than those living on trees with waxy barriers [9], presumably because ants in waxy trees are already isolated from potential intruder ants, which have difficulty walking on waxy surfaces.

Ants can also enhance growth of their host plant and obtain more resources for their colony by pruning nearby vegetation. Any plant growing close to the host acacia is a competitor for light, water, nutrients, or space. Therefore, killing neighboring plants or vines growing on the acacia reduces host plant competition [4]. Janzen suggested this hypothesis based on observations of acacias weakened or dying under the shadow of vines or trees. Besides the observations on *Acacia* by Janzen, it is known that *Tococa* trees inhabited by *Myrmelachista* ants die when the ants do

Figure 1: Clearing made by *Pseudomyrmex spinicola* ants around their host plant *Acacia collinsii* (center, diameter of 4 cm marked by the scale bar), showing three acacia sprouts (white arrows). A small portion of the clearing of a second acacia is also visible (top right corner). Growing outside the clearing is the grass species (*Oplismenus* sp., Poaceae) used as control in the experiments.

not kill the surrounding vegetation, apparently due to light attenuation resulting from overgrowth by neighboring plants [12].

Recently, a third function has been attributed to the clearings. If competition is reduced in the surroundings of the host tree, it may facilitate the establishment of host species sprouts (defined here as seedlings or shoots from rhizomes), a hypothesis called "sprout establishment hypothesis" [13]. Pruning ants can expand their colony to inhabit the recently established neighboring sprouts and benefit from the food and shelter provided by those sprouts growing in the clearing. To date, our knowledge about the seedlings growing inside the clearings is very limited. For several ant species, we know that they kill any plant inside the clearings except for seedlings of the mutualistic species [4, 12, 14], but little is known about the seedling's origin (dispersed seeds versus vegetative growth from the host plant), or how specific are ants in identifying or favoring host seedlings over seedlings of other plants. The ants kill any plant that is in contact with their host tree, apparently either to prevent the growth of encroaching vegetation [3], or to minimize invader entry points [11]. However, we do not know how they react when the contacting plant is an unrewarding seedling (i.e., a seedling that does not provide food or shelter), and whether they evaluate the long-term potential benefits of keeping a seedling that is not producing any reward against the short-term potential threat of having a seedling with leaves or branches in contact with the plant.

In this paper, I address several aspects of the sprout establishment hypothesis in the obligatory mutualism of acacia plants (*Acacia collinsii*) with *Pseudomyrmex spinicola* ants. I tested (1) whether the clearings favored the establishment of acacia sprouts, by comparing the density of sprouts near host plants with or without clearings; (2) whether the sprouts were inhabited by the same colony that made the clearing; (3) whether sprouts in a clearing were occupied by ants more often than sprouts growing near acacias without clearings. To understand whether the pruning behavior was favoring clones of the host acacia over seedlings coming from other plants, I evaluated the proportion of the sprouts established in the clearings that were growing from seeds or from rhizomes of the host plant. Additionally, I experimentally tested whether ants allowed saplings that were not clones or seedlings from their host tree to grow in the clearings. And finally, I evaluated whether ants kill or protect acacia seedlings that were not offering any immediate reward (nectar, protein bodies, or swollen thorns) but were functioning as bridges for potential intruders.

2. Methods and Materials

2.1. Study Site. The investigation was conducted in the dry forest of Palo Verde National Park (10 21 N, 85 21 W) in Guanacaste, Costa Rica. Palo Verde has a mean annual rainfall of 1500 mm and elevation ranging from 0 to 100 m. This area has a well-defined dry season from November to May and a rainy season from June to October. *A. collinsii* plants inhabited by *P. spinicola* occur in secondary growth forest where the lianas and vines are very common. These ants defend the colony against predators or intruders by stinging, and they kill vegetation around their host by biting and cutting the leaves or stems, producing a circular clearing around the host plant (radii between 30 cm up to 2 m; [3], this paper). In Palo Verde, it is possible to find acacias with clearings and acacias without clearings (normally inhabited by other *Pseudomyrmex* species, by the chemically defended *Crematogaster brevispinosa*, and few trees without ants). *A. collinsii* trees are able to reproduce sexually by seeds, or vegetatively by rhizomes that produce clones of the adult plant [3]. In the study site of the present investigation, the invasion threat for resident ants comes from both arboreal ants, which could displace them from the tree, and army ants that can predate on the brood. The sampling was carried out during the wet season of 2007 and 2008.

2.2. Density of Acacia Sprouts. In June 2007, I searched for solitary *Acacia collinsii* trees with clearings and inhabited by *P. spinicola* ants (Figure 1), and for acacia trees without clearings, to compare the density of acacia sprouts growing in the vicinity of the plant. A plant was considered to be solitary when it was separated by more than 4 m from another conspecific adult. Almost all of these clearings were approximately circular, so the radius was used as an estimate of the clearing's size. For each acacia, radii were measured (± 0.5 cm) from the trunk of the acacia (hereafter, central acacia) to the edge of the cleared area in the four cardinal directions, and the mean was used to calculate the area of the corresponding circle. I estimated the size of the acacia ($n = 60$) by measuring the diameter of the acacia (± 0.05 cm) at the ground level and counted all the acacia sprouts with swollen spines growing inside the clearing. For acacias without clearings ($n = 48$), I counted all sprouts growing within 1 m of the acacia. I used the estimated area of the clearing to calculate the density of acacia sprouts per square centimeter. Means ± standard deviations are presented. The density of acacia sprouts was compared with nonparametric ANCOVA test using ranks, following the procedure of McSweeney and Porter [15] and Conover and Iman [16], because the response variable did not meet normality and homoscedasticity. This statistical method takes into account the within-group and total-group regression when adjusting the dependent variable to the covariate [17]. The clearing (presence or absence) was considered a fixed factor, and plant diameter was used as a covariate. The covariate was included because the size of the plant could be correlated with the number of saplings growing into de clearing, for example, older plants could have more sprouts.

2.3. Inhabitants of the Sprouts Growing in the Clearing or Near Acacias without Clearings. To test whether ants on the sprouts were from the same colony that made the clearing, the sprouts from the density measurements were observed for ants. If the sprout had ants, I identified the species and verified whether they belonged to the same colony of ants on the central acacia. Colony identity was deduced by observing whether the ants on the sprout walked in a line back and forth between the central acacia and the sprout. If I did not find ants walking on the ground at that moment, they were encouraged to walk onto a stick from the sprout, allowing them to walk onto the central acacia. I checked whether the resident ants let the intruder walk on the tree or attacked it by biting and stinging (these ants recognize nestmates by chemical cues [18]). As control, I induced ants from the central acacia to walk onto a stick and then reintroduced them to the central acacia, in different place from where I placed the ant coming from the nearby sprout. The frequency of sprouts with nestmates, ants from other species, or unoccupied were compared by chi-square tests separately for plants with clearings or without clearings.

Another prediction is that sprouts in a clearing should be more often occupied by ants, than sprouts growing close to acacias without clearings. The density of sprouts occupied by ants (response variable) and the density of unoccupied sprouts (response variable) were compared by separate ANCOVA tests using ranks, where the fixed factor and covariate were clearing (presence or absence) and the plant diameter, respectively.

2.4. Identity of the Acacia Sprouts Established in a Clearing. To test whether plant killing was favoring host clones over seedlings (i.e., that ants were favoring the vegetative growth of their host plant), I determined the proportion of sprouts corresponding to clones and seedlings, on the clearings of 22 acacias. On each clearing, I dug about 25 cm deep around the main acacia and around the sprouts, looking for rhizomes. When rhizomes were found, they were followed to elucidate connections between the main acacia and the sprouts. Sprouts were classified as "independent" when its main root entered vertically into the ground, and it was not attached to a rhizome. When a horizontal rhizome between the sprout and the central acacia was found, the sprout was classified as a "clone of the main acacia". I classified some sprouts as "having horizontal roots" when the sprout lacked a main root growing vertical into the ground, and it was attached to a horizontal rhizome making an inverted "*T*" or an "*L*" with the stem but was not connected to the central acacia. In each clearing, the main acacia's diameter and the distance (± 0.5 cm) to the sprouts around it were measured. After corroborating that the diameter of the plant was not correlated with the proportion of clones (Spearman correlation, $R = -0.20$, $P = 0.37$), a Wilcoxon matched pairs test was used to compare the quantity of sprouts coming from seeds and those that were clones of the acacia. Means and standard deviations are presented.

Because the relation between established seedlings and the main acacia was impossible to determine with the previous observations, I performed field experiments where I placed acacia seedlings of known origin inside clearings and tested the reaction of the ants. I planted seeds of *A. collinsii* in bags with soil, and grew them on partially shaded tables protected from large herbivores (deer, horses, and cows). The *A. collinsii* seeds came from trees that were more than five kilometers away from the experimental trees. In similar bags, I also planted stolons of *Oplismenus* sp. (Poaceae) with 7-8 leaves, a grass native of the study area that is regularly killed by *Pseudomyrmex* ants. When the acacias had six or seven leaves (3-4 weeks after planting), they were introduced into the clearing of 12 solitary acacias (hereafter, experimental trees) that had less than three young acacias growing naturally in the clearing, to determine whether the ants will kill them or allow them to grow. In the clearing of each experimental tree, I placed two bags with *A. collinsii* seedlings at half of the clearings, and two bags with *Oplismenus* stolons as controls. Within each clearing, I placed bags with conspecific plants diametrically opposed from each other. Ants were able to walk on the vertical surface of the plastic bag without impediment. After placing bagged plants, I observed them for 10 days twice a day for 2 minutes, checking for *P. spinicola* ants pruning or chewing the plant. I checked the plants one more time after 20 days from the setup of the experiment. The experimental placement of plants in the clearings allowed me to evaluate the reaction of the ants to acacia seedlings that were not clones or seedlings from their host tree.

2.5. Unrewarding Acacia Seedlings in Contact with the Host Tree. To understand whether the decision of pruning a sprout changed when the acacia sprout also represented a potential bridge for intruders, I placed two plants in bags in contact with the trunk of solitary acacias inhabited by *P. spinicola* ants. One of the plants in the pair was an acacia seedling, and the other was either an *Oplismenus* grass stolon (7-8 developed leaves, $n = 22$) or a *Coursetia caribaea* shrub seedling ($n = 12$). I used the *C. caribaea* (Fabaceae) seedlings (aprox. 15 cm height) because it is a woody species with pinnate leaves like the acacia. Both plant species are common in the study area. Acacia seedlings used in the experiment did not have nectaries, food bodies or swollen spines, and, therefore, did not offer food or shelter to the ants. The diameter of the experimental acacias ranged from 2 to 2.5 cm at ground level. For all the plants, I placed the bag next to the trunk and arranged the leaves such that the second leaf touched the acacia. All colonies were sampled only once, and all bagged plants were used for a single colony. Similar observations to the previous experiment were done for 8 days.

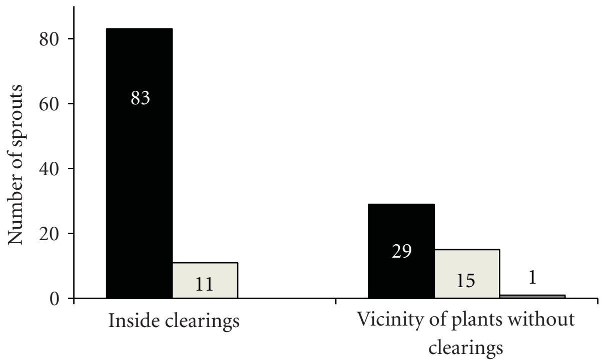


Figure 2: Absolute number of sprouts inhabited by workers from the same colony of the central acacia (black), unoccupied (white), or with ants from a different species (gray), for host plants with clearings ($n = 60$) or without them ($n = 48$).

3. Results

3.1. Density of the Sprouts Growing in the Clearing or Near Acacias without Clearings and Their Inhabitants. There was a higher sprout density in clearings (0.71 ± 0.15 sprouts/cm^2, $n = 69$) than in the vicinity of plants without clearings (0.40 ± 0.22 sprouts/cm^2, $n = 35$; nonparametric ANCOVA by ranks $F_{(1,101)} = 3.73$, $P = 0.05$). When looking at occupied sprouts (i.e., with ants), they were also at higher densities in clearings than close to acacias without clearings (0.46 ± 0.96 sprouts/cm^2 versus 0.26 ± 0.54 sprouts/cm^2, respectively; non parametric ANCOVA by ranks, $F_{(1,101)} = 4.09$, $P = 0.04$). On the other hand, there were similar numbers of unoccupied sprouts (without ants) per square meter within clearings and near acacias without clearings (0.23 ± 1.29 versus 0.13 ± 0.37 sprouts/cm^2, respectively; ANCOVA by ranks, $F_{(1,101)} = 0.003$, $P = 0.95$).

The majority (88%) of the A. *collinsii* sprouts growing inside clearings were occupied by ants from the same colony of the experimental acacia (not treated aggressively by the resident colony); the remaining 12% were unoccupied (Figure 2). The sprouts near acacias without clearings showed different proportions of sprouts on each category ($\chi^2 = 11.8$, d.f. $= 2$, $P = 0.003$): 65% were occupied by ants that were not attacked by the resident colony, 33% were unoccupied, and 2% were occupied by another species of ant (*Crematogaster brevispinosa* ants inhabited the main acacia, but the sprouts had *P. spinicola* ants).

3.2. Identity of the Acacia Sprouts Established in a Clearing. Inside the clearings, there was an equal amount of sprouts arising from seeds (4.3 ± 5.3 sprouts per acacia, median = 3) as clones from the acacia (2.9 ± 4.1, median = 1; Wilcoxon paired test, $T = 81$, $P = 0.37$). The results were consistent when the sprouts classified as "having horizontal roots" were incorporated as "clones" in the analysis (Wilcoxon paired test, $T = 98$, $P = 0.54$). It is very likely that these saplings are clones from the acacia, especially when the rhizome they come from was directed towards the central acacia.

None of the acacia seedlings placed in the clearings were pruned or severed, but all *Oplismenus* grasses were pruned. The majority of the colonies started pruning the grass on the same day that I first observed them on the plant, but some did not do so until after 9 days from the day that ants were first seen on the plants. Two grasses remained uncut by the ants during the first 10 observation days. But, by day 20, the ants had completely severed the main stem of all 24 grasses, whereas all 24 acacias were intact.

3.3. Unrewarding Acacia Seedlings in Contact with the Host Tree. All *Oplismenus* and *C. caribaea* plants were pruned, whereas all acacia seedlings were not damaged but were defended by the ants. All experimentally placed acacia seedlings were found by the ants on the same day I set them next to the host acacia, except for one of them that did not have ants until the third day. All these colonies were active pruners, because ants began to prune the grasses and the woody seedlings (*C. caribaea*) on the same day (8 cases) or the day following introduction of these plants (4 cases).

4. Discussion

The sprout establishment hypothesis proposes that by actively clearing vegetation around the acacia, the ants reduce plant competition, allowing the establishment of host species sprouts, which in turn benefits the ants with additional food and shelter [13]. The study findings support this hypothesis. Fonseca [19] found that nesting space was the main factor limiting colony size for *Pseudomyrmex concolor* associated with *Tachigali* trees (Fabaceae), and for seven other ant species that are obligatory mutualists of plants [20]. Food and shelter provided by *A. collinsii* are crucial for survival and colony growth of *P. spinicola* [3] and could also limit the colony growth rate or size. Relatively pure stands of acacia trees are common in the dry forest of Central America [3], and they were probably produced because of mutualistic ants killing other vegetation. In these patches, one colony (i.e., offspring of one queen) could occupy all surrounding shoots, and usually two or three colonies occupy larger patches in areas of more than 3 × 6 m [21]. Even beyond pure stands of acacia, colonies established on two neighboring plants (one much larger than the other) are frequently found. Therefore, *P. spinicola* ants sometimes expand their nest to more than one tree, suggesting that plant resources are limiting the colony size. Concordantly, I observed a higher density of acacia sprouts inside the clearings when compared with the density without clearings. Additionally, the sprouts were occupied by the same ant colony inhabiting the central acacia. However, the sprout-establishment hypothesis alone cannot fully explain this ant behavior, because the number of occupied sprouts in clearings is similar to the number of seedlings available for colonization in plants without clearings. The competition hypothesis proposed by Janzen [4], and the isolation against potential intruders, may also provide other benefits to the colony.

