The diversity and ecology of ant gardens (Hymenoptera: Formicidae; Spermatophyta: Angiospermae)

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Abstract

Mutualistic interactions between ants and plants are important features of many ecosystems, and they can be divided into three main categories: dispersal and protective mutualisms and myrmecotrophy. In both the Neotropics and the Southeastern Asian Paleotropics, ant gardens (AGs), a particular type of ant-plant interaction, are frequent. To initiate AGs, ants integrate the seeds of certain epiphyte species into the carton of their nest. The development of the plants leads to the formation of a cluster of epiphytes rooted in the carton. They have been defined as one of the most complex associations between ants and plants known because of the plurispecific, but also specialized nature of the association involving several phylogenetically-distant ant and plant species. The aim of this review is to provide a synthesis of the diversity and ecology of AGs, including the outcomes experienced by the partners in the interaction and the direct and indirect impacts ant-garden ants have on the plant and arthropod communities.

Key words: Ant-plant interactions, epiphytes, mutualisms, Neotropics, Paleotropics, phytotelm, parabiosis, seed dispersal, review.

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Introduction

Ants are ubiquitous and, in ecological terms, tremendously successful. The major consequence of this ecological success is the impact ants have on the other components of biomass. Besides being the principal predators of arthropods in tropical forests and even the principal herbivores in the Neotropics, ants are also involved in a diversity of interactions. Consequently, studying these interactions is of key importance in enabling us to determine ants' impact on the structure of ecological communities. Many of these interactions are mutualistic and most of these mutualisms are either based on the protection provided by the ants in exchange for food rewards and / or shelter (HEIL & MCKEY 2003, STADLER & DIXON 2008), or they are purely nutrition-based interactions with bacteria or fungi (KANE & MUELLER 2002, GIBSON & HUNTER 2010).

Ant-plant mutualisms are important components of tropical communities. Their diversity, associated with a similar global pattern of interactions, makes them useful model systems for understanding the origin and evolution of mutualisms. Ants and flowering plants have a long, shared history as the ants' diversification between ≈ 100 million years ago (mya) and ≈ 50 mya closely tracks the rise of Angiosperms (MOREAU & al. 2006, MOREAU 2009). The ecological dominance of ants is notable by the mid-Eocene (50 mya), suggesting an explosive radiation just before this period (WILSON & HÖLLDOBLER 2005, MOREAU & al. 2006). Today, ant-plant mutualisms either involve ants as dispersal agents of plant diaspores, the indirect protection of plants thanks to the predatory ability of ants, or the feeding on plants by ants.

Dispersal mutualisms occur in more than 3,000 plant species bearing elaiosomes (i.e., nutritive bodies attached to the seeds) that are dispersed by ants (BEATTIE & HUGHES 2002, GILADI 2006). The elaiosomes are consumed by the ants and the seeds are then either rejected or kept inside the nest (MARK & OLESEN 1996, GOMEZ & ESPADALER 1998, WILLSON & TRAVESET 2000, WENNY 2001). Such seeds can then be dispersed far from the parent plants into microhabitats suitable for their germination and growth (i.e., ant nests), and away from predators (reviewed in GILADI 2006).

Protective ant-plant mutualisms derive from the provision of food in the form of extrafloral nectar and / or a permanent shelter for the ants in specialized structures by the so-called myrmecophytic plants (HEIL & MCKEY 2003, RICO-GRAY & OLIVEIRA 2007). Extrafloral nectaries are present in 93 angiosperm and five fern families (BENTLEY 1977, KOPTUR 1992). In exchange for these food rewards, the ants generally protect the plants from herbivores (OLIVEIRA 1997, DE LA FUENTE & MARQUIS 1999, BEATTIE & HUGHES 2002, DIAZ-CASTELAZO & al. 2004, MODY & LIN-

SENMAIR 2004, RUDGERS & GARDENER 2004). In addition to these interactions in which a variety of partners are involved (BLÜTHGEN & al. 2000, APPLE & FEENER 2001, HOSSAERT-MCKEY & al. 2001), strict and obligatory mutualisms do exist. The constancy and specificity of these associations are facilitated by the presence of domatia and, often, such interactions are the result of co-evolutionary specializations (HEIL & MCKEY 2003, RICO-GRAY & OLIVEIRA 2007). In turn, the resident ants also protect their hosts from herbivory and / or competition, and they can also provide them with nutrients (HEIL & MCKEY 2003).

Nutrient provisioning to their host plant by the ants, called myrmecotrophy, has been demonstrated in several systems (BENZING 1991, TRESEDER & al. 1995, LETOURNEAU 1998, SAGERS & al. 2000, FISCHER & al. 2003). Ants provide the plant nutrients either through the accumulation of their waste in the domatia or by favouring the growth of epiphytic plants in the carton of their nest. Nitrogen and probably other nutrients are absorbed by the myrmecophytes through the walls of the domatia or by protuberances growing inside of them, and the plants can even benefit from ant respiration by absorbing carbon dioxide (TRESEDER & al. 1995, FISCHER & al. 2003, SOLANO & DEJEAN 2004). In carton-growing epiphytes, the growth of the plants is enhanced by the accumulation of the rich organic matter that the ants accumulate around the roots (LONGINO 1986, BENZING 1991, BLÜTHGEN & al. 2001).

Ant gardens (AGs) represent a particular type of interaction involving the three types of above-mentioned interactions between ants and plants (i.e., protective and dispersal mutualisms, and myrmecotrophy). They constitute an outstanding example of an ant-plant association, and also probably one of the most complex (BUCKLEY 1982, KLEINFELDT 1986). In this review, we summarize the diversity and ecology of AGs and we provide a synthesis of the outcomes experienced by the partners in the interaction and the direct and indirect impacts AG ants have on plant and arthropod communities.

Ant gardens

Ant gardens were first described by ULE (1901) based on his work in the Neotropics, and, subsequently, VAN LEEUWEN (1929a, b) demonstrated the same type of ant-epiphyte association in Southeastern Asia. They can be roughly defined as aggregates of epiphytes assembled by ants. More specifically, they refer to the particular mutualistic interactions between plants and ants in which ants integrate the seeds of certain epiphyte species into the carton of their arboreal nests. These epiphytes subsequently germinate and develop on this rich substrate to form hanging structures on the branches of host trees (Fig. 1).

