In: Beetles: Biodiversity, Ecology and Role in the Environment ISBN: 978-1-63463-380-2
Editor: Camilla Stack

Chapter 7

HOW A LOCALITY CAN HAVE SO MANY SPECIES? A CASE STUDY WITH DUNG BEETLES (COLEOPTERA: SCARABAEINAE) IN A TROPICAL RAIN FOREST IN COLOMBIA

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ABSTRACT

Dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae) are one of the most important insect groups in tropical regions because their relevant ecosystem role as organic recycling agents, biological pest controllers and secondary seed dispersers. However, our knowledge of the different mechanisms that maintain assemblage structure and allow species coexistence is poor. We lack such information because dung beetle assemblages are often sampled over the short term, there are few studies that cover extended periods of time and broad spatial areas, and it is common to use just one type of trap and bait. To better explore the mechanisms underlying dung beetle coexistence, it was studied a beetle assemblage found in a tropical rain forest located in Tinigua National Park in Colombia. Sampling was conducted in August 1992, May-July and December 1994, January and December 1995, January and July 1996, January-July 1997, and January and July 1998. Dung beetles were sampled in the three main habitats found in the study area: mature mainland forest, flooded lowland forest, and river beaches. Specimens were collected using baited pitfall traps, flight interception traps, and baited elevated traps placed at different heights using different type of baits. In addition, feces from different vertebrates, vegetation, logs, fungi, litter, and fallen fruit were checked for the presence of dung beetles. A total of 70 species belonging to 19 genera and 7 tribes were collected. Compared to other areas, previously sampled in Colombia, this area demonstrates a remarkable diversity and has a very high level of species richness (one of the highest in the country). Nevertheless, it cannot be considered a hotspot for endemism because there is a strong influence and contribution of species of nearby biogeographic

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provinces to its own fauna. Some of the mechanisms that may affect the richness and structure of the assemblage, favoring the coexistence of species are: spatial partitioning (habitats and microhabitats), temporal partitioning (seasonality and dial activity), resource partitioning, and guild-specific resource relocation behavior. The values of the Jaccard similarity index reveal low levels of species overlap. Therefore, these coexistence mechanisms appear to act in tandem to partition the ecosystem in a way that decreases overlap among similar species, thus allowing a large number of dung beetle species to coexist in the same area. These results demonstrate that it is necessary to carry out broad-ranging and exhaustive sampling to fully characterize the structure of tropical dung beetle assemblages. Finally, to completely describe the assemblage composition at this locality, the following additional improvements should be made to the sampling protocol: carrying out exhaustive sampling over one full year; using more specialized baits; studying the forest canopy; searching in specialized microhabitats, such as bromeliads and ant and termite nests; and characterizing potential phoretic interactions with mammals.

Keywords: Assemblage structure, coexistence mechanisms, Macarena, richness, Scarabaeidae, Tinigua National Park

INTRODUCTION

The study and inventory of diverse areas is a global priority that should be supported with as much research infrastructure as possible, especially when it comes to extremely diverse groups that could be useful bioindicators in monitoring and conservation studies (Maguran 1988, Halffter & Favila 1993, Gaston & Hudson 1994, Hammond 1994, Myers et al. 2000). Dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae) are one of the most commonly used groups of insect bioindicators because of the important ecological roles they play (Nichols et al. 2008). Adults and larvae feed on dung produced by mammals, thus helping to recycle organic matter (Halffter & Matthews 1966, Howden & Young 1981, Halffter & Halffter 1989, Gill 1991). Besides this function, dung beetles act as parasitic controllers of flies and nematodes (Waterhouse 1974) and also as secondary seed dispersers (Estrada & Coates 1991, Andresen 2001).