Selective pruning of foreign seedlings but not acacia seedlings placed inside the clearings also concurs with predictions of the sprout-establishment hypothesis. Food quantity has been shown to be a limiting factor for colony size of *Crematogaster* ants associated with *Macaranga* species [22], and Keeler [23] also found *Pseudomyrmex flavicornis* ants visiting the nectaries of *Ipomoea carnea* plants growing in contact with their host plantes and they did not sever it. *Myrmelachista* ants also selectively kill vegetation around their host tree, leaving alive saplings of the two plant species they inhabit [8]. Thus, it is likely that ants may allow other plants to grow close to their host as long as they obtain benefits from the intruder plant. For the acacia ants, Janzen [24] argued that ants would prune acacia sprouts only if they were not offering benefits to the ants, or if they were not clones from their host. However, the results from this investigation show that pruning behavior do not necessarily, or exclusively, benefit the ant's host plant, and that workers refrained from cutting acacias that were not sprouts from their host. There could be a potential conflict between the host acacia and its resident ants because the clones and seed of the host tree have to compete for the favorable conditions of the clearing with other acacia seedlings. The benefit for the ants could also be detrimental for the plants, because the aggregations of acacia sprouts may also be more vulnerable to predation (Janzen-Connell model [25, 26]), unless the defense of ants counteracts this effect. A study that follows the survival of acacia seedlings, both inside and outside clearings and solitary versus aggregated sprouts, is necessary to evaluate this potential conflict.

The ants still did not kill or prune saplings that were not providing immediate benefits, such as swollen thorns, nectarines, or food bodies, and these may be used as a bridge to get access to the host tree [11]. Potential intruder ants in the study area include workers of other colonies of *P. spinicola,* other acacia ants (*Pseudomyrmex flavicornis, Pseudomyrmex nigrocinctus,* and *Pseudomyrmex nigropilosus*), other arboreal species (*Pseudomyrmex gracilis* and *Crematogaster brevispinosa*) and predatory army ants (*Eciton burchelli parvispinum* and *Neivamyrmex pilosus mexicanus*). Even though other colonies of *Pseudomyrmex* are not predators, they represent potential threats because they use the same shelters (swollen thorns), and are attracted to both glucose-free nectar and Beltian bodies [27, 28]. Invasion of a colony by other *Pseudomyrmex* colonies is likely to occur via branches because of their arboreal habit, and, therefore, the clearings could deter these ants. In the experiments, ants did not kill acacia sprouts in contact with their plant, maybe because other *Pseudomyrmex* ants did not occupy them; hence the risk of invasions from the sprouts was low. The sprout-establishment hypothesis assumes that ants obtain delayed benefits for their pruning behavior, but this delay may be relatively short. The colony could receive the benefits of favoring acacia sprouts in the clearing very rapidly nectaries and food bodies are produced by the young acacias after 4 or 5 weeks (on their eighth or ninth leaf, Amador-Vargas unpublished data), and more rapidly from clones that develop faster because of the resources they receive from the host plant [3].

More studies that consider the reaction of resident ants to intruder plants of the host's species are necessary to understand the generality of the results found in this research (but see [14]). We still need to understand in the long-term whether clones are more successful than seedlings inside the clearings (because they are growing faster), and how the ants are able to identify and defend seedlings of the host species when they are not offering rewards.

Acknowledgments

The author thanks Frank Joyce, Gilbert Barrantes, Diane Davidson, Ulrich Mueller, Heather Ishak, José Luis Ponce de León and, especially, William Eberhard for extensive and valuable comments on previous versions of the manuscript, Frank Joyce and Rodolfo Aviles for help in the field, and Romelio Campos for taking care of the saplings in my absence. The staff of the Organization for Tropical Studies provided logistical support. This investigation would not have been possible without the financial support of the Organization for Tropical Studies, by the Don and Beverly Stone Fund and the Glaxo Fund. Research was conducted under scientific permit no. 74-2007 from the MINAE, in accordance with the laws of the Republic of Costa Rica.

References

[1] M. Heil and D. McKey, "Protective ant-plant interactions as model systems in ecological and evolutionary research," *Annual Review of Ecology, Evolution, and Systematics*, vol. 34, pp. 425–453, 2003.

[2] J. L. Bronstein, R. Alarcón, and M. Geber, "The evolution of plant-insect mutualisms," *New Phytologist*, vol. 172, no. 3, pp. 412–428, 2006.

[3] D. H. Janzen, "Coevolution of mutualism between ants and acacias in central america," *Evolution*, vol. 20, no. 3, pp. 249–275, 1966.

[4] D. H. Janzen, "Allelopathy by myrmecophytes: the ant azteca as an allelopathic agent of cecropia," *Ecology*, vol. 50, no. 1, p. 147, 1969.

[5] D. H. Janzen, "Protection of *Barteria* (Passifloraceae) by *Pachysima* ants (Pseudomyrmecinae) in a Nigerian rain forest," *Ecology*, vol. 53, no. 5, p. 885, 1972.

[6] E. W. Schupp, "Azteca protection of *Cecropia*: ant occupation benefits juvenile trees," *Oecologia*, vol. 70, no. 3, pp. 379–385, 1986.

[7] T. P. Young, C. H. Stubblefield, and L. A. Isbell, "Ants on swollen-thorn acacias: species coexistence in a simple system," *Oecologia*, vol. 109, no. 1, pp. 98–107, 1997.

[8] S. S. Renner and R. E. Ricklefs, "Herbicidal activity of domatia-inhabiting ants in patches of *Tococa guianensis* and *Clidemia heterophylla*," *Biotropica*, vol. 30, no. 2, pp. 324–327, 1998.

[9] W. Federle, U. Maschwitz, and B. Hölldobler, "Pruning of host plant neighbours as defence against enemy ant invasions: *Crematogaster* ant partners of *Macaranga* protected by "wax barriers" prune less than their congeners," *Oecologia*, vol. 132, no. 2, pp. 264–270, 2002.

[10] D. M. Larrea-Alcázar and J. A. Simonetti, "Why are there few seedlings beneath the myrmecophyte *Triplaris americana*?" *Acta Oecologica*, vol. 32, no. 1, pp. 112–118, 2007.

[11] D. W. Davidson, J. T. Longino, and R. R. Snelling, "Pruning of host plant neighbours by ants: an experimental approach," *Ecology*, vol. 69, no. 3, pp. 801–808, 1988.

[12] W. Morawetz, M. Henzl, and B. Wallnöfer, “Tree killing by herbicide producing ants for the establishment of pure *Tococa occidentalis* populations in the Peruvian Amazon,” *Biodiversity and Conservation*, vol. 1, no. 1, pp. 19–33, 1992.

[13] D. Varela, Y. Araya, Y. Di Blanco, C. Espinosa, and F. Joyce, “Formación de claros de *Acacia collinsii* por *Pseudomyrmex spinicola*,” in *Libro Curso Ecología Tropical y Conservación*, A. Farji-Brener and F. Chinchilla, Eds., pp. 197–200, OET, San José, Costa Rica, 2007.

[14] M. E. Frederickson, M. J. Greene, and D. M. Gordon, ““Devil”s gardens’ bedevilled by ants,” *Nature*, vol. 437, no. 7058, pp. 495–496, 2005.

[15] M. McSweeney and A. Porter, “Small sample properties of nonparametric index of response and rank analysis of covariance,” in *Annual meeting of the American Educational Research Association*, New York, NY, USA, 1971.

[16] W. J. Conover and R. L. Iman, “Analysis of covariance using the rank transformation,” *Biometrics*, vol. 38, no. 3, pp. 715–724, 1982.

[17] S. Maxwell, H. Delaney, and M. O’Callaghan, “Analysis of covariance,” in *Applied Analysis of Variance in Behavioral Science*, L. Edwards, Ed., pp. 63–100, CRC Press, New York, NY, USA, 1993.

[18] A. Mintzer, “Nestmate recognition and incompatibility between colonies of the acacia-ant Pseudomyrmex ferruginea,” *Behavioral Ecology and Sociobiology*, vol. 10, no. 3, pp. 165–168, 1982.

[19] C. R. Fonseca, “Nesting space limits colony size of the plant-ant *Pseudomyrmex concolor*,” *Oikos*, vol. 67, no. 3, pp. 473–482, 1993.

[20] C. R. Fonseca, “Amazonian ant-plant interactions and the nesting space limitation hypothesis,” *Journal of Tropical Ecology*, vol. 15, no. 6, pp. 807–825, 1999.

[21] D. H. Janzen, “*Pseudomyrmex ferruginea* (Hormiga del cornizuelo, acacia-ant),” in *Historia Natural de Costa Rica*, D. H. Janzen, Ed., pp. 776–778, 1991.

[22] T. Itino, T. Itioka, A. Hatada, and A. A. Hamid, “Effects of food rewards offered by ant-plant Macaranga on the colony size of ants,” *Ecological Research*, vol. 16, no. 4, pp. 775–786, 2001.

[23] K. H. Keeler, “Infidelity by acacia-ants,” *Biotropica*, vol. 13, no. 1, pp. 79–80, 1981.

[24] D. H. Janzen, “Swollen-thorn acacias of Central América/Daniel H. Janzen,” *Smithsonian Contributions to Botany*, vol. 13, pp. 1–130, 1974.

[25] D. H. Janzen, “Herbivores and the number of tree species in tropical forests,” *The American Naturalist*, vol. 104, no. 940, pp. 501–528, 1970.

[26] J. H. Connell, “On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees,” in *Dynamics of Populations*, P. J. den Boer and G. R. Gradwell, Eds., pp. 298–310, Oosterbeek: Centre for Agricultural Publishing and Documentation, Wageningen, DC, USA, 1971.

[27] M. Heil, B. Baumann, R. Krüger, and K. E. Linsenmair, “Main nutrient compounds in food bodies of Mexican Acacia ant-plants,” *Chemoecology*, vol. 14, no. 1, pp. 45–52, 2004.

[28] M. Heil, J. Rattke, and W. Boland, “Postsecretory hydrolysis of nectar sucrose and specialization in ant/plant mutualism,” *Science*, vol. 308, no. 5721, pp. 560–563, 2005.

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 183284, 10 pages
doi:10.1155/2012/183284

Research Article

Comparative Immature Morphology of Brazilian Fire Ants (Hymenoptera: Formicidae: *Solenopsis*)

Eduardo Gonçalves Paterson Fox,[1] Daniel Russ Solis,[2] Mônica Lanzoni Rossi,[3] Jacques Hubert Charles Delabie,[4] Rodrigo Fernando de Souza,[2] and Odair Correa Bueno[2]

[1] *Laboratório de Entomologia Médica, Centro de Ciências da Saúde, Federal University of Rio de Janeiro (UFRJ), 21.945-970 Ilha do Fundão, RN, Brazil*
[2] *Centro de Estudos de Insetos Sociais, Instituto de Biociências, Sao Paulo State University (UNESP), 13506-900 Rio Claro, SP, Brazil*
[3] *Laboratório de Histopatologia e Biologia Estrutural de Plantas, Centro de Energia Nuclear na Agricultura, University of São Paulo (USP), 13400-970 Piracicaba, SP, Brazil*
[4] *Laboratório de Mirmecologia, Centro de Pesquisa do Cacau, 45650-000 Itabuna, BA, Brazil*

Correspondence should be addressed to Eduardo Gonçalves Paterson Fox, ofoxofox@gmail.com

Received 18 March 2011; Accepted 29 April 2011

Academic Editor: Fernando Fernández

Although common in Brazil, the biology of the fire ant *Solenopsis saevissima* (Smith) is still poorly studied. Larval descriptions are useful to genus-level ant systematics and sometimes to species-level taxonomy. This study presents a detailed description of juveniles of *S. saevissima* from Brazil, which were compared with Brazilian specimens of *Solenopsis invicta* Buren, *Solenopsis geminata* (Fabricius), and *Solenopsis altipunctata* Pitts. Different larval instars were separated by diagnostic morphological traits which were confirmed by observing moults. Reproductive larvae could be easily sorted by their distinctive body dimensions and shape. Contrary to previous reports on this species, the larvae of *S. saevissima* proved to be generally identical to those of *S. invicta*, while a few specimens resembled those of other close species, such as *Solenopsis megergates* Trager. Mature larvae thus presented considerable intraspecific variation in some characters recently proposed to aid fire ant species separation (morphology of head hairs).

1. Introduction

The importance of immature morphology to insect systematics and taxonomy was extensively discussed in previous studies [1–3]. The present investigation is part of a series of studies on ant larvae which attempt to remedy the limitations in the available morphological information on immature ant morphology.

Solenopsis (Hymenoptera: Formicidae) is a cosmopolitan ant genus that includes approximately 300 species, of which over 108 occur in the New World [4]. Some of the largest species are aggressive, polymorphic ants commonly known as "fire ants" that are usually harmful in both their native and invasive geographical ranges. The *Solenopsis saevissima* species group (sensu [5]) includes some 13 species of fire ants which are markedly difficult to identify because of the plasticity of morphological characters, and because of their strong polymorphism. In an attempt to propose a phylogenetic hypothesis for species within the complex, Pitts et al. [5] revisited the morphological characters as originally proposed by Trager [6] and added new ones, including the use of head setae of last-instar larvae. Of the fire ant species analysed in his study, there are published larval descriptions only for *S. invicta* and *S. geminata* [7–9].

The fire ant *Solenopsis saevissima* Smith is widespread and common in Brazil, however still remains a generally poorly studied species. Their larvae are undescribed. Recently, a broad genetic study [10] demonstrated that it comprises a number of cryptic species along the Brazilian coast. This prompted the question of whether or not larvae of geographically distant populations of *S. saevissima* would be morphologically identical. The goal of the present study was to describe each immature stage of *S. saevissima* obtained from three distant localities, as well as to compare these larvae with specimens of *Solenopsis invicta* Buren, *Solenopsis geminata* (Fabricius), and *Solenopsis altipunctata* Pitts from Brazil.

2. Material and Methods

2.1. Collection of Samples. Whole nests of *S. saevissima* were obtained from three different localities in Brazil: (1) Pouso Alegre, Minas Gerais (MG) (22 13 S, 45 56 W), (2) Pedro do Rio, Rio de Janeiro (RJ) (22 20 S, 43 7 W), and (3) Ilhéus, Bahia (BA) (14 15 S, 39 13 W). In addition, whole nests of *S. geminata* were obtained at site (3); *S. invicta* was obtained from Rio Claro, São Paulo (SP) (22 23 S, 47 32 W) and at site (2); and *S. altipunctata* was obtained at site (2). Species identification was based on Trager [6] and Pitts et al. [5]; only "typical" morphs were used, that is, those clearly presenting the following set of characters. *Solenopsis saevissima*: a poorly developed central clypeal tooth, lack of a medial frontal streak, and absence of a frontal ocellus; *S. geminata*: all mentioned characters plus major workers with characteristically cordate enlarged heads, lacking the central clypeal tooth, and bearing shorter scapes and blunt mandibles; *S. invicta*: well-developed clypeal tooth and carinae, evident medial frontal streak, and absence of a frontal ocellus; *S. altipunctata*: similar to *S. invicta*, but with central clypeal tooth poorly developed, medial frontal streak feeble, and anterior wings of queens with medial cell open.

DNA was extracted and mtDNA sequencing followed the same methods described by Ross et al. [10], confirming species identifications. Species identification was corroborated using chemical characters (venom alkaloids and cuticular hydrocarbons) as described in a separate publication.

Voucher specimens of all immature and adult stages of the collected nests were deposited in the entomological collections of Instituto Biológico and Museu de Zoologia (MZUSP), SP, Brazil.

2.2. Determination of Larval Instars. The first instar and the last instar can be directly identified as hatching larvae and prepupae, and thus be used as reference to determine others. Other distinct instar characteristics used were based on Petralia and Vinson [9]. Larval instar characteristics were further validated during the descriptions from observing moulting larvae.

2.3. Differentiation of Larvae from Different Castes. Worker larvae only differed when mature in bodily dimensions, thus a size interval is given. Gyne and male larvae were considerably larger than worker larvae and presented typical body shapes of their own. These were directly confirmed as they moulted into male or female alate pupae.

2.4. Description of the Immature Forms. All collected samples were fixed in Dietrich's solution (900 mL distilled water, 450 mL 95% ethanol, 150 mL 40% formaldehyde, 30 mL acetic acid) for 24 h, and then preserved in 70% alcohol. Samples to be analysed under the scanning electron microscope were dehydrated in an alcohol graded series (80–100%; a 10-min-dip for each concentration), and critical-point dried (Balzers CPD/030). Dried specimens were then attached to aluminium stubs with double-faced conductive adhesive tape and gold-sputtered with a Balzers SCD/050 sputterer. Observations and images were obtained as soon as possible after sample preparation. Samples to be analysed under the compound microscope were warmed for 15 min in KOH 10% and placed in a small drop of glycerin on a microscope slide.

The morphological descriptions were based on over 10 larvae of each instar. The larvae were analyzed and described under a compound light microscope (Zeiss MC80 DX, with maximum magnification of 1000x), and illustrations were obtained with a scanning electron microscope (LEO 435 VP, at 20.0 kV). With a stereomicroscope (Zeiss Stemi SV11, with maximum magnification of 66x) equipped with a micrometric eyepiece, we obtained measures of every stage. All terminology used herein follows G. C. Wheeler and J. Wheeler [2], and measures are given either as approximate measures, size intervals, or mean ± SD followed by the number (n) of individuals analyzed, depending on sample size. Further specimens were later mounted on glass slides to rapidly check for intraspecific variations.