The complexity of these interactions comes from the plurispecific, but also specialized nature of the association. Indeed, several species of phylogenetically-distant ants can be associated with several, also phylogenetically-distant, epiphyte species, but none of them is found outside of AGs. Moreover, AG epiphytes lack obvious morphological adaptations, such as domatia (but see KAUFMANN & MASCHWITZ 2006, about the occurrence of ant-house epiphytes in AGs). Such an "apparent" absence of morphological adaptation, despite the specificity of their interactions with ants, might also have contributed to viewing AGs as complex systems. Finally, the commonness of one of the most intri-

guing interspecific associations between ant species within AGs, called parabiosis, contributes to the overall intricacy of AGs (FOREL 1898, MANN 1912, WEBER 1943).

Ant and plant diversities

Only a few ant species are known for their ability to initiate AGs. True AG ant species are defined as species sharing the following two behavioral characteristics: (I) the capacity to build an arboreal carton nest rich in humus, and (II) a retrieval behavior concerning the seeds of epiphytic plants that they retrieve to their nest and incorporate into its walls (CORBARA & al. 1999). Data in the literature are, however, lacking for many species recorded in AGs, so that such a definition applies to only a few ant species. Consequently, we will consider here that the definition of true AG ants can be also extended to species that have been recorded only in AGs and nowhere else. These AG ants belong to four ant subfamilies (i.e., the Dolichoderinae, Formicinae, Myrmicinae and Ponerinae) both in the Paleo- and in the Neotropics (see Tab. 1). In Southeastern Asia, the most abundant ant species is *Crematogaster* sp. with a prevalence of more than 80% (KAUFMANN & al. 2001, KAUFMANN & MASCHWITZ 2006), whereas in tropical America the parabioses between *Camponotus femoratus* (FABRICIUS, 1804) and *Crematogaster levior* LONGINO, 2003 and the AGs inhabited by *Pachycondyla goeldii* (FOREL, 1912) are by far the most frequent (DAVIDSON 1988, CORBARA & DEJEAN 1996, MARINI-FILHO 1999, DEJEAN & al. 2000).

A wide diversity of ant species can, however, inhabit AGs (KLEINFELDT 1978, 1986, DAVIDSON 1988, KAUFMANN & MASCHWITZ 2006). Indeed, even if true AG ants and plants are restricted to such associations, the epiphytes are, nevertheless, able to survive after the death of the ant colony that initiated the AG, and so can be colonized by opportunistic arboreal ant species. Moreover, because of the scarcity of suitable nesting sites in the arboreal environment, AGs represent appealing nesting structures for a variety of ant species and even for other insects (see CORBARA & DEJEAN 1998). During the expansion of their territories, dominant arboreal ant species are frequent secondary residents (DEJEAN & al. 1997, CORBARA & al. 1999), and several opportunistic species can also be found in AGs (DAVIDSON 1988, DEJEAN & al. 2000). Moreover, the secondary colonization of AGs by other ant species is facilitated when local ecological conditions change and drive a decrease in the population of AG ants (DEJEAN & al. 2000).

Of the 15,500 epiphyte species known from the Neotropics, some are regularly found in AGs. A review of the literature on Neotropical AGs resulted in the recording of a total of 53 epiphyte species from 12 families. True AG epiphytes represent only a subset of these species, and they are defined as plant species specifically incorporated into the nest at the seed stage by the ants (Tab. 2). As mentioned above for true AG ant species, data are also lacking for many epiphyte species, so that here we will consider several species as true AG epiphytes on the basis of their only having been observed in AGs. Because of the nutrient-rich composition of the carton nest and the probable absence of both pruning behavior by the ants and allelopathy by the plants, a variety of epiphytes can live on AGs if their seeds reach the carton nest. This is the case, for example, for the few Orchidaceae and Polypodiaceae species that are regularly found in AGs and whose seeds or spores are tiny and wind-
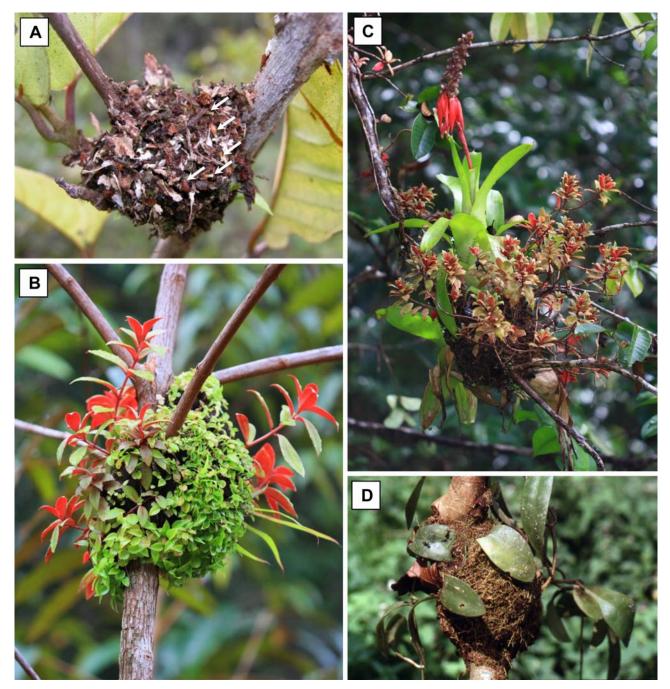
Fig. 1: The developmental stages of ant gardens. (A) Founding queens first build a carton nest from vegetal fibres into which they incorporate epiphyte seeds (arrows) – example from *Pachycondyla goeldii*; (B) Young ant garden inhabited by *Camponotus femoratus* and *Crematogaster levior* with numerous seedlings growing on the carton nest; (C) Mature Neotropical ant garden inhabited by *Ca. femoratus* and *Cr. levior* with the epiphytes *Codonanthe calcarata* and *Aechmea mertensii*; (D) Mature Southeastern Asian ant garden inhabited by the ant *Camponotus* sp. with the epiphyte *Hoya elliptica*.

dispersed (DAVIDSON 1988, DEJEAN & al. 2000, BLÜTH-GEN & al. 2001). A limited number of unrelated, true AG epiphytes can be found in AGs in a single location. Variations across locations (over a large geographical scale) affect the floristic composition of the AGs in terms of changes in species rather than through changes at a higher taxonomic level. Consequently, at the family and even the genus level, the floristic composition of Neotropical AGs is very similar with four families and six genera representing the vast majority of AG epiphytes (Bromeliaceae: *Aechmea*,

Streptocalyx; Areaceae: *Anthurium*, *Philodendron*; Gesneriaceae: *Codonanthe*; Piperaceae: *Peperomia*) (KLEINFELDT 1978, DAVIDSON 1988, MARINI-FILHO 1999, ORIVEL & DEJEAN 1999).