Among the countries located in the Neotropics, Colombia has one of the highest levels of dung beetles diversity. Knowledge about this group has been growing over the last two decades thanks to the publication of several important articles (Escobar & Medina 1996, Amat et al. 1997, Amezquita et al. 1999, Escobar 2000, Medina et al. 2001, 2002, Escobar 2004, Escobar et al. 2005, Fuentes & Camero 2006, Noriega et al. 2007, Martinez et al. 2009, Giraldo et al. 2011, Solis et al. 2011, Cultid et al. 2012, Delgado-Gómez et al. 2012, Noriega et al. 2012, Otavo et al. 2013). However, some of these studies cover only short time periods of sampling and use only a few different types of traps, frequently with just one kind of bait, which means that they are little more than rapid surveys of biodiversity; consequently, they provide an incomplete characterization of dung beetle assemblage richness.

In ecological classic literature is commonly assumed that the dynamic of the structure of an assemblage is influenced mainly by interspecific competition of a limiting resource in space and time, affecting the coexistence of more then two species (Hairston et al. 1960, Levins & Culver 1971, Hastings 1980, Tilman 1980, Atkinson & Shorrocks 1981, Connor & Simberloff 1983, Schoener 1983). Following the principal of competitive exclusion, two species cannot occupy the same ecological niche and if the resource they share is a limiting factor one of them will exclude the other one (Hardin 1960). In this sense, several studies with dung beetles have found that competition is an important factor that affects the composition, richness and abundance in assemblages (Hanski 1981, Holter 1982, Peck & Forsyth 1982, Giller & Doube 1989, Hanski & Cambefort 1991, Giller & Doube 1994, Montes de Oca & Halffter 1995, Hirschberger 1998, Krell-Westerwalbesloh et al. 2004, Feer & Pincebourde 2005, Horgan 2005, Horgan & Fuentes 2005, Vernes et al. 2005, Horgan 2006, Hernández et al. 2011). However, there is so few information that characterizes the mechanisms that support the coexistence in rich-species assemblages localities.

This study aimed to provide greater insight into this group by conducting a complete species inventory at one of the most biologically interesting areas in the country (Noriega et al. 2015). The study's main question was the following: how can a given area support such a large number of species? The goal was also to understand the coexistence mechanisms operating in the dung beetles assemblage that minimize interspecific competition, including spatial, temporal, and resource partitioning as well as resource relocation behavior.

MATERIALS AND METHODS

Study Area

The study was carried out at the Center for Ecological Research of La Macarena (Spanish abbreviation: CIEM); the study area (2º40' N - 74º10' W, 350-400 m.a.s.l.; Figure 1) was situated in a tropical rainforest found to the west of the Duda river, 13 km upstream from the Duda's junction with the Guayabero, and located near the eastern border of Tinigua National Park (201.875 ha; Meta Department, Colombia). The park was created in 1989 to establish a biological corridor between the parks of La Macarena and Picachos. The Serrania of La Macarena is part of the biogeographic province of the Guayana presenting a complex mosaic of faunal and floral elements (Hernandez et al. 1992).

The region is characterized by a high degree of seasonality (Kimura et al. 1994). The dry season lasts from December to March, and rainfall varies the rest of the year (>100 mm per month). Average annual rainfall is 2600 mm; monthly rainfall is lowest in January (as low as 0 mm) and highest in May (up to 530 mm). Average annual temperature is 25°C (Kimura et al. 1994). The area has soils with different and complex geological origins. They were largely created by Plio-Pleistocene alluvial plates, experiencing recent tectonic fracturing and water erosion; consequently, they have low fertility and a poor cationic exchange capacity, are oligotrophic and deficient in mineral elements (Hirabuki 1990).

Sampling was carried out in the study area's three main habitats (described by Hirabuki 1990; Figure 2):

- Mature mainland tropical rain forest (MF): primary tropical rainforest with a continuous canopy containing trees of 25–30 m and emergent trees that reach 35 m. This type of forest is associated with the highest diversity of tree species (Barbosa & Hirabuki 1992) and has the highest vegetative cover in the area (53%) (Hirabuki 1990, Stevenson et al. 2004).