2.5. Comparison with Other Samples. Last instar larvae of the following species were also rapidly analyzed for intraspecific variations: *S. invicta* from SP and RJ, *S. altipunctata* from RJ, and *S. geminata* from BA.

3. Results

3.1. Identification of Cryptic Species within S. saevissima. Mitochondrial DNA sequences were compared with accessions from the National Center for Biotechnology Information (NCBI/GenBank). Two of the three samples of *S. saevissima* could be amplified—BA and RJ—no sequences were recovered from MG. Their haplotypes were, respectively, W11 and W51, thus belonging to two different cryptic populations (refer to NCBI for further details on the haplotypes), and displayed different sets of cuticular hydrocarbons (not shown). Larvae of the different populations of *S. saevissima* proved identical, and are jointly described below.

3.2. Immature Morphology of Solenopsis saevissima (Smith, 1855)

3.2.1. Egg (Figure 1(a)). Widely ovoid in shape, about 0.18 mm × 0.25 mm, with whitish embryo showing through the transparent chorion. No outer ornamentation or orifices (Figure 1(a)). Eclosion by medial transverse rupture (Figure 1(b)), when first-instar larva outgrows chorion.

3.2.2. First Larval Instar (Figures 1(c)–1(f)). Body profile attoid, defined in [2] as: very short, stout, and curved, with segmentation indistinct; "diameter approximately equal to distance from labium to anus; anus being terminal."

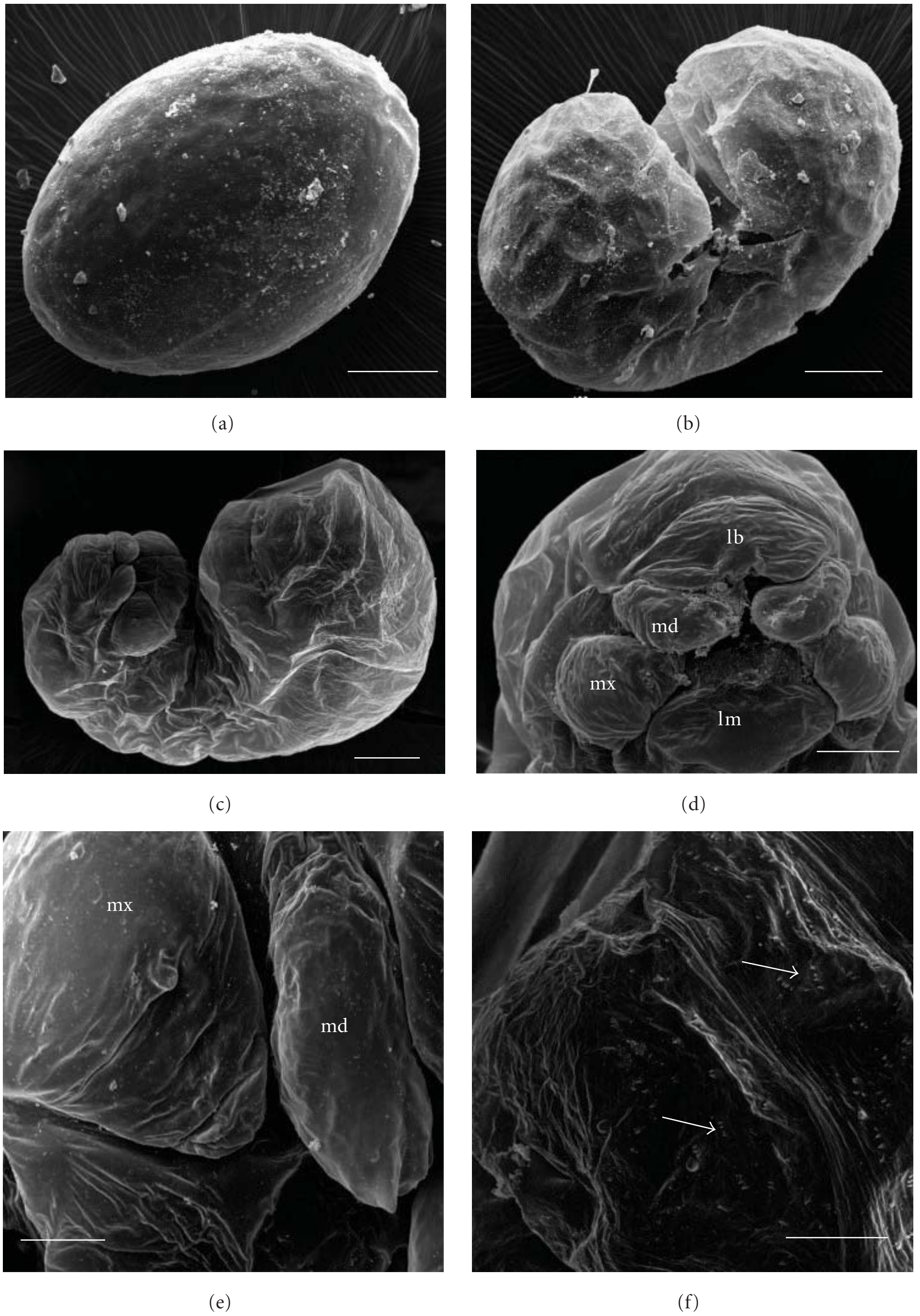


Figure 1: Egg and first instar larva of *Solenopsis saevissima*. (a) Egg. (b) Hatching larva. (c) Oblique view of first instar larva; inset: thoracic spiracle. (d) Head capsule and mouthparts; lb: labrum; md: mandible; mx: maxilla; lm: labium. (e) Detail of mouthparts, showing right maxilla and mandible. (f) Terminal region of body, showing anus (asterisk) and rows of spinules (setae). Respective sizes of scale bars (μm): 50, 25, 50, 20, 10, and 15.

Body about 0.290–0.340 mm long × 0.140–0.160 mm wide ($n = 5$); body length through spiracles 0.520 mm ($n = 1$) (Figure 1(c)). Ten inconspicuous pairs of spiracles, first one larger in diameter (0.002 mm) than others (0.001 mm). Integument surface smooth, without setation (Figure 1(c)), however with short spines over posterior abdominal region and around anus (Figure 1(f)). Head capsule subelliptical, 0.120–0.140 mm wide ($n = 5$), without setation or sensilla (Figure 1(d)). Clypeus and labrum fused to a single semicircular structure (0.035 mm wide) (Figure 1(d)); mandibles round and transparent, with two short apical teeth, about 0.025 mm long and 0.018 mm wide ($n = 2$; Figure 1(e)). Maxillae lobose about 0.020 mm long and 0.020 mm wide ($n = 1$); maxillary palps and galea indistinct (Figure 1(e)).

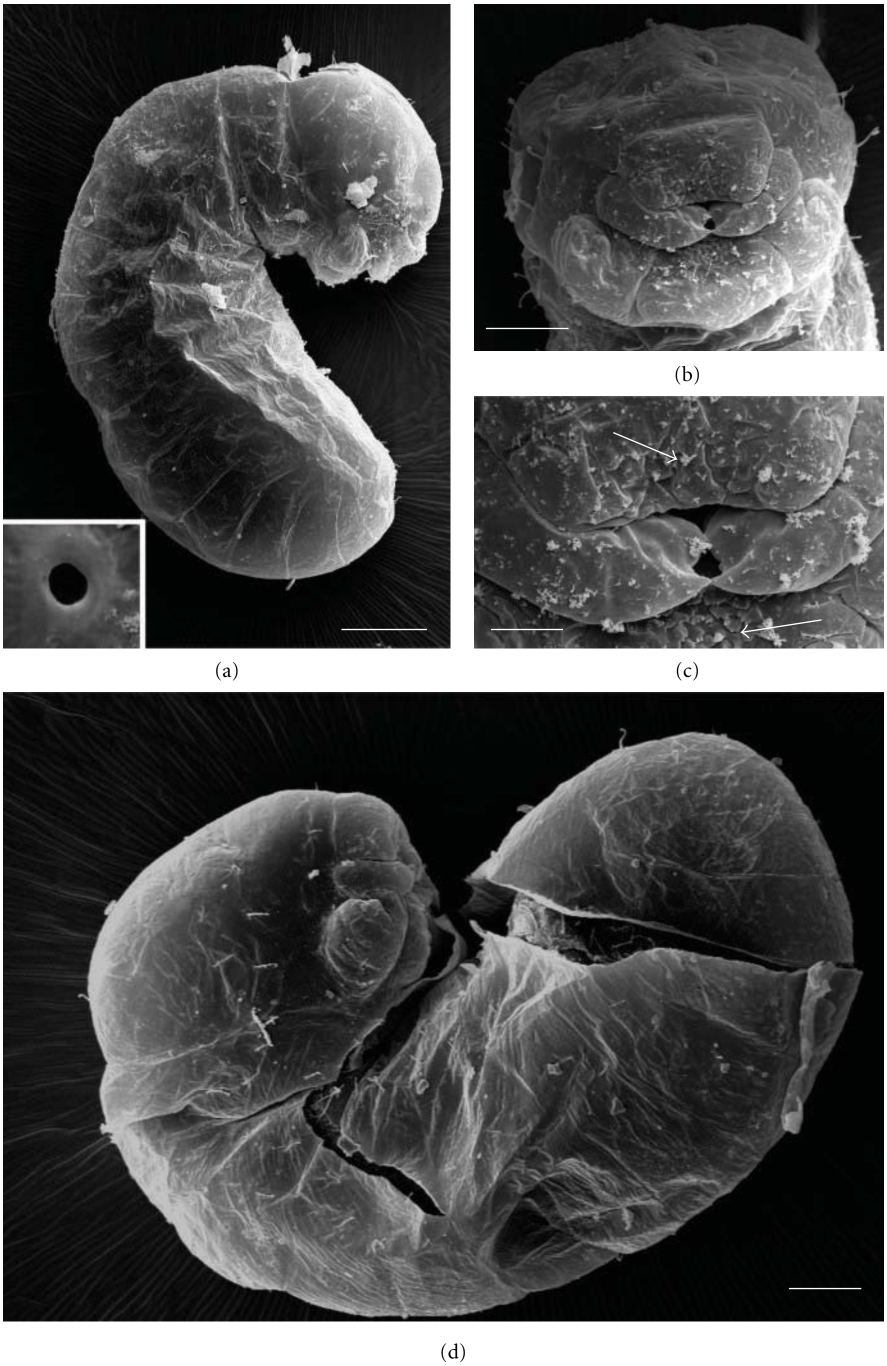
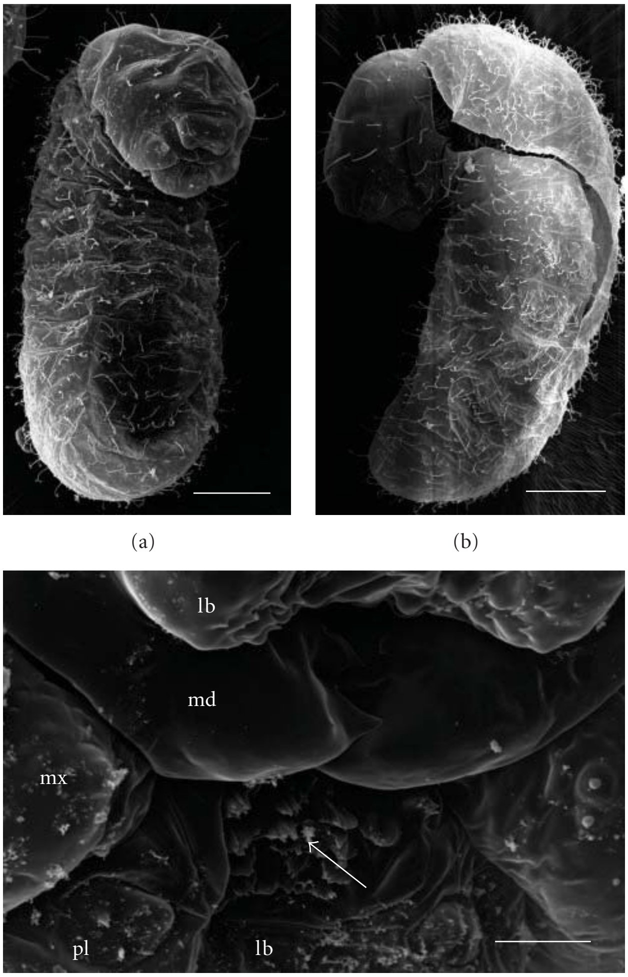


Figure 2: Second instar larva of *Solenopsis saevissima*. (a) Larva on side view; inset: thoracic spiracle. (b) Head capsule. (c) Mouthparts; arrows: spines around mouth entrance. (d) Larva moulting to third instar. Respective sizes of scale bars (μm): 100, 40, 15, and 50.

Labium ovoid, about 0.030 mm wide ($n = 3$) (Figure 1(d)); labial palps indistinguishable.

3.2.3. Second Larval Instar (Figures 2(a)–2(d)). Body profile attoid, greatly curved, with anus terminal; 0.480 ± 0.010 mm long and 0.230 ± 0.010 mm wide at widest somites ($n = 9$); body length through spiracles 0.640 mm ($n = 1$) (Figure 2(a)). Body hairs scarce and always simple, 0.026–0.030 mm long ($n = 47$), concentrated on the dorsal area of the first thoracic somite and over the terminal region of the body (not shown). Ten pairs of unornamented spiracles (inset in Figure 2(a)), first one slightly larger (0.010 mm) than the rest (0.006 mm) ($n = 7$). Head capsule subelliptical, 0.150–0.180 mm wide ($n = 9$; Figure 2(b)). Head hairs distributed as follows: between six and eight over the occipital border, two or three on vertex, and five on each gena. Antennae difficult to spot and bearing three basiconic sensilla (not shown). Mouthparts: Clypeus fused



(a) (b)

(c)

Figure 3: Third instar larva of *Solenopsis saevissima*. (a) Larva in frontal view. (b) Larva moulting to fourth instar. (c) Mouthparts; lb: labrum; md: mandible; mx: maxilla; lm: labium; arrow: spiny papillae at mouth entrance; asterisk: galea. Respective sizes of scale bars (μm): 100, 100, and 10.

with labrum into a single short trapezoidal structure about 0.080 mm wide and 0.090 mm long ($n = 2$), with a row of four simple hairs (Figures 2(b) and 2(d)); spiny papillae on dorsal surface near mouth entrance (Figure 2(c)). Maxillae lobose and 0.049 mm long and 0.050 mm wide ($n = 2$), with one simple hair at base (not shown). Mandibles unpigmented and roughly camponotus in shape, yet with pronounced apical tooth and one small subapical tooth; about 0.05 mm long and 0.033 mm wide at base ($n = 5$; Figure 2(c)). Labium a 0.06 mm-wide sphere, no visible palps or spinneret (not shown); densely spinulose near mouth entrance (Figure 2(c)). Moult occurs by apparently random rupture of tegument skin (Figure 2(d)).

3.2.4. Third Larval Instar (Figures 3(a)–3(c)). Body profile roughly dolichoderus, defined in [2] as "short, stout, plump (...) with both ends broadly rounded; anterior end formed by enlarged dorsum of prothorax; head ventral, near anterior end; no neck; somites indistinct." About 1.220 mm ± 0.010 mm long and 0.480 mm ± 0.010 mm wide ($n = 172$); length through spiracles about 1.300 mm ($n = 2$) (Figures 3(a) and 3(b)). Body hairs uniformly distributed and of three types: deeply bifid (0.020–0.03 mm long), bifid (0.030 mm long), and simple, with curved hook-like tips (0.010–0.050 mm long) (Figures 3(a) and 3(b)). Simple hairs predominant, except for ventral region of anterior somites ("food basket" area), which is naked and without spinules (not shown). Bifid hairs also found over most of body surface, but predominant on posterior body region. Ten pairs of spiracles, with the first slightly larger (0.100 mm) than the rest (0.070 mm) ($n = 26$). Head capsule 0.280 ± 0.010 mm wide ($n = 172$); subelliptical and presenting three types of hairs: simple with tip hooked (0.040 mm long), smooth and simple (0.007 mm long), and bifid (0.015–0.020 mm long) (not shown). Head hairs distributed as follows: six or seven hairs on occipital border, some (up to 1–3) bifurcated in some specimens, five hook-tipped simple hairs, and three or four bifid hairs on the vertex (some specimens had only simple hook-tipped hairs), two or three hook-tipped hairs on frons, five to eight simple hairs on each gena (bifid in some specimens, while one had one 3-branched hair). Antennae slight elevations with three basiconic sensilla (not shown). A conspicuous pair of enclosed sensilla on base of each mandible. Mouthparts (Figure 3(b)): clypeus and labrum fused into a single trapezoidal structure 0.087 mm wide ($n = 6$), slightly depressed mesad with a row of four simple hairs; four to six setaceous sensilla on anterior face of labrum, and six to seven basiconic sensilla on posterior face of labrum (not shown), the latter densely endowed with spinulose papillae (Figure 3(c)). Maxillae paraboloidal, about 0.050 mm long and 0.037 mm wide, with a hook-tipped hair near the base (some specimens with one additional short simple hair) and two setaceous sensilla; maxillary palpus a simple elevation with four basiconic sensilla, and galea represented by a pair of basiconic sensilla (Figure 3(c)). Mandibles poorly sclerotized, about 0.057 mm long and 0.037 mm wide at base (Figure 3(c)). Labium elliptical, about 0.1 mm wide, with one or two setaceous sensilla on the surface below the opening of the sericteries—not shown, an horizontal slit about 0.040 mm—and a conspicuous cluster of spiny papillae towards mouth entrance (Figure 3(c)).