By contrast, information on AG associations from the Paleotropics remains scarce (KAUFMANN & al. 2001, KLEIJN & VAN DONKELAAR 2001, KAUFMANN & MASCHWITZ 2006). While AGs are locally abundant and widespread in the Neotropics, the so-called ant-house epiphytes (*Hydnophytum* sp. and *Myrmecodia tuberosa* JACQ., both Rubi-

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Tab. 1: True ant-garden ant species (i.e., species able to initiate ant gardens or restricted to AGs) in both the Paleo- and the Neotropics.

References: a BENSON (1985), b CORBARA & DEJEAN (1996), c DAVIDSON (1988), d DEJEAN & al. (2000), e KAUFMANN & al. (2001), f KAUFMANN (2002), g KAUFMANN & MASCHWITZ (2006), h KLEINFELDT (1978), i KLEINFELDT (1986), j LONGINO (1999), k LONGINO (2003c), l LONGINO (2003a), m LONGINO (2003b), n MANN (1912), o MARINI FILHO (1999), p ORIVEL & al. (1997), q ORIVEL & al. (1998), r ORIVEL & al. (1999), s SCHMIT-NEUERBURG & BLÜTHGEN (2007), t WEBER (1943), u WHEELER (1921), v WILSON (2003), w YOUNGSTEADT & al. (2009).

[1] The number in parentheses represents the number of species of the genus recorded as specialists of ant gardens (see KAUFMANN 2002, KAUFMANN & MASCHWITZ 2006).

[2] *Crematogaster limata*, *Cr. carinata* and *Cr. levior* belong to the *Cr. limata* complex (see LONGINO 2003c), and are difficult to differentiate at the morphological level (especially *Cr. carinata* and *Cr. levior*). Moreover, the species have often been recorded as *Cr. limata* and / or *Cr. limata parabiotica* in the literature, so that these three species are listed together with the same references. It should be noted, however, that *Cr. levior* is a specialized parabiotic associate of *Camponotus femoratus*, while *Cr. carinata* and *Cr. limata* are parabiotic associates of *Odontomachus panamensis* and *Dolichoderus debilis* or *D. inermis* (although not in AGs in these two latter cases) or *O. mayi*, respectively.

[3] References that explicitly support the role of the ant species as an AG initiator.

Subfamily	Species	Geographic area	References
Dolichoderinae	*Philidris* spp. (6) [1]	Peninsular Malaysia	e, f [3], g
Formicinae	*Camponotus* spp. (4) [1]	Peninsular Malaysia	e, f [3], g
Myrmicinae	*Crematogaster* spp. (6) [1]	Peninsular Malaysia	e [3], f [3], g
	Pheidole spp. (2) [1]	Peninsular Malaysia	e, f [3], g
Ponerinae	*Diacamma* sp. (1) [1]	Peninsular Malaysia	e, f [3], g
Dolichoderinae	*Azteca trailii* EMERY, 1893, *Azteca* sp.	Brazil, Peru	c [3], i, o [3], s
Formicinae	*Camponotus femoratus* (FABRICIUS, 1804)	Brazil, French Guiana, Peru, Venezuela	c [3], d, i, o, r [3], s, t, u, w [3]
Myrmicinae	*Crematogaster limata* F. SMITH, 1858 [2] *Crematogaster levior* LONGINO, 2003 [2] *Crematogaster carinata* MAYR, 1862 [2]	Brazil, French Guiana, Peru, Venezuela	c, d, i, k, o, s, t, u, w
	Crematogaster longispina EMERY, 1890	Costa Rica	d, h [3], i, k
	Crematogaster jardinero LONGINO, 2003	Costa Rica	l
	Pheidole violacea WILSON, 2003	Costa Rica	m, v
Ponerinae	*Odontomachus mayi* MANN, 1912	Brazil, French Guiana	d, n, o, q [3]
	Odontomachus panamensis FOREL, 1899	Costa-Rica, Panama	j, k
	Pachycondyla goeldii (FOREL, 1912)	Brazil, French Guiana	a, b, d, p, q [3], r [3]

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Tab. 2: True ant-garden epiphyte species (i.e., species that are specifically incorporated into the nest ➔ at the seed stage by the ants and / or observed only in AGs) in both the Paleo- and the Neotropics.

References: a BLÜTHGEN & al. (2001), b CATLING (1995), c CEDENO & al. (1999), d CORBARA & DEJEAN (1996), e DAVIDSON (1988), f DAVIDSON & EPSTEIN (1989), g DEJEAN & al. (2000), h KAUFMANN & al. (2001), i KAUFMANN (2002), j KAUFMANN & MASCHWITZ (2006), k KLEIJN & VAN DONKELAAR (2001), l KLEINFELDT (1978), m LONGINO (1999), n LONGINO (2003b), o NIEDER & al. (2000), p ORIVEL & DEJEAN (1999), q SCHMIT-NEUERBURG & BLÜTHGEN (2007), r YOUNGSTEADT & al. (2009).

[1] Some of the *Dischidia* species cited in KAUFMANN (2002) are not included here because they can be found outside of AGs (see WEIR & KIEW 1986).

[2] These species have been rarely observed in AGs, and no data are available on the incorporation of their seeds into the carton nest by the ants. Although data are also lacking about their occurrence outside of AGs, these species are still included as true AG species.

[3] References that explicitly support the dispersal of the seeds by AG ants.