- Flooded lowland tropical rain forest (FF): lowland forest located on flatlands that are partially flooded during the rainy season by the river. It has a discontinuous canopy that is dominated by *Ficus* spp., *Inga* spp., and *Cecropia* sp. and an underbrush that contains mainly *Heliconia* spp. In this area, vegetative cover is 11% in this type of forest (Hirabuki 1990).
- River beaches (RB): beaches located on the banks of the Duda river. Their number and size vary throughout the year depending on rainfall seasonality. During the rainy months, the river increases in volume and covers the beaches completely within a few days. In the dry season, the beaches reappear, although the river never dries up completely. During the dry months, sand surface temperatures reach 50–55°C. These beaches are characterized by a type of early successional riparian forest containing *Tessaria integrifolia* and young trees of *Cecropia* sp.

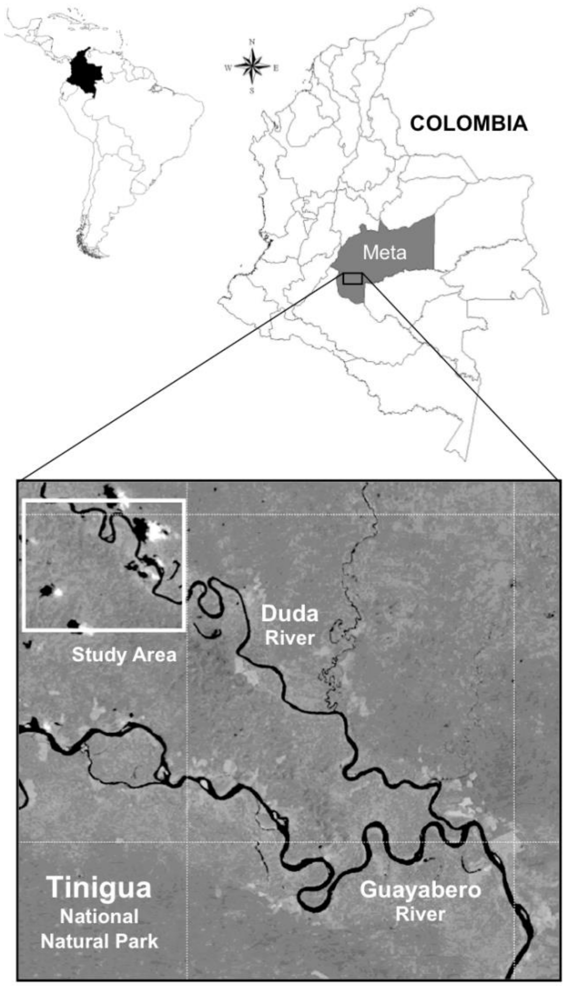

Figure 1. Geographical location of the study area: CIEM - Tinigua National Park, Meta Department, Colombia.