3.2.5. Fourth Larval Instar of Worker (Figures 4(a)–4(d)). Body profile pheidole, defined in [2] as with "abdomen short, stout, and straight; head ventral near anterior end, mounted on short stout neck, which is the prothorax; ends rounded, one end more so than the other." Larvae varying from 1.350 to 2.850 mm long ($n = 77$) and 0.580 to 1.30 mm wide ($n = 77$) (Figure 4(a)). Dimensions of spiracle peritremes and mandibles of larvae of different sizes always about the same ($n = 20$ specimens of different sizes). All measurements given below were taken from a 3.00-mm-long worker larva, unless stated otherwise. Body length through spiracles 0.630–4.220 mm ($n = 7$ larvae of different sizes). Body hairs uniformly distributed, of three types: deeply

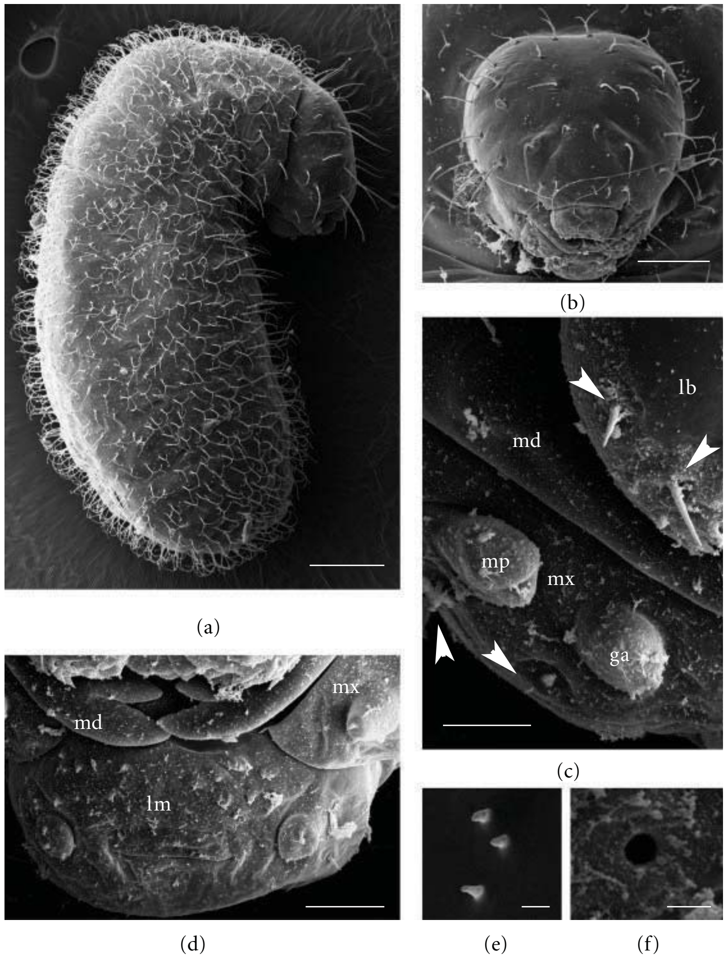
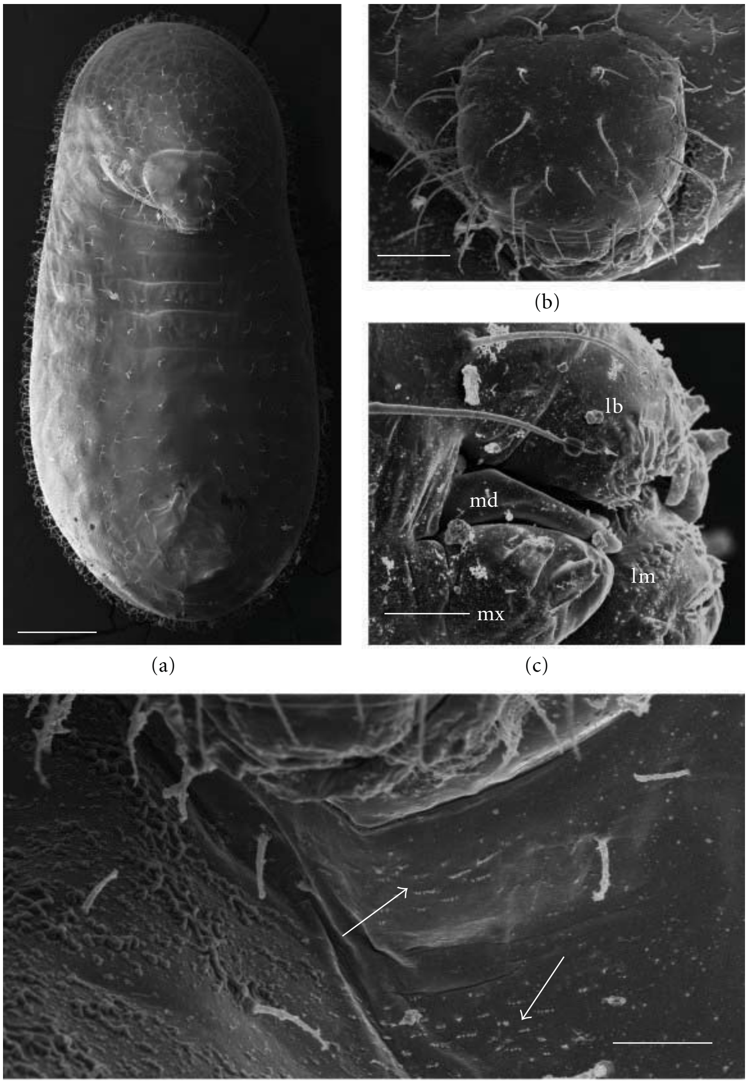


Figure 4: Fourth instar larva of *Solenopsis saevissima* worker. (a) Larva in side view. (b) Head capsule in full frontal view. (c) Frontal view of right mouthparts; lb: labrum; mx: maxilla; md: mandible; mp: maxillary palp; ga: galea; arrowheads: setaceous sensilla. (d) Lower mouthparts; md: mandibule; mx: maxilla; lm: labium. (e) Antennal sensilla (setaceous). (f) thoracic spiracle. Respective sizes of scale bars (μm): 200, 100, 10, 15, 5, and 3.

bifid (0.075 mm), bifid (0.700 mm), and simple (0.055 mm). Simple hairs predominate on ventral region of anterior somites, while bifid hairs predominate over the rest of the body (Figure 4(a)). "Food basket" area usually naked and without spines, except in larger specimens (not shown). Ten pairs of unornamented spiracles (Figure 4(f)), the first slightly larger (0.016 mm) than others (0.014 mm), and last pair smallest (0.100 mm). Head capsule 0.370 ± 0.020 mm wide ($n = 13$); subelliptical and with 20–30 hairs of two types: simple (0.100–0.120 mm) and bifid (0.570 mm), distributed as follows: seven or eight (rarely nine) hairs on occipital border, usually bifid (central hairs sometimes simple, see Figure 8), two or three hairs on each side of vertex (one usually bifid), two to four simple hairs on frons, five to seven simple hairs on each gena (Figure 4(b)). Antennae with three 1 μm-long setaceous (often basiconic) sensilla (Figure 4(e)). A pair of enclosed sensilla near base of mandibles (not shown). Clypeus poorly delimited from cranium and rectangular, with a row of four simple hairs at midheight (Figure 4(b)). Mouthparts: Labrum clearly delimited and roughly rectangular, slightly depressed mesad, 0.100–0.126 mm wide, with six basiconic sensilla and seven to eight setaceous sensilla on anterior face, ventral surface densely covered with rounded, spiny papillae (not shown). Maxilla roughly parabolic in shape, about 0.085 mm long and 0.047 mm wide, with two setaceous sensilla near base of palps (Figure 4(c)). Galea paxiliform and 0.015 mm long, and maxillary palpus digitiform and 0.22 mm long, the first tipped with two setaceous sensilla and the latter with four sensilla, two basiconic, one setaceous, and one enclosed (Figures 4(c) and 4(d)). Mandibles ectatommoid in shape, heavily sclerotized, and stout (0.100 mm long and 0.037 mm wide) with two apical teeth (Figure 4(d)) and two prominent subapical teeth followed by a long blade with two or three molar denticles (not shown). Labium rounded, about 0.8 mm wide; labial palps being simple elevations about 0.012 mm wide with four basiconic sensilla and one setaceous sensillum on top; labial surface below palps with two or three basiconic sensilla and one or two setaceous sensilla at varied positions; labial surface above the palps



(a) (b) (c) (d)

Figure 5: Last instar larva of *Solenopsis saevissima* gyne. (a) Body in frontal view. (b) Head capsule in full frontal view. (c) Mouthparts in oblique view; lb: labrum; md: mandibule; mx: maxilla; lm: labium. (d) Food basket area, asterisk: lower mouthparts; arrows: rows of spinules. Respective sizes of scale bars (μm): 400, 100, 50, and 50.

endowed with sparse spines directed to the mouth entrance (Figure 4(d)). Opening of sericteries a horizontal slit about 0.035 mm long with an inconspicuous, enclosed sensillum by the end of each extremity (Figure 4(d)).

3.2.6. Reproductive Larvae (Figures 5 and 6). The reproductive larvae differed from worker larvae only in the last instar by their greater size and unique shape (compare Figures 4(a), 5(a), and 6(a)). Mature larvae (prepupae) of males measured 3.80–4.50 mm ($n = 12$), with greatly engorged thoraxes (Figure 6(a)), and a whitish hue because of the development of a thicker integument (not shown). Mature larvae of gynes are longer (4.80–6.20 mm long) ($n = 7$) and swollen (Figure 5(a)). Also, greater body size results in a decrease in density of body hairs, thus reproductive larvae look distinctly less hairy than worker larvae.

A few morphological particularities were noted, probably deriving from their further increase in size, as described below.

3.2.7. Gyne Larvae (Figures 5(a)–5(d)). Antennal sensillae always setaceous, longer (not shown). Tentorial pits clearly discernible on cranium (Figure 5(b)). Labial surface under mouth entrance and posterior face of labrum densely spinulose (Figure 5(c)). Food basket area with rows of short spines (Figure 5(d)).

3.2.8. Male Larvae (Figures 6(a)–6(f)). First thoracic spiracle much larger than the remaining ones (inset of Figure 6(a)), peritreme opening with valve-like projections. Antennal sensillae always setaceous, longer; well-developed tentorial pits (Figures 6(b) and 6(d)). Maxillary palps slightly longer

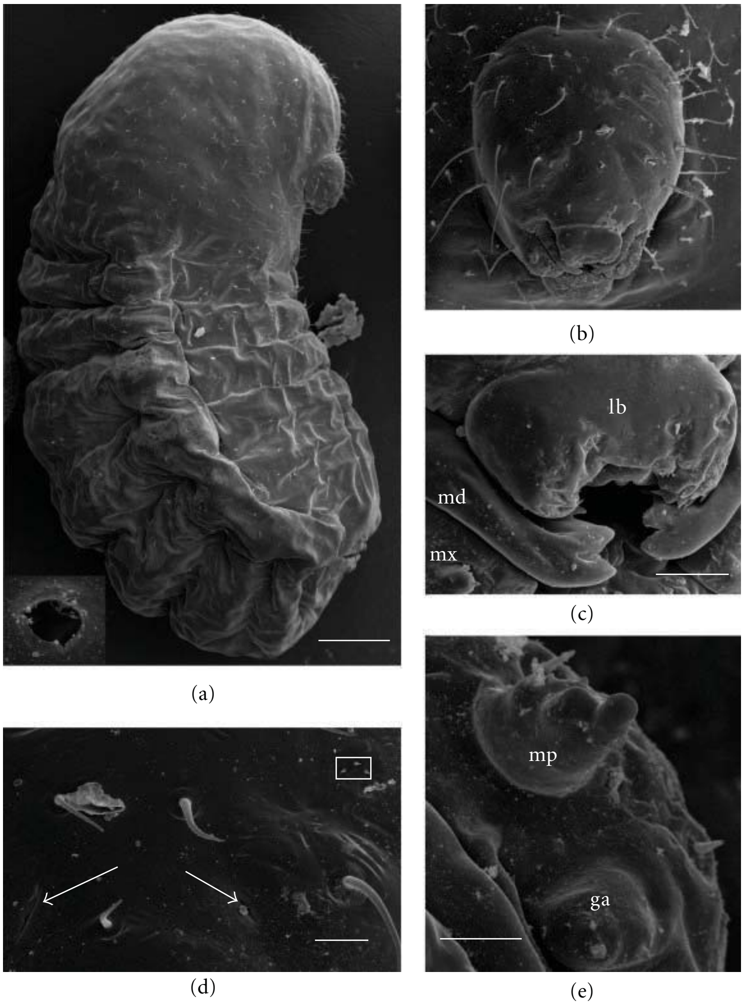


Figure 6: Last instar larva of male of *Solenopsis saevissima*. (a) Body in side view. (b) Head capsule in full frontal view. (c) Mouthparts in oblique view; lb: labrum; mx: maxilla; md: mandible. (d) Detail on frons of head capsule; arrows: tentorial pits; white box: left antenna. (e) Detail on right maxilla, showing maxillary palp (mp) and galea (ga). Respective sizes of scale bars (μm): 400, 100, 20, 30, and 10.

and paxilliform, due to the presence of a well-developed, enclosed apical sensillum (Figures 6(c) and 6(e)). Similarly, galea with a distinct shape due to enlarged apical sensilla (Figure 6(e)).

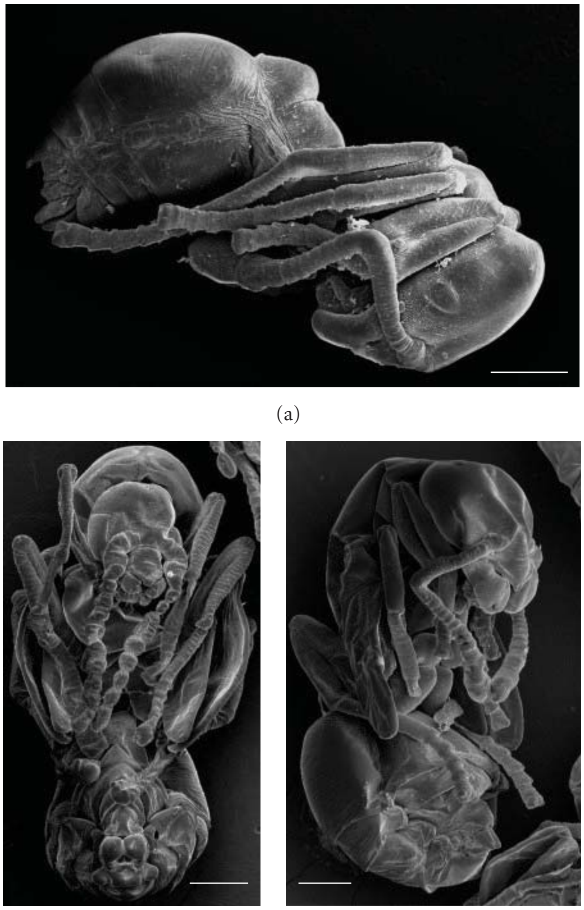
3.2.9. Pupae (Figures 7(a)–7(c)). Young pupae yellowish white, colour darkening with age as they mature into imagoes. Always exarate and without cocoons, yet pupal skin clearly discernible detached from the developing exoskeleton, particularly upon petiole (Figure 7(a)). Worker pupae (Figure 7(a)) varied 2.00–4.00 mm long ($n = 29$), while male pupae (Figure 7(b)) averaged 4.20 mm ($n = 4$), and gyne pupae (Figure 7(c)) measured 5.30–5.50 mm long ($n = 6$).

3.3. Comparisons with Other Species. From comparing numerous last instar larvae of *S. saevissima* with *S. invicta* and *S. altipunctata*, we were unable to pinpoint specific character states that could be used to differentiate between these species—that is, they are identical. All presented marked intraspecific variation in the morphology of head setae (i.e., "hairs" according with the terminology of the Wheelers), in which occipital and even vertexal hairs can be either simple, bifid, or at times 3-branched. Variations occurred among specimens from within the same nests and geographical locations. It is worth noting that a few specimens of *S. saevissima* and *S. invicta* had all head hairs simple, which is reminiscent of other species (read further notes in discussion).

Head hairs of specimens of *S. geminata* proved less variable than in other species, with occipital hairs usually bifid, sometimes 3-branched at random positions. Other characteristics were as described for *S. saevissima*.