Family	Species	Geographic area	References
Asclepiadaceae[1]	*Dischidia acutifolia* Maingay	Peninsular Malaysia	h[3], i[3]
	Dischidia albida Griff.	Peninsular Malaysia	h, i[3], j
	Dischidia bengalensis Colebr.	Peninsular Malaysia	h, i[3]
	Dischidia fruticulosa Ridl.	Peninsular Malaysia	i[3]
	Dischidia hirsuta Decne.	Peninsular Malaysia	h, i[3]
	Dischidia imbricate Steud.	Peninsular Malaysia	h, i[3]
	Dischidia longepedunculata Ridl.	Peninsular Malaysia	i[3]
	Dischidia punctata Decne.	Peninsular Malaysia	h, i[3], j
	Dischidia subalata Warb.	Peninsular Malaysia	i[3]
	Dischidia sp.	Peninsular Malaysia	i[3]
	Hoya brevialata Kleijn & Donkelaar	Sulawesi	k
	Hoya elliptica Hook. f.	Peninsular Malaysia	h, i[3], j
	Hoya lacunosa Blume	Peninsular Malaysia, Sulawesi	h, i[3], j, k
	Hoya micrantha Hooker	Peninsular Malaysia	i[3]
	Hoya mitrata Kerr	Peninsular Malaysia	i[3], j
	Hoya multiflora Blume	Peninsular Malaysia	i[3], j
	Hoya parvifolia Schltr.	Sulawesi	k
	Hoya picta Hort.	Sulawesi	k
	Hoya pubera Blume	Sulawesi	k
	Hoya spp.	Peninsular Malaysia	i[3]
Gesneriaceae	*Aeschynanthus albidus* Steud.	Peninsular Malaysia	h[3], i, j
	Aeschynanthus fecundus P. Woods	Peninsular Malaysia	h[3], i
	Aeschynanthus myrmecophilus P. Woods	Peninsular Malaysia	i[3]
	Aeschynanthus spp.	Peninsular Malaysia	i[3]
Melastomataceae	*Medinilla crassifolia* Blume	Peninsular Malaysia	i[3]
	Pachycentria constricta Blume	Peninsular Malaysia	i[3], j, k
	Pachycentria glauca Triana	Peninsular Malaysia	i[3], j, k
Moraceae	*Ficus* sp.	Peninsular Malaysia	i[3]
Urticaceae	*Poikilospermum cordifolium* Merr.	Peninsular Malaysia	i[3], j, k
	Poikilospermum microstachys Merr.	Peninsular Malaysia	i[3], j, k
Zingiberaceae	*Hedychium longicornutum* Griff. ex Baker	Peninsular Malaysia	i[3]
Araceae	*Anthurium gracile* Lindl.	Brazil, French Guiana, Peru, Venezuela	a, c d, e[3], g, o, p[3], q
	Anthurium ernestii Engl.	Peru	f
	Philodendron deflexum Poepp.	French Guiana, Peru, Venezuela	a, c, e[3], g, o, q
Bromeliaceae	*Aechmea mertensii* Schult. f.	Brazil, French Guiana	d, g, p[3],
	Aechmea tillandsioïdes Baker	Belize, Venezuela	a, b, q
	Neoregelia sp.	Peru	e[3], f
	Streptocalyx longifolius (Rudge) Baker	Brazil, French Guiana, Peru	e[3], f, g,
Cactaceae	*Epiphyllum phyllanthus* (L.)	Brazil, Peru, Venezuela	e[3], f, o, q
Gesneriaceae	*Codonanthe calcarata* Hanst.	Brazil, French Guiana, Venezuela	a, c, g, o, p[3], q
	Codonanthe crassifolia (Focke)	Costa Rica, French Guiana	c, d, l[3],
	Codonanthe macradenia Donn.Sm.	Belize	b
	Codonanthe uleana Fritsch	Brazil, Peru	e[3], f
	Columnea linearis Oerst.[2]	Costa Rica	m
	Columnea verecunda C.V. Morton[2]	Costa Rica	n
Moraceae	*Ficus paraensis* Miq.	Brazil, French Guiana, Peru	e[3], f, g
Orchidaceae	*Coryanthes speciosa* (Hook.)[2]	Belize	b
	Epidendrum imatophyllum Lindl[2]	Belize	b
Piperaceae	*Peperomia macrostachya* A. Dietr.	Brazil, French Guiana, Peru, Venezuela	e[3], f, g, p[3], r[3]
Solanaceae	*Markea ulei* (Dammer)	Peru	e[3], f
	Markea formicarum (Dammer)[2]	Brazil, French Guiana	g, p

aceae, and *Dischidia* spp., Asclepiadaceae) are common in Southeastern Asia and even often recorded in AGs (KAUFMANN & MASCHWITZ 2006). Those species that are restricted to AGs and whose seeds are dispersed by AG ants can thus be considered as true AG epiphytes (DAVIDSON & EPSTEIN 1989, KAUFMANN & MASCHWITZ 2006). The total number of epiphyte species in the Paleotropics, including Africa, is estimated at 12,600 (RICHARDS 1996). KAUFMANN (2002) recorded 84 epiphyte species from 16 plant families in AGs in Peninsular Malaysia, of which around 40 species have been defined as true AG species (Tab. 2). Nevertheless, further studies are still necessary to arrive at a more meaningful classification of true versus facultative AG epiphytes.

Creation of the association

When he discovered their existence, ULE (1901, 1905) hypothesized that AGs developed thanks to ants. He conducted seed-dispersal experiments that demonstrated that the ants transport the seeds of the epiphytes, and also postulated that the epiphyte species were AG specialists, cultivated by the ants and unable to grow elsewhere. Later, WHEELER (1921) rejected Ule's view, stating that the epiphytes' presence on the trees must precede the arrival of the ants. Subsequent studies have all demonstrated that Ule's findings were correct. Ants do indeed initiate AGs, both in the Neotropics and in the Paleotropics (DAVIDSON 1988, CORBARA & DEJEAN 1996, ORIVEL & DEJEAN 1999, KAUFMANN & MASCHWITZ 2006). The ants first build a carton nest from plant fibres and then incorporate epiphyte seeds into them. Seeds are also added continuously during the lifetime of the ant colony, thus ensuring a permanent turnover of the epiphytes if some were to die.