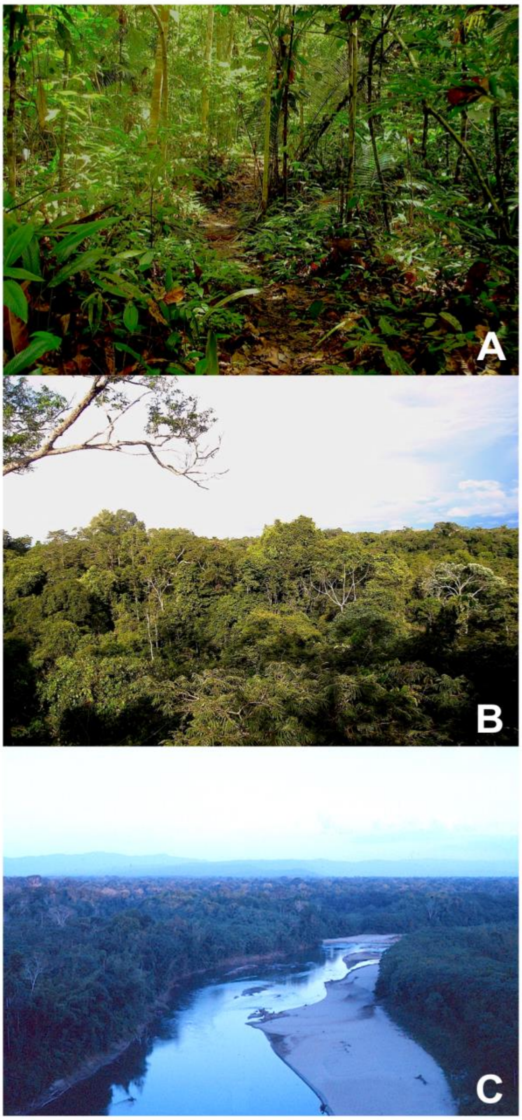

Figure 2. Habitats sampled at CIEM - Tinigua National Park, Meta Department, Colombia. A) Mature mainland tropical rain forest - MF, B) Flooded lowland tropical rain forest – FF and C) River beaches – RB.

In terms of vertebrates this area is a diverse spot with high species richness in different orders as Artiodactyla (3 spp.), Carnivora (9 spp.), Lagomorpha (1 sp.), Perissodactyla (1 sp.), Rodentia (6 spp.) and Xenarthra (5 spp.) (Stevenson 2002). In addition, it is home to seven coexisting species of primates: *Lagothrix lagothricha* (Humboldt, 1812 – common woolly monkey), *Sapajus apella* (Linnaeus, 1758 - brown capuchin), *Ateles belzebuth* Geoffroy, 1806 - spider monkey, *Alouatta seniculus* (Linnaeus, 1766 - red howler monkey), *Saimiri sciureus* (Linnaeus, 1758 - squirrel monkey), *Callicebus cupreus* (Spix, 1823 - red titi) and *Aotus brumbacki* Hershkovitz, 1983 - brumback´s night monkey (Stevenson 2002). Woolly monkeys and howler monkeys have the highest densities and levels of biomass (Stevenson & Quiñones 1993).

Dung Beetles Sampling, Data Review and Food Relocation Guilds

The author collected specimens in the habitats described above between June to July 1994, December 1994 to January 1995, December 1995 to January 1996, as well as in July 1996 and January 1998. Besides, other researchers studying dung beetles in the same area also collected some samples (from January to July 1997 and in July 1998) that were included in the analyses. In addition, it was included data from specimens that were found while going through the review of the largest entomological collections in Colombia: Entomological Collection Instituto Alexander von Humboldt (IAvH), Entomological Collection Instituto de Ciencias Universidad Nacional de Colombia (ICN-MHN), Entomological Collection Universidad de Antioquia (CEUA), Entomological Collection Universidad del Cauca (MHN-UC), Entomological Collection Pontificia Universidad Javeriana (MPUJ), Entomological Collection Universidad de Nariño (PSO), Entomological Collection Universidad de Tunja (CCM-FM) and Entomological Collection Natural History Museum of Universidad de Los Andes (EANDES). These collections contain some specimens that were collected during some of the same time periods as those mentioned above as well as some specimens collected in August 1992 and May 1994. Furthermore, data were added from any published reports or studies for which dung beetles in this area were sampled (Castellanos et al. 1999, Laverde et al. 2002, Noriega 2002b, 2004, Noriega & Calle 2008, Noriega 2011, Noriega & Acosta 2011, Noriega 2012).

Specimens were collected using pitfall trap arrays (Noriega & Fagua 2009); traps were baited with human excrement, carrion (rotten fish, squid, calamari, and chicken), or fruit (banana) and were left at least 48 hours (20160 hours/traps; Noriega et al. 2005). Flight interception traps were also used. Arrays of elevated traps placed at different heights were baited with human excrement, rotten fish, mushrooms, and decaying fruit (Noriega, unpubl. data). Additionally, dung from different vertebrates—such as *L. lagothricha, A. seniculus, Hydrochaeris hydrochaeris* (Linnaeus, 1766) (capybara), *Crocodylus intermedius* (Graves, 1819) (Orinoco crocodile), and *Tapirus terretris* (Linnaeus, 1758) (brazilian tapir)—was visually inspected for the presence of beetles. In addition, individuals were manually collected from vegetation, logs, flowers, fungi, leaf litter, and fallen fruit along the CIEM's trail system.