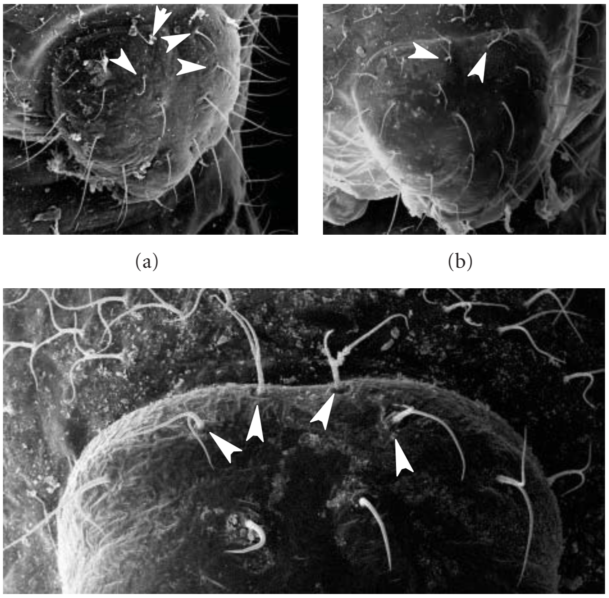
4. Discussion

This is the first description of juvenile stages in *S. saevissima*, and the first larval description of a fire ant to include specimens of different castes and geographical locations.


(a)

(b) (c)

Figure 7: Pupae of major worker (a), male (b), and gyne (c) of *Solenopsis saevissima*. Respective sizes of scale bars (μm): 300, 500, and 500.


(a) (b)

(c)

Figure 8: Head hairs (= setae) of fourth instar larvae from different fire ant species. Medial hairs of second row of vertex and occipital region are indicated with arrowheads. (a) *Solenopsis saevissima* with medial hairs simple (compare with Figures 4(b), 5(b), and 6(b), in which specimens had bifid hairs). (b) *Solenopsis invicta* with bifid hairs. (c) *Solenopsis geminata* with bifid hairs. Respective sizes of scale bars (μm): 80, 100, and 30.

Younger first- and second-instar larvae were always found in low frequencies in the collected nests, suggesting that they may last only for a few hours before moulting, or may reside in part of the nest not typically collected. This can only be determined by direct experimentation and observation of the duration of each larval instar.

The extensive similarities between reproductive and worker larvae were previously noted by G. C. Wheeler and J. Wheeler [2]. These authors reported only being able to distinguish reproductive from worker ant larvae using the last instar, as by this stage reproductive larvae are considerably larger. The distinct body shape acquired by the sexual larvae of males and gynes of *S. saevissima* makes sexual separation usually quite easy. It is certainly caused by the inner developing pupa. The greatly enlarged thoracic spiracle of male prepupae is probably related to intense metabolism in that somite (e.g., development of flight muscles?). This and the alterations in the integument of male larvae merit direct investigation.

The larval instars of *S. invicta* were previously described by O'Neil and Markin [8], who also presented descriptions of larvae of all castes, yet a later study by Petralia and Vinson [9] added SEM images of all juvenile stages along with detailed descriptions, correcting several flaws in the original description by O'Neil and Markin [8]. Moreover, O'Neil and Markin [8] claimed that head widths of larvae of different castes were significantly different, but our observations do not support this assertion. In fact, it is clear from our results that Dyar's rule should be applicable for instar separation in fire ants using not only head width, but also mandible length and spiracle diameter, despite the pronounced worker polymorphism. Direct demonstration of this fact is warranted.

In a recent revision of morphological characters and phylogenetic relationships within fire ants, Pitts et al. [5] proposed the use of different sets of character states of the head setae (= hairs) of fourth instar larvae to facilitate species separation. Proposed head hairs to be used were those above the antennal level, individualized in the "first and second rows on vertex" and the "occipital row." The series of larval characters described by Pitts et al. [5] indicates that 4th-instar larvae of *S. invicta* would differ from those of *S. saevissima* and *S. geminata* in the morphology of the medial head hairs of the occipital region: in *S. geminata* and *S. saevissima* such hairs would always be bifid, yet larvae of *S. invicta* would vary in having simple or bifid hairs (for further details, see Pitts et al. [5]). These three species can alternatively be easily recognized based on other traits of major workers. In *S. altipunctata*, mature larvae would have the occipital row with inner hairs always bifid, with others simple; adult forms are, however, difficult to separate from *S. invicta* and *S. saevissima* without examining the queens.

However, in the present investigation we found considerable variation in the pattern of head hairs of mature larvae of *S. saevissima* from different nests from Rio de Janeiro, Minas Gerais and Bahia. As noted, some specimens even had all medial head hairs above antennal level simple, which should be diagnostic of *Solenopsis richteri* Forel [5]. By relying on the larval characters proposed by Pitts et al. [5], one would have mistaken the specimen of Figure 7(a) for *Solenopsis megergates*, many others for *S. invicta*, and a few for *S. richteri*. Our observations, thus, confirm the larval characters proposed by Pitts et al. [5] for *S. invicta* and *S. geminata*, but demonstrate that larvae of *S. saevissima* cannot be differentiated from other species because of extensive intraspecific (even intranest) variation. Also, similar intraspecific variation was observed with larvae of *S. altipunctata*. Similar marked intraspecific variation was also recently observed in larvae of *Paratrechina longicornis* Latreille [11], thus the phenomenon is most likely universal (among ants?).

As mentioned, subsequent to the study of Pitts et al. [5], Ross et al. [10] demonstrated the existence of cryptic species within *S. saevissima.* It should be noted that there is considerable molecular evidence that some of the other fire ant species might also include cryptic species [12]. It should be stressed that the present study was based on at least two different haplotypes of *S. saevissima* (samples from MG were not sequenced) and considerable intraspecific variation in this character state was detected in all of them, thus the morphology of head hairs is definitely not a reliable character for sorting between fire ant species given the present state of knowledge. We suspect that the samples examined by Pitts et al. [5] included only a few larvae of each species (the exact number of observations was not given), thus leading to biased conclusions.

In summary, the present description adds to the limited body of knowledge about juvenile stages of ants. Some of the observed traits found may have taxonomic importance (best suited for genus-level comparison), and probably reflect specializations in the life history of the group. We would not recommend the use of fire ant larvae for species identification in South America given the present state of knowledge, as one of the most common fire ant species, *S. saevissima*, exhibits considerable intraspecific variation that overlaps with other species, and there is significant evidence that this is also the case in closely related species.

Acknowledgments

The authors would like to thank Elliot Watanabe Kitajima and Francisco André Ossamu Tanaka (NAP/MEPA/ESALQ/USP) for granting access to the electron microscopes, and Andrigo Monroe, Sandra Frances Fox Lloyd, and Maria Helena dos Santos for assistance in the field in locating fire ant nests. Dietrich Gotzek provided useful tips in the molecular identification of specimens and discussion insights. Several anonymous reviewers contributed useful critiques; Scott E. Solomon kindly polished the narrative in the final version of the manuscript.

References

[1] T. Finlayson, "A classification of the subfamily Pimplinae (Hymenoptera: Ichneumonidae) based on final-instar larval characteristics," *The Canadian Entomologist*, vol. 99, pp. 1–8, 1975.

[2] G. C. Wheeler and J. Wheeler, "Ant larvae: review and synthesis," *Memories of the Entomological Society of Washington*, vol. 7, pp. 1–108, 1976.

[3] T. R. Schultz and R. Meier, "A phylogenetic analysis of the fungus-growing ants (Hymenoptera: Formicidae: Attini) based on morphological characters of the larvae," *Systematic Entomology*, vol. 20, pp. 337–370, 1995.

[4] B. Bolton, G. Alpert, P. S. Ward, and P. Naskrecki, *Bolton Catalogue of Ants of the World: 1758–2005*, Harvard University Press, Cambridge, Mass, USA, 2006.

[5] J. P. Pitts, M. C. J. Hugh, and K. G. Ross, "Cladistic analysis of the fire ants of the Solenopsis saevissima species-group (Hymenoptera: Formicidae)," *Zoologica Scripta*, vol. 34, no. 5, pp. 493–505, 2005.

[6] J. C. Trager, "A revision of the fire ants of the Solenopsis geminata group (Hymenoptera: Formicidae: Myrmicinae)," *Journal of the New York Entomological Society*, vol. 99, pp. 141–198, 1991.

[7] G. C. Wheeler and J. Wheeler, "The ant larvae of the myrmicine tribe Solenopsidini," *The American Midland Naturalist*, vol. 54, pp. 119–141, 1955.

[8] J. O'Neal and G. P. Markin, "The larval instars of the imported fire ant Solenopsis invicta (Hymenoptera: Formicidae)," *Journal of the Kansas Entomological Society*, vol. 48, pp. 141–151, 1975.

[9] R. S. Petralia and S. B. Vinson, "Developmental morphology of larvae and eggs of the imported fire ant, *Solenopsis invicta*," *Annals of the Entomological Society of America*, vol. 72, pp. 472–484, 1979.

[10] K. G. Ross, D. Gotzek, M. S. Ascunce, and D. D. Shoemaker, "Species delimitation: a case study in a problematic ant taxon," *Systematic Biology*, vol. 59, no. 2, pp. 162–184, 2010.

[11] E. G. P. Fox, D. R. Solis, C. M. Jesus, O. C. Bueno, A. T. Yabuki, and M. L. Rossi, "On the immature stages of the crazy ant *Paratrechina longicornis* (Latreille 1802) (Hymenoptera: Formicidae)," *Zootaxa*, no. 1503, pp. 1–11, 2007.

[12] K. G. Ross, M. J. B. Krieger, L. Keller, and D. D. Shoemaker, "Genetic variation and structure in native populations of the fire ant Solenopsis invicta: evolutionary and demographic implications," *Biological Journal of the Linnean Society*, vol. 92, no. 3, pp. 541–560, 2007.

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 145743, 5 pages
doi:10.1155/2012/145743

Research Article

First Record of *Lenomyrmex inusitatus* (Formicidae: Myrmicinae) in Ecuador and Description of the Queen

T. Delsinne[1] **and F. Fernández**[2]

[1] *Biological Evaluation Section, Royal Belgian Institute of Natural Sciences, 29 rue Vautier, 1000 Brussels, Belgium*
[2] *Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Apartado 7495, Bogotá D.C., Colombia*

Correspondence should be addressed to T. Delsinne, thibaut.delsinne@sciencesnaturelles.be

Received 12 March 2011; Accepted 20 April 2011

Academic Editor: Jacques H. C. Delabie

The rarely collected ant *Lenomyrmex inusitatus* Fernández 2001 is recorded for the first time in Ecuador. The queen is described. The new record is the southernmost limit of distribution for the genus. A key to the workers of the six *Lenomyrmex* species and a key for the known queens are provided.

1. Introduction

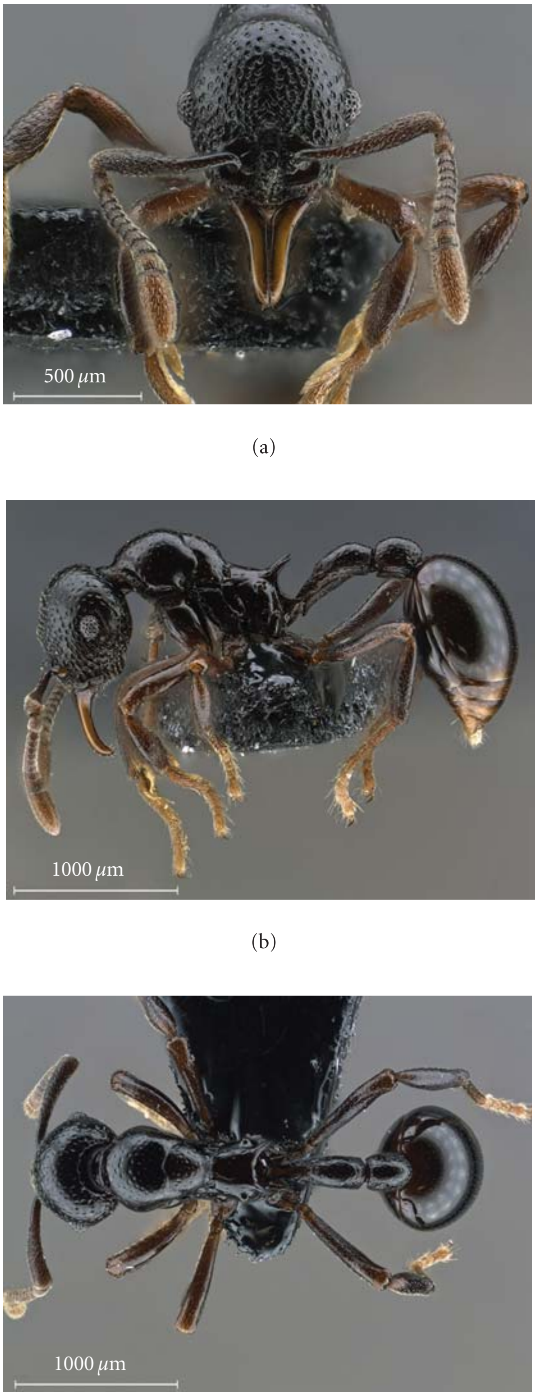
The myrmicine ant genus *Lenomyrmex* Fernández and Palacio 1999 includes six species rarely collected from Costa Rica to Ecuador [1–3]. The genus is characterised by elongate mandibles bearing a series of minute peg-like denticles that arise behind the masticatory margin, by frontal lobes that are poorly expanded laterally, by large and deep antennal fossae, and by pedunculate petiole, with a poorly defined node [1]. The fact that *Lenomyrmex* possesses both primitive (e.g., promesonotal suture well developed) and derived (e.g., specialized morphology of the mandibles) characters makes ascertaining its correct phylogenetic position challenging [1, 2, 4]. The genus was tentatively placed in its own tribe, Lenomyrmecini [5], but its position within the Myrmicinae remains to be determined [5]. Preliminary results of a phylogenetic analysis (Ant-AToL project, http://www.antweb.org/atol.jsp) indicate that *Lenomyrmex* falls within a clade of predominantly New World ants that includes the tribes Attini, Cephalotini, Dacetini, and the genus *Pheidole* (T. Schultz and P. Ward, comm. pers.).

The worker of *Lenomyrmex inusitatus* Fernández 2001 is distinguished from other *Lenomyrmex* workers by smooth and shiny mesosoma with well-developed propodeal spines and by the foveolate-striate sculpture covering all the dorsal surface of its head [2]. *L. inusitatus* has an unusual distribution since it is the single *Lenomyrmex* species recorded east of the Andes [2]. Nevertheless, it was previously only known from the type locality (“Territorio Kofanes”, Nariño, Colombia). Here, the species is recorded for the first time in the Eastern Cordillera of the South-Ecuadorian Andes.

Among *Lenomyrmex* species, the queen caste has been described only for *L. mandibularis* Fernández and Palacio 1999 and *L. wardi* Fernández and Palacio 1999. In this paper, we provide the first record and a description of the queen of *L. inusitatus*.

2. Materials and Methods

The sampling of *Lenomyrmex* in the Ecuadorian Andes is part of a rainfall exclusion experiment [6] and was based on the Winkler extraction method. The leaf litter inside a 0.25 or 0.5-m^2 quadrat was collected and sifted and its fauna was extracted during 48 h. All specimens were collected close to the Podocarpus National Park, within the “Copalinga” property, at 1420 m (Zamora-Chinchipe province, Ecuador). Vegetation corresponds to an evergreen lower montane forest [7]. Mean annual precipitation is about 2100 mm. Mean temperature in the leaf litter from December 2009 to May 2010 was 18.5 C (min–max: 15.7–22.2 C).



(a)

(b)

(c)

Figure 1: Worker (specimen number 4042619) of *Lenomyrmex inusitatus* Fernández 2001: in (a) frontal, (b) lateral, and (c) dorsal views. Note the predominantly smooth and shiny mesosoma, with no erect hairs (b, c) and the foveolate head, with median longitudinal striae (a).

A worker (no. 4042619, from sample no. 40426) and a queen (no. 4042602, from the same sample) have been imaged (Figures 1 and 2, resp.) and are available at http://projects.biodiversity.be/ants.

Measurements and Indices. All measurements are in millimeters. The abbreviations are as follows:

HL: Head length, measured in full face view, from the anterior margin of the medial lobe of the clypeus to the posterior border of the head (excluding the mandibles).

HW: Head width, the maximum width of the head measured in full face view, excluding the compound eyes.

ML: Mandible length, the maximum length of the mandible measured in dorsal view, from the anteriormost portion of the head to the apex of closed mandibles.

EL: Eye length, the maximum diameter of the eye in frontal view.

SL: Scape length, excluding the basal condyle and the neck.

WL: Weber's length, measured diagonally in lateral view from the anterior edge of the pronotum to the posterior edge of the propodeal lobe.

PL: Petiole length, the axial distance from the dorsal corner of the posterior peduncle to the nearest edge of the propodeal lobe.

PW: Petiole width, the maximum transverse distance across the node measured in dorsal view.