How ants initiate AGs has only been studied to date for a single species from the Neotropics, the ponerine ant *Pachycondyla goeldii* (see CORBARA & DEJEAN 1996, ORIVEL & al. 1998), but the process is probably similar for other AG ants. In this species, colony foundation is pleometrotic (i.e., multiple queens are involved). The queens start to build a small carton nest on the upper surface of a leaf, between two leaves or on a small branch. At this stage, the queens already begin to incorporate seeds collected from the surroundings, mostly from vertebrate-dispersers' droppings. Later, the workers enlarge the nest as the colony and the epiphytes grow. As for most AG ants, the colonies of *P. goeldii* are frequently polycalic, and the nests are distributed in the same or in several host trees (DENIS & al. 2006).

Although almost every epiphyte species can be associated with any ant species able to initiate AGs, preferential associations between ant and epiphyte species do exist (KLEINFELDT 1978, MARINI-FILHO 1999, ORIVEL & DEJEAN 1999, KAUFMANN & MASCHWITZ 2006). Even if abiotic factors might favour or limit the growth of the epiphyte seedlings, the observed preferential associations result mostly from seed selection by the ants, at least in the Neotropical AGs (ORIVEL & DEJEAN 1999). As a result, each species is preferentially attracted to and transports the seeds of the epiphyte species with which it is mainly associated. Such preferences do not result from differences in the quality or quantity of the food rewards, as the same preferences can be observed when the elaiosomes are removed (ORIVEL & DEJEAN 1999) and also as these seeds are not retrieved by ant species that do not build AGs (DAVIDSON

1988, YOUNGSTEADT & al. 2009). Consequently, seed retrieval and preferences in AG ants are mainly related to chemical cues on the surface of the seed.

An investigation into the chemicals on AG seeds showed that volatile attractants are present on the seed surface, and that the chemical compounds are sufficient to attract AG ants (YOUNGSTEADT & al. 2008). Among these volatiles, methyl 6-methylsalicylate [6-MMS] is common to most AG epiphytes, and might, thus, at least partly explain the retrieval of AG seeds by AG ants (SEIDEL & al. 1990). Interestingly, 6-MMS has never been reported in plants other than those restricted to AGs, but it has been isolated in the glandular secretions of several ant species (BRAND & al. 1973, DUFFIELD & BLUM 1975, MORGAN & al. 1990, SEIDEL & al. 1990, GREENBERG & al. 2007). Nevertheless, bioassays conducted on this compound alone showed that 6-MMS is surely not solely responsible for seed selection and retrieval (DAVIDSON & al. 1990). Moreover, several other volatiles have been isolated from AG seeds, although their occurrence might not be constant across species (SEIDEL & al. 1990, YOUNGSTEADT 2008). The bioassays performed with single compounds did not elicit seed selection (DAVIDSON & al. 1990), and, if the mixture of active molecules identified by gas chromatography-electroantennographic detection in the epiphyte *Peperomia macrostachya* A. DIETR. was attractive to *Camponotus femoratus*, no seed retrieval could be induced (YOUNGSTEADT & al. 2008). Such results confirm the role of volatiles in the attraction of AG ants toward the seeds of AG epiphytes, but also point out that further studies are needed to identify the role of volatiles versus contact cues in triggering seed-carrying behaviour. Moreover, the role of volatiles has been demonstrated in a single epiphyte species, *Pe. macrostachya*, and in a single ant species, *Ca. femoratus*. The diversity of Neotropical AG ants and epiphytes suggests the existence of shared properties in the AG seed chemicals, which also points to the need for further investigation. On the one hand, YOUNGSTEADT (2008) identified several volatiles common to AG seed species and absent from non-AG plants. On the other hand, preliminary results also suggest, however, that the behavioural and ecological convergence observed in the interactions between AG ants and seeds could result from different chemicals (KAUFMANN 2002, YOUNGSTEADT 2008). In addition, the nature of the attractive cues involved in the dispersal of seeds in Paleotropical AGs is still mainly unknown, and also deserves further study to highlight any possible convergence with Neotropical AGs. The only study that investigated these cues in Paleotropical AGs showed that specific chemical cues produced by AG seeds and not present on the seeds of non-AG epiphytes may be involved; moreover these semiochemicals seem to act at contact rather than from a distance (KAUFMANN 2002).

Shared benefits

The association between ants and epiphytes in AGs is the result of a mutualistic interaction in which, by definition, both parties benefit. The main plant benefits are quite obvious and combine the principal positive outcomes found in both dispersal interactions (i.e., myrmecochory) and protective mutualisms. First, as shown above, the seeds are collected by the ants either directly from the fruits, or, after a first dispersion phase by vertebrates (MACEDO & PRANCE

1978, MADISON 1979, DAVIDSON 1988), or they are transported by the wind (KAUFMANN 2002). These seeds are, however, not only dispersed by the ants, but they are also integrated into a nutrient-rich carton structure (BLÜTHGEN & al. 2001). This carton is made of various organic materials and is much richer in N, P and K than the subjacent soil thus favouring the growth of the plants (BELIN-DEPOUX 1991, BENZING 1991, BLÜTHGEN & al. 2001, KAUFMANN 2002). Indeed, the survival of seedlings and the growth of AG plants are strongly and negatively affected by the loss of the carton substrate (KLEINFELDT 1978, SCHMIT-NEUERBURG & BLÜTHGEN 2007). Moreover, this substrate is continuously cared for by the ants, which also aids in the survival and maturation of AG epiphytes (LONGINO 1986, SCHMIT-NEUERBURG & BLÜTHGEN 2007). The other difference with most common examples of myrmecochory is linked to the specificity of the interactions. While most terrestrial myrmecochores are dispersed by a variety of ant species with little or no specificity (BEATTIE & HUGHES 2002, GILADI 2006), AG plant species represent only a subset of epiphytes and they are dispersed by only a few ant species (YOUNGSTEADT & al. 2009). Second, these seeds and later the plants not only benefit from dispersal, but also from biotic protection as in myrmecophytic mutualisms (HEIL & MCKEY 2003). The ants provide a constitutive defence to the plants through their constant patrolling of the AG epiphytes, but little induced defence (i.e., mass-recruitment of nestmates following leaf damage) has been observed (VANTAUX & al. 2007). Such low response to foliar damages contrasts with similar studies conducted on myrmecophytes (see AGRAWAL & DUBIN-THALER 1999, CHRISTIANINI & MACHADO 2004, ROMERO & IZZO 2004, GRANGIER & al. 2008). Nevertheless, specialized predators of the epiphytes are able to circumvent the biotic protection provided by the ants (CORBARA & al. 1999, ORIVEL & DEJEAN 2000). Also, in terms of costs, ants may hinder the reproduction of the plants because the protection they provide to the plant can also deter pollinators, and thus interfere with the pollination process (BEATTIE & HUGHES 2002, NESS 2006). Potential conflicts between plant reproduction and ant activity seem to be prevented by the high level of autogamy in the epiphyte species recorded in Neotropical AGs (MADISON 1979, DAVIDSON 1988).