PPL: Postpetiole length, the axial distance from the base of the node in front to the tip of the posterior peduncle measured in lateral view.

PPW: Postpetiole width, the maximum transverse distance across the postpetiole in dorsal view.

GL: Gaster length, in lateral view, from the anterior edge of the first tergum to the posterior edge of the last visible tergum.

GW: Gaster width, in dorsal view, the maximum transverse distance across the gaster.

TL: Total length measured in lateral view (ML + HL + WL + PL + PPL + GL).

OI: Ocular index, EL/HW × 100.

CI: Cephalic index, HW/HL × 100.

SI: Scape index, SL/HL × 100.

Queens and workers have been deposited at the Royal Belgian Institute of Natural Sciences, Brussels, Belgium, (RBINS), the Laboratorio de Entomología—Universidad Técnica Particular de Loja, Loja, Ecuador (UTPL), and the Museo de Insectos, Instituto de Ciencias Naturales—Museo de Historia Natural, Universidad Nacional de Colombia, Santafé de Bogotá D.C., Colombia (ICN).

3. Results (Tables 1 and 2)

3.1. Material Examined. A total of 34 workers and two dealated queens of *Lenomyrmex inusitatus* were collected. The worker (Figure 1) corresponds to the description of the holotype [2], except that it is slightly smaller.

Table 1: Key to the workers of the six described *Lenomyrmex* species.

1. Mesosoma predominantly smooth and shiny, with no erect hairs	2
–Mesosoma with conspicuous sculpture and at least a pair of erect hairs	3
2(1). Propodeum without spines; head only foveolate (SW Colombia)	*foveolatus*
–Propodeum with a pair of acute and well-defined spines; head foveolate, with median longitudinal striae (Cordillera Oriental of the Andes in S Colombia and S Ecuador)	*inusitatus*
3(1). Dorsum of head and petiole with longitudinal conspicuous costae; erect hairs of antennal scape as long as or longer than maximum diameter of scape; body ferruginous yellow (W Panama)	*costatus*
–Dorsum of head densely rugo-reticulate; sculpture of the petiole variable, rugulate to rugo-reticulate or longitudinally striate but never costate; erect hairs of antennal scape not longer than maximum diameter of the scape; body brownish black or dark red brown	4
4(3). Length of propodeal spines approximately equal to distance between their bases; mesopleuron with some irregular longitudinal striae, but mostly smooth and shiny; metapleuron with irregular longitudinal striae; HL > 0.80 mm; mesosoma with only two suberect hairs on the pronotum (SW Colombia)	*mandibularis*
–Length of propodeal spines variable, either shorter or longer than distance between their bases; metapleuron and subsequent portion of mesopleuron with fine transverse rugulae or rugo-reticulate, without smooth areas; HL < 0.80 mm; mesosoma with numerous erect to suberect hairs	5
5(4). Propodeal spines shorter than distance between their bases; eyes with six or seven facets in maximum diameter; petiolar node protruding over the peduncle and well defined; postpetiolar dorsum with longitudinal striae (NW Ecuador, SW Colombia)	*wardi*
–Propodeal spines longer than distance between their bases; eyes with about nine facets in maximum diameter; petiolar node undifferentiated from the peduncle; postpetiolar dorsum smooth and polished (Costa Rica)	*colwelli*

Table 2: Key for the known queens of *Lenomyrmex*.

1. Head foveolate, with median longitudinal striae; mesosoma predominantly smooth and shiny, with sparse punctures on pronotum, mesopleuron, metapleuron, and propodeum, scutellum and axillae foveolate, mesoscutum foveolate-striate, no erect hairs	*inusitatus*
–Head densely rugo-reticulate; mesosoma covered by sculpture, mesopleuron, scutellum, and propodeal dorsum with striae, axillae rugo-reticulate, mesoscutum rugulose, erect hairs	2
2(1). Propodeal spines approximately equal in length to distance between their bases; integument predominantly shiny; HL > 0.80	*mandibularis*
–Propodeal spines notably shorter than distance between their bases; integument predominantly opaque; HL < 0.80	*wardi*

Workers. ECUADOR: Zamora-Chinchipe province: Zamora: Bombuscaro: Copalinga property; Lat: – 4.083; Long: – 78.967; 26.IV-01.V.2010; collected by Delsinne T. and Arias Penna T.; 34 workers in 23 Winkler samples (number of specimens/Winkler sample: 1–4); sample codes: 40343, 40367, 40369, 40374, 40375, 40382, 40387, 40391, 40395, 40417, 40418, 40424, 40426, 40428, 40437, 40439, 40440, 40446, 40449, 40453, 40455, 40457, 40459, 40461; RBINS, UTPL, ICN.

Worker Measurements (no. 4042619). TL 4.23, HL 0.74, HW 0.64, ML 0.41, SL 0.60, EL 0.16, WL 1.15, PL 0.62, PW 0.20, PPL 0.30, PPW 0.24, GL 1.11, GW 0.76, CI 86, OI 24, SI 81.

Queens. ECUADOR: Same data as workers; two queens in two Winkler samples; sample codes: 40426 and 40343; RBINS, UTPL.

Queen Measurements (no. 4042602). TL 4.34, HL 0.75, HW 0.65, ML 0.41, SL 0.59, EL 0.20, WL 1.16, PL 0.64, PW 0.21, PPL 0.27, PPW 0.24, GL 1.11, GW 0.78, CI 86, OI 31, SI 79.

Queen Diagnosis (Figure 2). The queen is similar to the worker [2] but differing in the following characters: anterior margin of clypeus mostly convex, with a slight median notch or concavity; compound eyes bigger, with 11-12 facets in maximum diameter; three ocelli present; mesosoma robust; dorsum of pronotum smooth and shiny, with sparse punctures; mesoscutum foveolate, with longitudinal striae; scutellum and axillae foveolate, with smooth and shiny interspaces; dorsum of propodeum completely smooth and polished; propodeal spines long and stout but shorter than distance between their bases; mesopleuron with anepisternum clearly separated from katepisternum by a suture; lateral face of pronotum, anepisternum, katepisternum, metapleuron, and

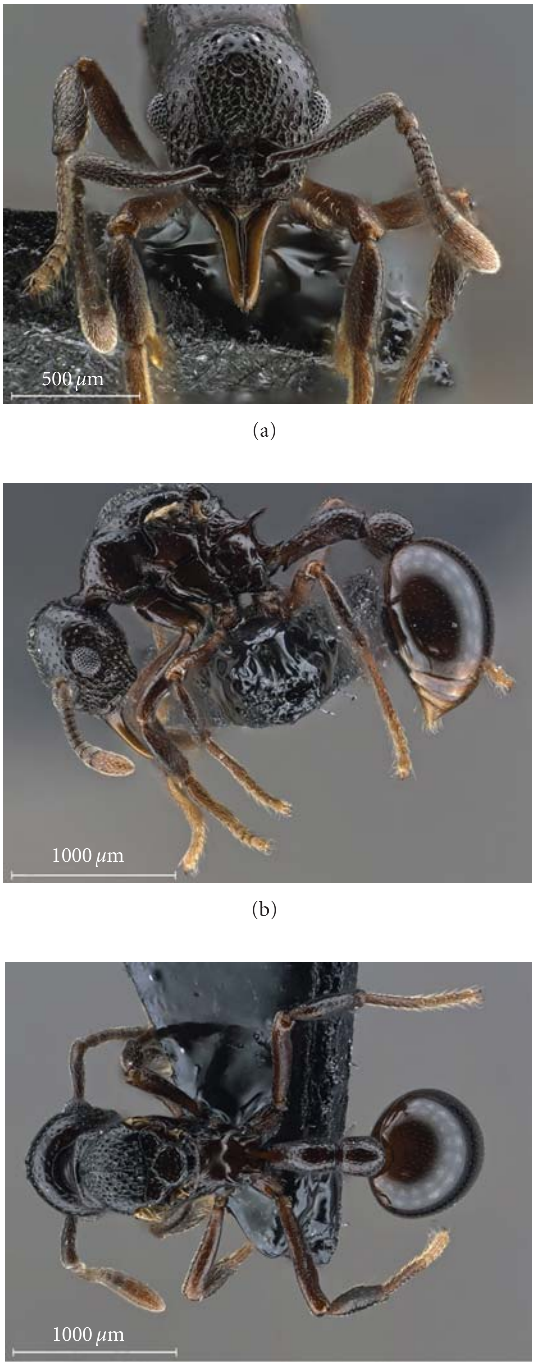


Figure 2: Queen (specimen number 4042602) of *Lenomyrmex inusitatus* Fernández 2001: in (a) frontal, (b) lateral, and (c) dorsal views. Note the predominantly smooth and shiny mesosoma, with mesoscutum foveolate-striate and without erect hairs (b, c) and the foveolate head, with median longitudinal striae (a).

lateral face of propodeum mostly smooth and shiny, with some sparse punctures; punctures of lateral and dorsal faces of petiole and postpetiole more defined and deeper than in workers; short and appressed pilosity more abundant on mesosoma than in workers.

4. Discussion

Lenomyrmex inusitatus is, with *L. wardi* and *L. foveolatus*, the third *Lenomyrmex* species collected in Ecuador [1, 8]. To our knowledge, the new record represents only the tenth locality known for the entire genus and constitutes its southernmost limit of distribution. The range of the species and of the genus increases nearly 510 km and 415 km to the South, respectively. Although data remain insufficient to understand the biogeography of *Lenomyrmex*, it is interesting to note that the new record confirms the presence of *L. inusitatus* on the Eastern side of the Cordillera Oriental of the Andes.

Lenomyrmex species were collected from elevations close to sea level to 1800 m but seem to be mainly restricted to mid-elevations, that is, 1100–1500 m ([1–3], this study). The degree of queen-worker dimorphism is weak, suggesting small colony sizes and absence of claustral independent colony foundation [9]. *Lenomyrmex* ants seem always locally rare and it is in fact the first time that up to 34 workers have been collected within a relatively small area (400 m^2). A thorough inspection of the dead wood laying on the ground and of soil samples failed to uncover any nest of *L. inusitatus*. This and the fact that both workers and dealate queens were extracted from the leaf litter (Winkler method) may indicate that this species nests and forages in the leaf litter. The unusual morphology of the mandibles suggests that *Lenomyrmex* is a specialist predator on an unknown prey. This habit is possibly linked to its apparent rarity and restricted elevational distribution. More data are needed to accurately determine the biology and biogeography of these interesting ants.

N.B. After submitting the paper, two additional workers were found within a soil sample, at slightly higher elevation (1500 m), within the “Copalinga” property. The two workers were maintained alive during six days. They moved relatively slowly and feigned death when disturbed. They did not feed on any offered food items (alive and dead termites, millipedes, mites, various insect parts, sugar/water, tuna, biscuits). The information for these specimens are ECUADOR: Zamora-Chinchipe province: Zamora: Bombuscaro: Copalinga property; Lat: − 4.082; Long: − 78.968; 13.IV.2011; collected by Delsinne T. and Arias Penna T.; two workers in one soil sample (= a thorough visual search for ants for twenty person-minutes from a 15 × 15 × 15-cm core of soil); specimen codes: 4649901 and 4649902; RBINS.

Acknowledgments

The authors thank C. Vits and B. de Roover from “Copalinga” for allowing them to sample ants within their property, J. Bendix, the “Deutsche Forschungsgemeinschaft” (DFG)-Research Unit 816, and the team of the “Estación Científica San Francisco” for allowing and extensively facilitating their work, I. Bachy, Y. Laurent, and M. Leponce for ant digitization, J. Peña and T. M. Arias Penna for assistance with fieldwork, and two anonymous referees for helpful suggestions on the paper. This research was funded by the Belgian Science Policy (BELSPO) and was carried out in

the framework of EDIT (European Distributed Institute of Taxonomy). In accordance with section 8.6 of the ICZNs International Code of Zoological Nomenclature, printed copies of the edition of Psyche containing this article are deposited at the following six publicly accessible libraries: Green Library (Stanford University), Bayerische Staatsbibliothek, Library—ECORC (Agriculture & Agri-Food Canada), Library—Bibliotheek (Royal Belgium Institute of Natural Sciences), Koebenhavns Universitetsbibliotek, University of Hawaii Library.

References

[1] F. Fernández C. and E. E. Palacio G., "*Lenomyrmex*, an enigmatic new ant genus from the Neotropical Region (Hymenoptera: Formicidae: Myrmicinae)," *Systematic Entomology*, vol. 24, no. 1, pp. 7–16, 1999.

[2] F. C. Fernández, "Hormigas de Colombia. IX: Nueva especie de *Lenomyrmex* (Formicidae: Myrmicinae)," *Revista Colombiana de Entomología*, vol. 27, pp. 201–204, 2001.

[3] J. T. Longino, "New species and nomenclatural changes for the Costa Rican ant fauna (Hymenoptera: Formicidae)," *Myrmecologische Nachrichten*, vol. 8, pp. 131–143, 2006.

[4] F. Fernández, "Subfamilia myrmicinae," in *Introducción a Las Hormigas de la Región Neotropical*, F. Fernández, Ed., pp. 307–330, Instituto de Investigación de Recursos Biológicos Alexander von Humbold, Bogotá, Colombia, 2003.

[5] B. Bolton, "Synopsis and classification of Formicidae," *Memoirs of the American Entomological Institute*, vol. 71, pp. 1–370, 2003.

[6] T. Delsinne, T. M. Arias Penna, and M. Leponce, "Effects of experimental rainfall exclusion on a diverse ant assemblage along an elevational gradient in the Ecuadorian Andes," in *Proceedings of the 5th International conference of the International Biogeography Society*, p. 97, Crete, Greece, 2011.

[7] J. Homeier, F. A. Werner, S. R. Gradstein, S.-W. Breckle, and M. Richter, "Potential vegetation and floristic composition of Andean forests in South Ecuador, with a focus on the RBSF," in *Gradients in a Tropical Mountain Ecosystem of Ecuador*, E. Beck, J. Bendix, I. Kottke, F. Makeschin, and R. Mosandl, Eds., vol. 198, pp. 87–100, Ecological Studies, 2008.

[8] D. Donoso and G. Ramón, "Composition of a high diversity leaf litter ant community (Hymenoptera: Formicidae) from an Ecuadorian pre-montane rainforest," *Annales de la Société Entomologique de France (numéro spécial)*, vol. 45, pp. 487–499, 2009.

[9] C. Peeters and M. Molet, "Colonial reproduction and life histories," in *Ant Ecology*, L. Lach, C. L. Parr, and K. L. Abbott, Eds., pp. 159–193, Oxford University Press, New York, NY, USA, 2010.

Hindawi Publishing Corporation
Psyche
Volume 2012, Article ID 594302, 8 pages
doi:10.1155/2012/594302

Research Article

Distribution and Diversity of the Cryptic Ant Genus *Oxyepoecus* (Hymenoptera: Formicidae: Myrmicinae) in Paraguay with Descriptions of Two New Species

T. Delsinne,[1] W. Mackay,[2] A. Wild,[3] Y. Roisin,[4] and M. Leponce[1]

[1] *Biological Evaluation Section, Royal Belgian Institute of Natural Sciences, 29 street Vautier, 1000 Brussels, Belgium*
[2] *Laboratory for Environmental Biology, The University of Texas, El Paso, TX 79968, USA*
[3] *Department of Entomology, University of Illinois, 505 South Goodwin Avenue, Urbana, IL 61801, USA*
[4] *Department of Evolutionary Biology and Ecology, Université Libre de Bruxelles, 50 Avenue Roosevelt, 1050 Brussels, Belgium*

Correspondence should be addressed to T. Delsinne, thibaut.delsinne@sciencesnaturelles.be

Received 2 April 2011; Accepted 19 April 2011

Academic Editor: Fernando Fernández

We discuss the diversity and distribution of the ant genus *Oxyepoecus* in Paraguay. *Oxyepoecus inquilinus* is recorded for the first time, and new distribution data are given for *O. rastratus* and *O. vezenyii*. Published data for *O. bruchi*, *O. rastratus*, *O. reticulatus*, and *O. vezenyii* are summarized. Two new species are described (*O. bidentatus* n. sp. and *O. striatus* n. sp.), and a key to the workers of the seven Paraguayan *Oxyepoecus* species is provided. At Teniente Enciso National Park, four species cooccur. This locality appears as a promising site for studies documenting the biology of this poorly known ant genus, and because of the IUCN "vulnerable" Red List classification of *O. inquilinus*, the importance of the Teniente Enciso National Park for biological conservation is clearly established.

1. Introduction

Oxyepoecus [1] is a genus of cryptobiotic ants collected infrequently from Colombia to Chile [2–5]. The genus is a member of the tribe Solenopsidini in the subfamily Myrmicinae [6]. It currently includes 20 species [3, 4, 7], including two species described as new in this paper. Four *Oxyepoecus* species were previously recorded in Paraguay: *O. bruchi* [1], *O. rastratus* [8], *O. reticulatus* [7], and *O. vezenyii* [9, 10].