As the epiphytes grow, their roots strengthen the structure of the nest. Their leaves constitute a physical barrier against heavy rains, and they can act as living sump pumps by transpiring the water out of the rain-soaked carton between rain showers (YU 1994, SCHMIT-NEUERBURG & BLÜTHGEN 2007). Several epiphyte species can also provide the ants with food resources in the form of extrafloral and floral nectar, elaiosomes and fruit pulp (KLEINFELDT 1978, MADISON 1979, DAVIDSON 1988, KAUFMANN 2002). Most of the true AG epiphyte species in the Neotropics present common characteristics including fleshy fruits (except in the genus *Peperomia* where the fruits are achenes) and small seeds (less than 5 mm) with elaiosomes (MACEDO & PRANCE 1978, MADISON 1979, DAVIDSON 1988). It should be noted, however, that such elaiosomes differ from those on typical myrmecochorous seeds as they are not needed to elicit the dispersal of the seeds by AG ants (ORIVEL & DEJEAN 1999). In the Paleotropics, two types of AG epiphyte seeds can, however, be distinguished: (I) wind-dispersed seeds equipped with a hairy appendage,

and (II) bird-dispersed seeds enclosed in a fleshy, fruit pulp (KAUFMANN 2002).

Nevertheless, in most cases, the amount of food supplied by the epiphytes to the ants cannot be considered as major. On the one hand, some of these resources can be indeed seasonal if flowering does not occur throughout the year. On the other hand, several ant species are mostly or even solely predatory (ORIVEL & al. 1998, 2000), while other species rely mainly on carbohydrates for their diet. In these cases, they rely mostly on the honeydew of hemipteran trophobionts that very rarely feed on the AG epiphytes (J. Orivel & C. Leroy, unpubl.).

Parabiosis

In both the Neo- and the Paleotropics, two ant species can frequently live in association within an AG. Such associations, called parabioses (FOREL 1898), differ from the other associations between ant colonies (WHEELER 1901). They result in non-obligatory, mixed colonies where the two ant species tolerate each other and share the same nest, but keep their brood separate. Moreover, the associated species can exploit the same food sources (FOREL 1898, WHEELER 1921).

Parabiotic associations have also been discovered outside of AGs and even between insects other than ants (RASA 1994, LENOIR & al. 2001, ERRARD & al. 2003, MENZEL & al. 2008b). Studies of the cases involving ants have highlighted the global pattern of reciprocal, interspecific tolerance between two partners sharing the same nest. Moreover, such tolerance exists regardless of a congruency in the cuticular hydrocarbon profile, contrary to the general strategy developed by ant symbionts and parasites for entering into ant colonies (LENOIR & al. 2001, ERRARD & al. 2003, MENZEL & al. 2008b). Note, however, that the parabiotic colonies in AGs differ from other cases of parabiosis for at least two characteristics. First, and at least in the association between *Odontomachus mayi* MANN, 1912 and *Crematogaster limata* F. SMITH, 1858, mutual tolerance in parabiotic AG ants is limited to the individuals belonging to the associated colony (ORIVEL & al. 1997), while the absence of aggressiveness can extend to allocolonial individuals from the associated species in the other cases (ERRARD & al. 2003, MENZEL & al. 2008b). Second, selective tolerance in parabiotic Asian species is linked to the acquisition of allospecific, cuticular substances (hydrocarbons and steroids). Even if these substances do not induce a chemical mimicry in the cuticular profiles of the species, they suffice to ensure acceptance by the partner colony (MENZEL & al. 2008a, 2009). Only cuticular hydrocarbons have been studied, however, in parabiotic colonies in AGs, and thus studies on the presence and subsequent role of steroids or other unusual classes of cuticular compounds would be of interest in understanding these systems.

Parabioses are also the only known example of mutualistic associations between ant species. In AGs, if *Cremato-gaster levior* benefits from nest building, including seed-carrying behaviour and protection by the larger and more aggressive *Camponotus femoratus*, the latter species benefits from the ability of *Crematogaster levior* to discover food sources during foraging. *Camponotus femoratus* workers are indeed able to follow *Crematogaster levior* trails – although this has not yet been demonstrated experimentally – and to steal prey thanks to their competitive superi-

ority (SWAIN 1980, VANTAUX & al. 2007). Moreover, both species participate in the biotic protection of their nest epiphytes, demonstrating the existence of reciprocal beneficial outcomes for each interacting partner in AGs (DAVIDSON & EPSTEIN 1989, VANTAUX & al. 2007). The study of shared benefits in Asian parabioses has also demonstrated the better foraging abilities of the *Crematogaster* species (*Cr. modiglianii* EMERY, 1900) and the ability of the *Camponotus* species (*Ca. rufifemur* EMERY, 1900) to follow *Ca. modiglianii* trails and to take advantage of the food source. In the same way as it does in AGs (WHEELER 1921, DAVIDSON 1988), *Ca. modiglianii* might benefit from the defensive abilities of the larger species (MENZEL & BLÜTHGEN 2010).

Epiphyte distribution and phorophytes

As carton-nest builders and seed dispersal agents, AG ants play a crucial role in epiphyte distribution. AGs are common in areas with relatively high light intensity, and AG ants are often the dominant organisms in the canopy fauna in several natural and disturbed environments, such as along natural and artificial corridors and in natural and disturbed forest areas (WILSON 1987, BELIN-DEPOUX 1991, DEJEAN & al. 2000). Moreover, because AG ant colonies are frequently polydomous, the distribution of epiphytes is highly clumped and not random (NIEDER & al. 2001). The vertical distribution of epiphytes also varies among most species. Such vertical distribution patterns can be linked to both the light requirements of the species and the preference of the ant species for light-intense or more shaded environments. Consequently, some groups of epiphyte species can be considered as light-demanding species while others are more shade tolerant (DAVIDSON 1988, DEJEAN & al. 1997, NIEDER & al. 2001). It should be noted, however, that this separation is not strict, and that most epiphyte species can survive and reproduce in most environmental conditions where AGs are found. Nevertheless, this might not be without consequences for the interaction (see below).