The genus is differentiated from other Solenopsidini by the 11-segmented antennae with a three-segmented apical club, the clypeus with four teeth, and the dentate propodeum [3]. In addition, the petiole and postpetiole nodes are high and often anteroposteriorly compressed [3].

The biology of the genus is poorly known, but three species (*O. inquilinus* [11], *O. daguerrei* [12], and *O. bruchi* [1]) are suspected to be inquilines of *Pheidole* or *Solenopsis* [1, 7, 11], although the exact nature of the relationship is unclear [3]. These three species are considered as "Vulnerable D2" [13], meaning they are suspected to be "facing a high risk of extinction in the wild in the medium-term future" because "their populations are characterized by an acute restriction in their area of occupancy (typically less than 100 km^2) or in the number of locations (typically fewer than five)." Due to the current rapid loss of biodiversity and uncertainty concerning the conservation status of social insects [14], data to increase our knowledge of threatened species are desperately needed.

Here, we report *Oxyepoecus inquilinus* for the first time from Paraguay and provide new distribution data for *O. vezenyii* and *O. rastratus*. Two new species are described.

2. Materials and Methods

The sampling of ant assemblages in the Chaco region of Paraguay was based on 560 Winkler and 720 pitfall samples collected between 2001 and 2004 in 11 localities along a 410 km transect beginning at Río Verde and ending at Fortín Mister Long close to the Bolivian border (Figure 1) [15, 16]. Sampling was always carried out at the end of the dry season (September–November). For Winkler extractions, the leaf litter present inside a one m^2 quadrat was collected and sifted and its fauna was extracted for 24 h. Pitfall traps consisted of 70 mm diameter drinking cups, containing water and a drop of detergent, operating for at least 24 hours. Vegetation corresponds to relatively well-preserved xeromorphic forests [17]. Elevation, mean annual rainfall and temperature, mean maximal temperature of the warmest month, and mean minimal temperature of the coldest month are provided for each locality [16].

Specimens from the Paraguayan oriental region were collected following previous techniques [10]. Data were supplemented by the examination of existing museum material [10]. Finally, data from the literature and the online specimen database http://www.antweb.org/ were added in order to provide a complete overview of the diversity and distribution of *Oxyepoecus* in Paraguay.

3. Measurements and Indices

All measurements are in millimeters. The abbreviations are as follows.

TL: Total length from the anterior margin of the head (in vertical position) to the posterior edge of the gaster measured in lateral view.

HL: Head length, measured in full face view, from the anterior margin of the medial lobe of the clypeus to the posterior border of the head (excluding the mandibles).

HW: Head width, the maximum width of the head measured in full face view, excluding the eyes.

EL: Eye length, the maximum diameter of eye.

SL: Scape length, excluding the basal condyle.

PL: Petiole length, the maximum length of the node measured in dorsal view, starting at the base of the anterior face and ending at the base of the posterior edge.

PW: Petiole width, the maximum width of the node measured in dorsal view.

PPL: Postpetiole length, the maximum length of the node measured in dorsal view, as above.

PPW: Postpetiole width, the maximum width of the node measured in dorsal view.

WL: Weber's length, measured from the anterior edge of the pronotum to the posterior edge of the metapleural lobe.

CI: Cephalic index, HW/HL × 100.

SI: Scape index, SL/HL × 100.

The terminology is based on [18].

Holotypes, paratypes, and voucher specimens have been deposited at the Royal Belgian Institute of Natural Sciences, Brussels, Belgium, (RBINS), the University of Texas at El Paso (CWEM), the Alexander L. Wild personal collection (ALWC), the Museum of Comparative Zoology, Harvard University (MCZC), the Los Angeles Country Museum, Los Angeles, California, USA (LACM) and the "Museo Nacional de Historia Natural del Paraguay", San Lorenzo, Paraguay (INBP).

4. Results

The following species of *Oxyepoecus* were collected in Paraguay (Figure 1).

4.1. Oxyepoecus bidentatus. Delsinne and Mackay, n. sp. (Figures 2 and 3).

Diagnosis. Its worker morphology places this species within the *rastratus* species-group [4]. The reticulate-costulate dorsal surface of the head (Figures 2(a) and 2(d)) and the well-defined subpostpetiolar process, forming a pair of prominent blunt teeth (Figure 3), separate *O. bidentatus* from all the other species of *Oxyepoecus*. The gyne and male are unknown.

Description of the Worker. Measurements of holotype, paratypes ($n = 2$) between parentheses: TL 1.94 (1.86–1.90), HL 0.52 (0.51–0.55), HW 0.44 (0.42–0.46), EL 0.07 (0.06-0.07), SL 0.32 (0.32–0.35), PL 0.07 (0.07–0.11), PW 0.17 (0.19–0.23), PPL 0.09 (0.08–0.12), PPW 0.22 (0.25–0.28), WL 0.63 (0.60–0.64), CI 85 (83-84), and SI 62 (63-64).

Lateral clypeal teeth are well developed, directed anteriorly; eye small, about 16–18 ommatidia, five ommatidia in greatest diameter; scape in repose failing to reach posterior border of head by about two maximum widths; sides of head nearly straight, parallel; frontovertexal margin slightly convex; pronotal shoulder gently angulate, marked with striae; notopropodeal (=metanotal) groove indistinct; propodeal angles developed, with two medium-sized acute teeth; subpetiolar process well-developed, lobe-like, directed ventrally; subpostpetiolar process well-developed, forming pair of blunt teeth, directed ventrally; nodes of petiole and postpetiole high and dorsally rounded, compressed anteroposteriorly; in lateral view, petiolar node higher than postpetiolar node; as seen from above, postpetiole much broader than petiole.

Long erect hairs abundant on clypeus, vertex, dorsum of mesosoma, petiole, postpetiole, all surfaces of gaster; mandibles, antennae, legs, and dorsal surface of head with abundant shorter semierect hairs.

Mandibles smooth and shiny, with few scattered punctures; head dorsum reticulate-costulate, lateral costulae attain compound eye and posteriorly vertexal margin; dorsopronotum and mesonotum longitudinally costate; dorsopropodeum transversely costate (about 10–12 costae on dorsal face), anterior half of the lateropronotum mostly smooth and glossy, sometimes with faint longitudinal costae; posterior half of the lateropronotum, mesopleuron and lateropropodeum covered by sparse longitudinal costae; nodes of petiole and postpetiole transversely costate; gaster smooth and glossy with sparse punctures.

Body Color. Concolorous Reddish Brown.

Etymology. From Latin, *bidens*, referring to the subpostpetiolar process forming a pair of well-defined teeth.

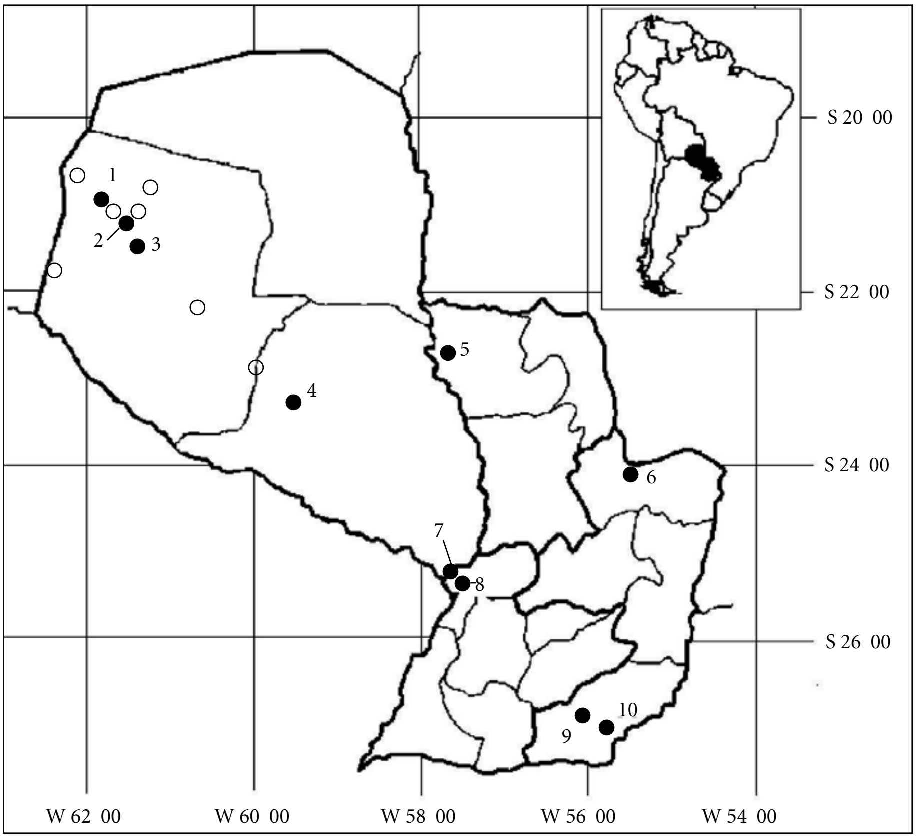


Figure 1: Distribution of *Oxyepoecus* in Paraguay. In this country, seven species have been reported: *O. bidentatus* n. sp. (collected at localities 2, 3, 4), *O. bruchi* (7), *O. inquilinus* (1, 2), *O. rastratus* (2, 3, 6, 10), *O. reticulatus* (9), *O. striatus* n. sp. (4), and *O. vezenyii* (2, 3, 5, 8). Localities are (1) Nueva Asunción, (2) Teniente Enciso National Park, (3) Garrapatal, (4) Río Verde, (5) Puerto Max, (6) Reserva Natural del Bosque Mbaracayú, (7) San Lorenzo, (8) Luque, (9) Santa María, and (10) Pastoreo. For information, localities of the Paraguayan dry Chaco sampled by Delsinne et al. [15, 16] but where no *Oxyepoecus* species were collected are also shown on the picture (empty symbols).

Distribution. Oxyepoecus bidentatus was found in three localities of the Paraguayan dry Chaco (Figure 1). Because the maximal distance between localities was 340 km, *O. bidentatus* is suspected to be widely distributed in xeromorphic Chacoan forests, even if rarely found.

Type Series

Holotype worker. Paraguay: Presidente Hayes: Río Verde, Lat: S 23.22, Long: W 59.20, 15-16.X.2003, Delsinne T., 24-hour pitfall sample (specimen number 29272, SIDbase [19], RBINS). Images of the holotype are available at http://projects.biodiversity.be/ants.

Paratype workers. Paraguay: Presidente Hayes: Río Verde, Lat: S 23.22, Long: W 59.20, 15-16.X.2003, Delsinne T., one worker, 24-hour pitfall trap, specimen number 32013, MCZC; Boquerón: T. Enciso N.P., Lat: S 21.21, Long: W 61.66, 03–05.XI.2001, Leponce M., five workers in three Winkler samples, RBINS, INBP, specimen numbers 7598, 7683, 7684, 7698, and 32605 (scanning electron microscope (SEM) pictures of the specimen number 7684 are available at http://projects.biodiversity.be/ants); Boquerón: Garrapatal, Lat: S 21.45, Long: W 61.49, 05-06.XI.2001, Leponce M., one worker, Winkler sample, specimen number 24606, RBINS.

Comparison. Oxyepoecus bidentatus is the only species of the genus to have both the dorsal surface of the head entirely covered by sculpture and a bidentate subpostpetiolar process. The anterior subpostpetiolar process of *O. bruchi* of the *vezenyii* species-group is also prominent and bidentate [1, 3], but the dorsal surface of the head is mainly smooth and shining except for two patches of fine, longitudinal rugulae which do not reach posteriorly to the vertex margin nor laterally to the compound eye. Criteria separating *O. bidentatus* from other species of the *rastratus* species-group are the mesopleuron and lateropropodeum covered by longitudinal costae (and not reticulate as for *O. myops, O. rosai,* and *O. reticulatus*), and the presence of a reticulate-costulate sculpture on the dorsal surface of the head reaching posteriorly to the vertexal margin and laterally to the compound eye.

Biology. The fact that workers were extracted from leaf litter (Winkler method) or were collected in pitfall samples, while

(a) (b)

(c) (d)

Figure 2: *Oxyepoecus bidentatus* Delsinne and Mackay, n. sp.; holotype worker (number 29272): in frontal (a), lateral, (b) and dorsal views (c); paratype worker (number 7684): detail of the vertex sculpture (d). Note the dorsal surface of the head entirely reticulate-costulate (a, d) and the subpostpetiolar process bidentate (b).

no gynes were found, suggests that this species nests in the soil, but workers forage in the leaf litter when abiotic conditions are favorable. Localities where the species was found have a mean annual rainfall and temperature ranging from 593 to 887 mm and from 23 to 25 C, respectively [16].

4.2. Oxyepoecus bruchi [1]. Paraguay: Central: San Lorenzo, Lat: S 25.33, Long: W 57.55, 4.X.1979, Vaucher C., one worker, specimen code CASENT0178098, ALWC. The specimen has been imaged and is available on AntWeb (http://www.antweb.org/).

4.3. Oxyepoecus inquilinus [11]. Paraguay: Boquerón: T. Enciso N.P., Lat: S 21.21, Long: W 61.66, 03–05.XI.2001, Leponce M., two workers from one Winkler sample, specimen numbers 7617, and 7619, RBINS (SEM photographs of the specimen number 7617 are available at http://projects.biodiversity.be/ants); Boquerón: Nueva Asunción, Lat: S 20.70, Long: W 61.93, 02–06.XI.2001, Leponce M., two workers in two four-day pitfall traps, specimen numbers 30660, 30678, RBINS.

4.4. Oxyepoecus rastratus [8]. Paraguay: Canindeyú: Reserva Natural del Bosque Mbaracayú, Jejuimi, Lat: S 24.1, Long: W 55.53, 02.V.1996, Wild A., seven workers and one dealate queen, collection code AW0129, ALWC, INBP, LACM (nest in red rotting log; wood was too hard for a full excavation; one chamber uncovered with gyne and brood), humid subtropical tall forest, one worker and the dealate gyne have been imaged and are available on AntWeb (http://www.antweb.org/), specimen codes CASENT0178099 and CASENT0178100, respectively; Boquerón: Teniente Enciso National Park, Lat: S 21.21, Long: W 61.66, 03–05.XI.2001, Leponce M., 28 workers and one gyne in eight Winkler samples, worker numbers 7302, 7303, 7746, 7633, 7634, 32602, 7646, 7647, 7674, 23778, 7669, 25221, 405701, RBINS, INBP, CWEM, gyne number 7662, RBINS (SEM photographs of the specimen number

23778 are available at http://projects.biodiversity.be/ants); Boquerón: Garrapatal, Lat: S 21.45, Long: W 61.49, 05-06.XI.2001, Leponce M., one worker, Winkler sample, specimen number 25221, RBINS.

In addition, data from the literature [4] include: Paraguay: Itapúa: Pastoreo, Lat: S 25.38, Long: W 55.83, 03.X. 1974, Duelli P., collection code 399, three workers.

4.5. Oxyepoecus reticulatus [7]. Paraguay: Itapúa: Santa María, no specific location information, 25.X.1982, Baud F., three workers, ALWC, one worker has been imaged and is available on AntWeb (http://www.antweb.org/), specimen number CASENT0178101.

4.6. Oxyepoecus striatus. Mackay and Delsinne, n. sp. (Figure 4).

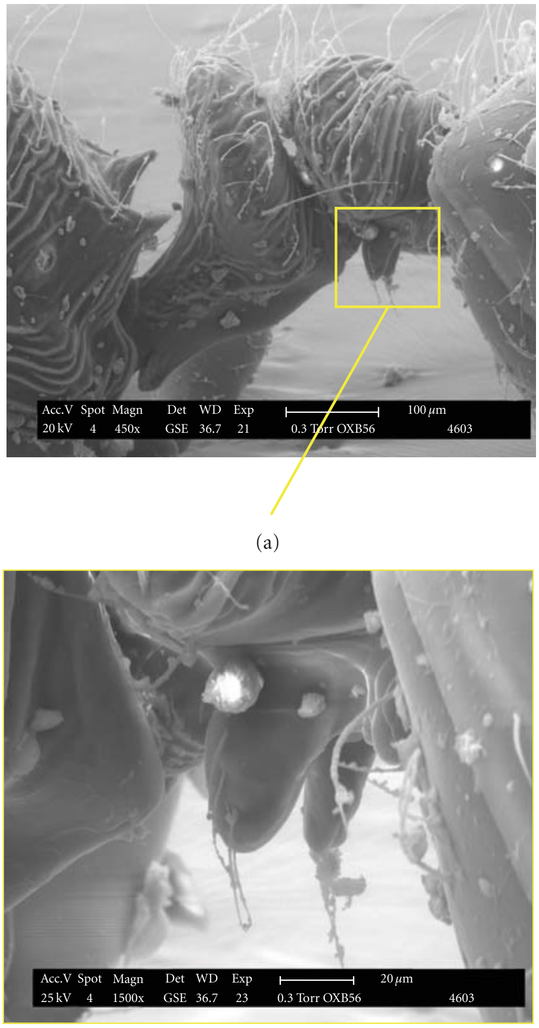
Diagnosis. Its worker morphology places this species within the *vezenyii* species-group [3]. The worker is a small specimen with longitudinal striae covering the promesonotum (Figures 4(c) and 4(d)) and transverse striae on the dorsopropodeum. The clypeal teeth are well defined and sharp. The gyne and male are unknown.