Besides their preferences for certain habitats, AG ants can also exhibit some preferences or specificities towards certain phorophyte species (i.e., host tree species). In Southeastern Asia, two species of *Crematogaster* are specifically associated with different species of giant bamboo (KAUFMANN & al. 2001). In the Neotropics, several preferential associations have also been found involving species of phorophytes that bear extrafloral nectaries or are able to sustain populations of Hemiptera (DAVIDSON 1988, DEJEAN & al. 1997). In all cases, AGs are abundant in areas where the level of productivity of the resources made available to the ants is especially high (DAVIDSON 1988, KAUFMANN & MASCHWITZ 2006). Also, in pioneer forest areas of French Guiana, the spatio-temporal distribution of AG ants changes during the development of the vegetal formations (DEJEAN & al. 2000). The ponerine *Pachycondyla goeldii* is predominant in young pioneer vegetal formations, whereas *Camponotus femoratus* and *Crematogaster levior* are more abundant in older formations.

Ants mediate epiphyte traits and the diversity of invertebrate communities

As mentioned above, the distribution of AGs varies according to the initiating ant species. In French Guiana, *P. goeldii* preferentially colonizes small trees in light-intense environments, whereas *Camponotus femoratus* rather colo-

nizes larger trees in more shaded areas. Such a difference in habitat preferences is echoed in the shape and leaf structure of AG epiphytes, as demonstrated for the tank-bromeliad *Aechmea mertensii* SCHULT. f. (Bromeliaceae) (LEROY & al. 2009a). In this epiphyte, the interlocking leaves form a well (or "phytotelm") that holds rainwater, and, therefore, provides a habitat for aquatic macro- and microorganisms (Fig. 2; RICHARDSON 1999, KITCHING 2000). Light-exposed bromeliads associated with *P. goeldii* are smaller and limit direct light incidence by adopting an amphora shape, whereas those growing in partial shade and associated with *Ca. femoratus* are larger and forage for light by developing a wider canopy (LEROY & al. 2009a). This phenotypic variability has a direct influence on the amount of rainwater and leaf litter intercepted by the tank-forming leaves. By coexisting on a local scale, the two ant species generate a gradient of habitat conditions (space and food) for the aquatic invertebrates, and the diversity of invertebrate communities increases with greater volumes of water and fine detritus (CÉRÉGHINO & al. 2010). Invertebrate species richness and abundance are significantly higher in *Ca. femoratus*-associated bromeliads. The source of nutrients for the aquatic food web, as well as for the bromeliad, comes from the detritus (e.g., windborne particulates, faeces, and dead leaves and animals) that enter into the tanks (BENZING 2000, NGAI & SRIVASTAVA 2006). LEROY & al. (2009a) showed that nitrogen acquisition is significantly higher in *Ca. femoratus*-associated bromeliads in relation to the higher diversity of aquatic communities. Thus, in an AG-associated bromeliad, the species of the ant partner indirectly influences nitrogen assimilation (and consequently plant fitness) through a kind of plant-invertebrate-plant feedback loop (LEROY & al. 2009a, b, CÉRÉGHINO & al. 2010).

Conclusion and prospects

AGs are the only example of an interaction between ants and plant in which the plants experience a net outcome that encompasses the three main categories of benefits generally found in such mutualisms. The plants are dispersed, protected from enemies and fed by the nutrient-rich carton of the ant nest. In turn, the ants benefit mainly from a structural protection provided by the plants and this acts as a buffer against abiotic factors. Moreover, the AG model system exemplifies the global complexity that interspecific interactions can exhibit (Fig. 2). Carton-nest building and associations with epiphytes are two common traits in ants (LONGINO 1986, DEJEAN & al. 1995, STUNTZ & al. 2003, GIBERNAU & al. 2007), but the transport and integration of epiphyte seeds into a previously built carton nest can be considered as a key feature of AGs (but see MAEYAMA & MATSUMOTO 2000, KAUFMANN & MASCHWITZ 2006). Some other ant species can nevertheless be attracted to and transport the seeds of AG epiphytes, but in such cases the survival and / or maturation of the plants is strongly affected (DAVIDSON 1988, DAVIDSON & EPSTEIN 1989, YOUNGSTEADT & al. 2009). AGs can thus be considered as special cases of ant-epiphyte interactions, representing a subset of the community of arboreal ant and epiphyte species in all of the areas where they occur. Nonetheless, the ecology of AGs is still only partially understood to date, mostly because of the lack of data on both the ability of most ant species to initiate AGs and on the retrieval and integration into the carton of the seeds of most AG-re-
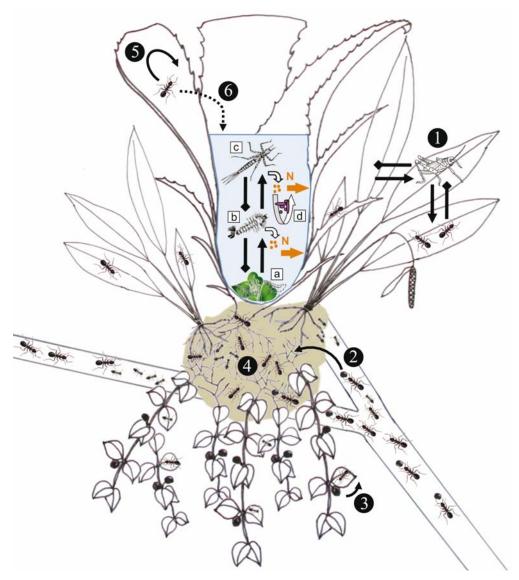
Fig. 2: Summary of the interactions between the ants, plants and aquatic community living in the phytotelm of the bromeliad *Aechmea mertensii* in Neotropical ant gardens. Bullets indicate negative interactions caused by consumption (top-down effect), arrowheads indicate positive effects (bottom-up effect) and dotted lines indicate indirect effects. Plants benefit from (1) protection from defoliating insects, (2) seed dispersal and incorporation into the carton nest by the ants. The plants provide (3) food rewards such as pulp fruits or elaiosomes to the ants, and (4) an increase in the structural stability of the nest from the roots. Ants modulate (5) the plant phenotype directly, and (6) the phytotelm structure of the bromeliad indirectly. (a) Vegetal and organic animal matter, (b) detritivores (shredders or collectors), (c) predators, and (d) microorganisms. N: nitrogen is made available to the bromeliad through the bacterial decomposition of faeces, and organic matter.

stricted epiphyte species. Such data are, however, crucial to shedding light on the ecological interaction networks in AGs, and thus to understanding the evolution of traits that determine relationships across species.