Description of the Worker. Measurements of holotype; paratypes ($n = 2$) between parentheses: TL 1.58 (1.6-1.7), HL 0.46 (0.46–0.48), HW 0.35 (0.35-0.36), EL 0.05 (0.07-0.07), SL 0.29 (0.29–0.31), PL 0.06 (0.06-0.06), PW 0.16 (0.17-0.18), PPL 0.08 (0.09-0.09), PPW 0.19 (0.21-0.22), WL 0.51 (0.49–0.51); CI 76 (75-76), SI 63 (62–65).

Mandible with four teeth, with diastema (gap) between basal and subbasal teeth; lateral clypeal teeth well-developed but small, not lobe-like, directed anteriorly; eye small, with about 18 ommatidia, five ommatidia in greatest diameter; scape in repose failing to reach posterior border of head by about two maximum widths; sides of head nearly straight, parallel, frontovertexal margin slightly convex; pronotal shoulder slightly marked with stria; inferior pronotal process well developed; notopropodeal groove poorly developed; propodeal angles developed, acute; subpetiolar process well developed, lobe-like, directed ventrally, anterior and posterior faces of petiole nearly parallel; two subpostpetiolar angles present, anterior and posterior faces of postpetiole nearly parallel; as seen from above, postpetiole much broader than petiole, postpetiole slightly angulate laterally.

Erect hairs abundant on mandibles, clypeus, dorsal surface of head, dorsum of mesosoma, petiole, postpetiole, all surfaces of gaster, legs with semierect hairs; appressed pubescence sparse, few hairs noticeable on head and gaster.

Mandibles smooth and shiny, with few scattered punctures, most of dorsum of head with scattered coarse punctures, medial area smooth and glossy, mesonotum with longitudinal parallel striae, dorsopropodeum with fine transverse striae, lateropronotum mostly smooth and glossy, mesopleuron and lateropropodeum striolate, nodes of petiole and postpetiole smooth and glossy, posterior face of postpetiole transversely striolate, gaster smooth and glossy.



(a)

(b)

FIGURE 3: *Oxyepoecus bidentatus* Delsinne and Mackay, n. sp.; paratype worker (number 7684): detail of petiole and postpetiole (a) and detail of the bidentate subpostpetiolar process (b).

Body color. Concolorous Medium Reddish Brown.

Etymology. From Latin, *stria*, referring to the striae covering the dorsum of the mesosoma.

Distribution. Known only from the type locality.

Type Series

Holotype worker. Paraguay: Presidente Hayes: Río Verde, Lat: S 23.22, Long: W 59.20, 15-16.X.2003, Delsinne T., 24-hour pitfall sample, specimen number 32606, MCZC.

Paratypes. Same data as holotype, three workers, in three 24-h pitfall samples, specimen numbers 29523, 29531, 29667, RBINS, INBP. Images of the specimen number 29531 are available at http://projects.biodiversity.be/ants.

(a) (b) (c) (d)

Figure 4: *Oxyepoecus striatus* Mackay and Delsinne, n. sp.; paratype worker (number 29531): in frontal (a), lateral, (b) and dorsal views (c, d). Note the longitudinal striae covering the promesonotum (c, d).

Comparison. This species is a member of the *vezenyii* species-group [3] defined principally in having a predominantly smooth and glossy dorsum of the head. It is very similar to the relatively common *O. vezenyii*, but can be easily distinguished as the promesonotum of *O. vezenyii* is nearly completely smooth and glossy (the dorsopropodeum of *O. vezenyii* has transverse striae as in *O. striatus*).

Oxyepoecus striatus appears most similar to *O. browni*, which has a similar sculptured promesonotum, short posterior propodeal face, moderately well-developed costulae between the frontal carinae, and a large lobe-like subpetiolar process. *Oxyepoecus striatus* can be separated as being smaller; the clypeal teeth are well defined, sharp, and directed anteriorly (not lobe-like and directed inward). The frontal lobes are more widely spaced than those of *O. browni* (separated by 0.11 mm) and the head is covered by coarse punctures (except for the smooth medial area).

Biology. The specimens were collected in three separate pitfall samples. The mean annual rainfall and temperature of the locality where the species was found were 887 mm and 23 C, respectively [16].

4.7. Oxyepoecus vezenyii [10]. Paraguay: Boquerón: T. Enciso N.P., Lat: S 21.21, Long: W 61.66, 03–05.XI.2001, Leponce M., 23 workers and five gynes in 12 Winkler samples, worker numbers 7692, 7726, 7737, 7738, 7744, 7690, 7691, 7599, 32603, 32604, 7659, 7660, RBINS, INBP, CWEM, (SEM photographs of the specimen number 7737 are available at http://projects.biodiversity.be/ants), gyne numbers 7753, 7731, 22806, 7661, 7618, RBINS; Boquerón: Garrapatal, Lat: S 21.45, Long: W 61.49, 05-06.XI.2001, Leponce M., one worker, Winkler sample, specimen number 24598, RBINS; Central: Luque, Lat: S 25.27, Long: W 57.57, 11.VIII-6.X. 1982, Kochalka J., Pitfall trap, sample code IBN230, two workers, one of them has been imaged and is available on AntWeb (http://www.antweb.org/), specimen code CASENT0178102, ALWC.

In addition, the type specimen (worker) was collected in Paraguay (Concepción: Puerto Max Forel) [9].

5. Key to the Workers of Oxyepoecus in Paraguay

(1) Cephalic dorsum entirely sculptured (Figure 2(a); 2).

(1) Cephalic dorsum completely smooth or with at least a smooth median frontal stripe (Figure 4(a); 4).

(2) Mesopleuron and lateropropodeum covered by longitudinal costae (Figure 4(b); 3).

(2) Mesopleuron and lateropropodeum irregularly reticulate and punctuate *O. reticulatus.*

(3) Cephalic dorsum with dense costulae, subpostpetiolar process shaped as transverse crest, triangular in side view, not bidentate *O. rastratus.*

(3) Cephalic dorsum with reticulated costulae, subpostpetiolar process prominent and bidentate (Figure 3) *O. bidentatus* n.sp.

(4) Eyes large, with more than 40 ommatidia in total *O. inquilinus*.

(4) Eyes small, with about 20 ommatidia in total (Figure 4(b); 5).

(5) Subpostpetiolar process prominent and bidentate with anteriormost process much larger than posterior tooth *O. bruchi.*

(5) Subpostpetiolar process with two subparallel crests of approximately equal size (Figure 4(b); 6).

(6) Promesonotum nearly entirely smooth and glossy *O. vezenyii*.

(6) Promesonotum covered with longitudinal striae (Figures 4(c) and 4(d)) *O. striatus* n. sp.

6. Discussion

Seven *Oxyepoecus* species are recorded from Paraguay. Two of them are new species described in this paper: *O. bidentatus* and *O. striatus* from the *rastratus* and *vezenyii* species-groups, respectively. These species-groups now include eight and 12 species, respectively. *Oxyepoecus bidentatus* was found in three localities, 20 to 340 km away from each other, indicating that this species may be widely distributed within the Paraguayan dry Chaco. *Oxyepoecus striatus* is only known from the type locality.

Oxyepoecus rastratus was documented from South and South-East Brazil and from Eastern Paraguay [4]. Its presence at T. Enciso N.P. increases its range nearly 700 km to the West. In addition, samples in the dry Chaco and in the Paraná forest suggests that this species may be present in a variety of biomes.

Oxyepoecus reticulatus has been recorded in a dozen localities in South and Southeastern Brazil, mainly in relatively dry forests [4]. The Paraguayan data increase its distribution by nearly 360 km to the West.

Oxyepoecus bruchi was collected in 1948 and 1953 in Argentina (Córdoba and Tucumán provinces) and more recently (2003) in Brazil (Palhoça, Santa Catarina State) [3, 4, 7]. Only one specimen was collected in 1979 in Paraguay (Central). Although the species was rarely collected, its distribution seems potentially large. Nevertheless, *O. bruchi* appears locally rare, justifying its vulnerable status [13]. This species is suspected to be an inquiline of the ants *Pheidole rosae* (named *Ph. silvestrii* in [7]) and *Ph. obtusopilosa* [1, 7, 11], but these species were not present in our samples and, to our knowledge, have not been collected in Paraguay [10].

Oxyepoecus inquilinus was sampled in two localities of the Paraguayan dry Chaco. In the literature, *O. inquilinus* was reported from two savanna localities of the Brazilian Cerrado [7], one Brazilian pasture [4], one anthropogenic area (i.e., the "Jardin del Instituto Miguel Lillo") from the Argentinean Tucumán province [11], and one locality in the Bolivian Bení Department [7]. In addition, one worker closely related to *O. inquilinus* was collected in a savanna-morichal habitat from Colombia, but its specific status awaits further investigation [2]. Finally, *O. inquilinus* was recently sampled in a Valdivian forest of Chile [5]. If the identity of the Colombian specimen is confirmed, *O. inquilinus* is the most broadly distributed species of the genus. In fact, its Colombian and Chilean localities represent both the northernmost and southernmost limits of distribution for the entire genus. Although data are insufficient to determine the exact requirements of this species, *O. inquilinus* seems to be present both in open and closed habitats, in degraded and pristine ecosystems, and in dry and wet areas. The distribution of this species seems large but discontinuous, and *O. inquilinus* is apparently locally rare, justifying its vulnerable status [13]. *O. inquilinus* is suspected to be inquiline in *Pheidole radozskowskii* nests [11]. At T. Enciso N.P., the same Winkler sample collected two workers of *O. inquilinus* and 11 workers of *Ph. radozskowskii.* However, at Nueva Asunción the latter was not recorded in our 60 Winkler and 60 pitfall samples, suggesting that *O. inquilinus* is not restricted to this host species.

With the exception of the Paraguayan type specimen [9], *Oxyepoecus vezenyii* is exclusively known from Brazil where it was sampled in different ecosystems over a large spatial scale [3, 4]. The presence of this species in the Paraguayan dry Chaco increases its range nearly 400 km to the West.

In this study, *Oxyepoecus* individuals were mainly collected using the Winkler extraction method. This technique is highly effective for sampling minute and cryptic ant species which were previously suspected to be rare before the development of the method [20, 21]. This may be the case for *Oxyepoecus* species [3]. Nevertheless, in dry forests the Winkler sampling is strongly influenced by the rainfall regime, and a recent rainfall may increase its efficiency both in terms of species collected and species occurrences [15]. Teniente Enciso National Park was the single locality of the dry Chaco sampled a day after a rainfall. This bias may be the reason why a relatively large number of *Oxyepoecus* species and individuals were collected in this park and just a few in the other dry Chacoan localities. We hypothesize that using the Winkler method during the rainy season of the Paraguayan dry Chaco (December–April) [22] will increase the probability of collecting *Oxyepoecus*.

Oxyepoecus ants appear diversified and well established at Teniente Enciso National Park, where 58 individuals representing four species were collected during a single sampling session (03–05.XI.2001). This locality may hence constitute a promising reference site to undertake studies concerning these poorly known myrmicinae. Moreover, the presence of *O. inquilinus* at T. Enciso N.P. emphasizes the biological conservation importance of this park.

Acknowledgments

This paper was made possible by financial support from the "Fonds pour la Formation à la Recherche dans l'Industrie et l'Agriculture" and the "Fonds de la Recherche Scientifique-FNRS" (Belgium). The Ernst Mayr Fund of the Museum of Comparative Zoology funded a visit to the MCZC to examine types and other specimens. The authors thank J. Kochalka, B. Garcete Barrett, V. Filippi, J. Jara, C. Bénilez, and C. Aguílar Julio from the IBNP, the guards of T. Enciso N.P., and V. Olivier for their help during fieldwork or administrative procedures, J. Cillis from the RBINS for performing the electron microscope photographs, I. Bachy and Y. Laurent for ant images, and T. Arias Penna, D. Arias Penna, and two anonymous referees for comments and helpful suggestions on the paper.

References

[1] F. Santschi, "Deux nouvelles fourmis parasites de l'Argentine," *Folia Myrmecologica et Termitologica*, vol. 1, pp. 6–8, 1926.

[2] F. Fernández, "Ant records for Colombia and South America (Hymenoptera: Formicidae)," *Revista Colombiana de Entomología*, vol. 28, p. 215, 2002.

[3] N. L. Albuquerque and C. R. F. Brandão, "A revision of the Neotropical Solenopsidini ant genus *Oxyepoecus* Santschi 1926 (Hymenoptera: Formicidae: Myrmicinae). 1. The *vezenyii* species-group," *Papéis Avulsos de Zoologia*, vol. 44, pp. 55–80, 2004.

[4] N. L. Albuquerque and C. R. F. Brandão, "A revision of the Neotropical Solenopsidini ant genus *Oxyepoecus* Santschi, 1926 (Hymenoptera: Formicidae: Myrmicinae). 2. Final. Key for species and revision of the *rastratus* species-group," *Papéis Avulsos de Zoologia*, vol. 49, pp. 289–309, 2009.

[5] F. Cuezzo, "First record of the ant genus *Oxyepoecus* (Formicidae: Myrmicinae: Solenopsidini) in Chile, with remarks on its geographical range," *Revista de la Sociedad Entomológica de Argentina*, vol. 66, pp. 165–167, 2007.

[6] B. Bolton, "Synopsis and classification of Formicidae," *Memoirs of the American Entomological Institute*, vol. 71, pp. 1–370, 2003.

[7] W. W. Kempf, "A review of the Neotropical ant genus *Oxyepoecus* Santschi (Hym., Formicidae)," *Studia Entomologica*, vol. 17, pp. 471–512, 1974.

[8] G. Mayr, "Südamerikanische Formiciden," *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien*, vol. 37, pp. 511–632, 1887.

[9] A. Forel, "Formicidés du Musée National Hongrois," *Annales Historico-Naturales Musei Nationalis Hungarici*, vol. 5, pp. 1–42, 1907.

[10] A. L. Wild, "A catalogue of the ants of Paraguay (Hymenoptera: Formicidae)," *Zootaxa*, no. 1622, pp. 1–55, 2007.

[11] N. Kusnezov, "Acerca de las hormigas simbióticas del género *Martia* Forel (Hymenoptera, Formicidae)," *Acta Zoológica Lilloana*, vol. 10, pp. 717–722, 1952.

[12] F. Santschi, "Fourmis de la République Argentine, en particulier du territoire de Misiones," *Anales de la Sociedad Científica Argentina*, vol. 116, pp. 105–124, 1933.

[13] IUCN (Species Survival Commission of the World Conservation Union), "IUCN Red List of Threatened Species, Version 2010.4," February 2011, http://www.iucnredlist.org.

[14] R. E. Chapman and A. F. G. Bourke, "The influence of sociality on the conservation biology of social insects," *Ecology Letters*, vol. 4, no. 6, pp. 650–662, 2001.

[15] T. Delsinne, M. Leponce, L. Theunis, Y. Braet, and Y. Roisin, "Rainfall influences ant sampling in dry forests," *Biotropica*, vol. 40, no. 5, pp. 590–596, 2008.

[16] T. Delsinne, Y. Roisin, J. Herbauts, and M. Leponce, "Ant diversity along a wide rainfall gradient in the Paraguayan dry Chaco," *Journal of Arid Environments*, vol. 74, no. 10, pp. 1149–1155, 2010.

[17] M. F. Mereles, "Una aproximación al conocimiento de las formaciones vegetales del Chaco boreal, Paraguay," *Rojasiana*, vol. 6, pp. 5–48, 2005.

[18] F. Serna and W. MacKay, "A descriptive morphology of the ant genus *Procryptocerus* (Hymenoptera: Formicidae)," *Journal of Insect Science*, vol. 10, no. 111, pp. 1–36, 2010.

[19] M. Leponce and C. Vander Linden, "SIDbase: a database built for the management of social insects diversity inventories," in *Proceedings of the Colloque de la Section Française de l'IUSSI*, p. 38, Poster, Tours, France, Septemper 1999.

[20] C. R. F. Brandão, J. L. M. Diniz, D. Agosti, and J. H. Delabie, "Revision of the Neotropical ant subfamily Leptanilloidinae," *Systematic Entomology*, vol. 24, no. 1, pp. 17–36, 1999.

[21] F. Fernández, "First record of the myrmicine ant genus *Paedalgus* Forel, 1911 (Hymenoptera: Formicidae) from the Western Hemisphere," *Entomotropica*, vol. 17, pp. 181–182, 2002.

[22] L. Ramella and R. Spichiger, "Interpretación preliminar del medio físico y de la vegetación del Chaco Boreal. Contribución al estudio de la flora y de la vegetación del Chaco. I," *Candollea*, vol. 44, pp. 639–680, 1989.