The interaction between ants and epiphytes is clearly mutualistic. The lack of obvious adaptations does not suggest that they result from coevolutionary processes (i.e., reciprocal evolutionary changes). Further studies on the chemicals involved in seed dispersal might, however, help in deciphering the putative role of co-evolution in these interactions. The chemical similarity of the compounds involved across species and their specific attractiveness for AG ants are the two key elements needed to favour evolutionary specialization and co-adaptation in this interacting system. Such chemicals have only been partly identified, and much effort still remains to be made on this subject (DAVIDSON & al. 1990, SEIDEL & al. 1990, KAUFMANN 2002, YOUNGSTEADT 2008, YOUNGSTEADT & al. 2008). Alternatively, comparative studies on the geographic variations in the identity of the interacting partners, in their biological traits and in the outcomes of the interactions would reveal the relative importance of reciprocal evolutionary changes versus pre-adaptations in these systems. In the Neo- and the Paleotropics, AGs are found across large geographic areas. Both the identities of the interacting partners and / or their abundance vary across the entire range, and, if historical factors might have influenced the actual observed patterns, other factors such as co-adaptations

might be of importance. Future studies on species-interaction networks across a large geographical range and including the intensity of the interactions would be of interest in demonstrating the role and importance of local adaptation versus pre-adaptation in these systems.

Moreover, several true AG ant species generally coexist on a local scale and they interact with the same epiphyte species – although preferential associations have been observed (ORIVEL & DEJEAN 1999). Such coexistence, associated with differences in the ecology and behaviour of the species might select for different seed traits. Studies on the population genetic structure of both the ants and their associated plants would then be of interest in highlighting possible correlations in the kin structures of both partners. In French Guiana, for example, *Camponotus femoratus* and *Pachycondyla goeldii* are two frequent AG ant species that are sympatric. They differ in their seed retrieval behaviour (directly from the fruits versus vertebrates' droppings, respectively). The beneficial outcomes for the epiphytes also vary according to the associated ant species, at least in *Aechmea mertensii* (see LEROY & al. 2009b). Such differences could have a strong impact on the association. If seed traits are under selection pressure by the ants, then being associated with an ant species (*Ca. femoratus*) that provides greater benefits and favours the growth of the offspring of this plant in similar conditions are arguments for selection and thus co-adaptation.

Another level of complexity in AGs depends on the commonness of the parabiotic associations between ant species. Although not restricted to AGs, parabioses are frequent and this unique type of interaction between ant species makes AGs multipartite and mutualistic associations. Recent advances in the understanding of parabioses have focused on the behavioural interactions and recognition cues used by the ant species, but much remains to be done towards understanding the evolutionary origin of the phenomenon and the genetic structure of the populations and its consequences for the epiphytes. The development of molecular markers for the most frequent parabiotic species, *Ca. femoratus* and *Crematogaster levior*, will surely help in the clarification of these aspects (BOOTH & al. 2009a, b).

Finally, AGs are also a striking example of the way an ant-plant mutualism can increase the population density of the partners and affect community patterns (WILSON 1987, DAVIDSON 1988, NIEDER & al. 2000). As ecologically dominant species, most AG ants directly or indirectly affect the entire invertebrate community located within their territory. Such an impact has already been thoroughly examined in studies on the arboreal ant mosaic (LESTON 1973). Ant mosaics are driven by direct interactions between ant species, dominance hierarchies and resource utilisation, and lead to positive and negative associations between species pairs (ROOM 1971, MAJER & al. 1994, BLÜTHGEN & STORK 2007). AG ants also have an indirect impact on the invertebrate community because of their interaction with epiphytes. As epiphyte gardeners, AG ants directly shape epiphyte distribution and dispersal (NIEDER & al. 2000). Context dependency, however, strongly modulates the beneficial outcomes for the plant as the habitat preferences of the dispersers (ant species) may influence the plant phenotype (CHAMBERLAIN & HOLLAND 2009, LEROY & al. 2009a, CÉRÉGHINO & al. 2010). This is clearly demonstrated when the invertebrate community living in an AG phytotelm af-

fects nitrogen acquisition by the plant, and, thus, its fitness. Such a context-dependent effect might not be without consequences for the outcomes of the ant-plant interaction, although this interaction remains globally mutualistic (LEROY & al. 2009b).

Zusammenfassung

Mutualistische Interaktionen von Ameisen und Pflanzen sind wichtige Merkmale vieler Ökosysteme. Sie können in drei übergeordnete Kategorien eingeteilt werden: Myrmekochorie, Mutualismus zum Schutz der Pflanzen und Myrmekotrophie. Sowohl in den Neotropen als auch den südostasiatischen Paläotropen sind Ameisengärten, ein besonderer Typ von Ameisen-Pflanzen-Interaktionen, häufig. Um Ameisengärten zu gründen, integrieren Ameisen die Samen bestimmter Epiphyten in den Karton ihres Nests. Die Entwicklung der Pflanzen führt dann zu einer Anhäufung von Epiphyten, die im Karton wurzeln. Ameisengärten zählen wegen der plurispezifischen aber gleichzeitig spezialisierten Assoziation mehrerer phylogenetisch entfernter Ameisen- und Pflanzenarten zu den komplexesten Beziehungen zwischen Ameisen und Pflanzen. Das Ziel dieses Überblicksartikels ist die Synthese der Diversität und Ökologie von Ameisengärten, einschließlich der Effekte auf die einzelnen Partner in den Interaktionen und der direkten und indirekten Auswirkungen von Ameisengärten auf die Pflanzen- und Arthropodengemeinschaften.

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