All specimens were preserved in 70% ethanol upon collection. They were later dried and identified to species using different taxonomic keys (Halffter & Martinez 1977, Howden & Young 1981, Kohlmann 1984, Jessop 1985, Edmonds 1994, Genier 1996, Kohlmann & Solis 1997, Cook 1998, Edmonds 2000, Medina & Lopera 2000, Kohlmann & Solis 2001, Solis & Kohlmann 2002, Edmonds & Zidek 2004, Solis & Kohlmann 2004, Kohlmann & Solis 2006, Vaz-de-Mello 2008, González et al. 2009, Camero 2010, Edmonds & Zidek 2010, Molano & Medina 2010, Vaz-de-Mello et al. 2011, Cupello & Vaz-de-Mello 2013, Solis & Kohlmann 2013), reference specimens in entomological collections, and the assistance of taxonomic experts. A reference collection was deposited at the EANDES in Bogotá, Colombia, and specimens from almost all the species collected were distributed to various entomological collections in Colombia: IAvH, ICN-MHN, and Universidad Pedagógica Nacional (MHNUPN). Specimens were also placed in the personal reference collections of Alejandro Lopera (CAL) and the author (CJAN).

Dung beetles food-relocation groups incorporated in the analysis where defined using the guilds described by Bornemissza (1976) and Halffter & Edmonds (1982): paracoprids (T, tunnelers)—species that dig a vertical tunnel below the food resource and transport a fraction of it into the bottom of the burrow to build their nests; telecoprids (R, rollers)—species that make a ball from the resource, roll it horizontally and later bury it into the ground building a nests; and endocoprids (D, dwellers)—species that occur within the food resource and make their nests there or in the interphase soil – resource. Since, for some species, it was impossible to directly observe specific relocation behaviors in the field, the distinctive behavior of the genus was assumed to occur.

In addition, the beetles were placed in three researcher-defined size categories: small (<10 mm), medium (10–18 mm) and large individuals (>18 mm). This was an adaptation of the system proposed by Doube (1990).

Data Analysis

An Excel matrix was constructed using the information on the niche characteristics of all of the 70 species sampled (habitat, season, dial activity, resource preferences, and guild-resource relocation behavior). These niche characteristics (coded as 14 grouped binomial variables placed in 6 ecological categories) were transformed into orthogonal components by performing a principal coordinates analysis on a matrix of Jaccard similarities. The five first components that accounted for more than 5% of the variability of the original matrix (70 species x 14 variables) and that, in addition, fulfilled the "broken stick" criterion were retained (Peres-Neto et al. 2006). Ecological patterns were interpreted by examining the five components obtained and comparing the positions of each species in each component based on the variable states (0-1); for each component, variables were selected using ANOVAs ($p<0.001$).

Using all of the species positions (derived from the principal coordinates analysis), a matrix of the Euclidean distances between the different pairs of species was obtained. Using this new matrix, it was possible to calculate the overall average distance between species as well as the average of the top 1% of distances between species ($C_{70,2}=2415$). These two measurements reveal the average and maximum degree of ecological divergence between species, respectively.

The matrix of 70 species x 5 components, which defined the ecological niches of the species in the study area, was used to generate 9999 neutral matrices of the "ecological positions" of the species. The neutral positions of the 70 species in each of the five orthogonal components were determined by randomly redistributing the values of the species within each component; consequently, because species values were not correlated across components, it was ensured that the different components would not be related (i.e., $r\approx0$).

These neutral matrices had the same dimensions (70 x 5) and contained the same amount of information as the original matrix of observed values. However, because they described randomly generated species, whose niches were not determined by real-life interspecific ecological interactions, they served as controls that could be used to determine if the observed degree of ecological packing was greater or less than what would be expected according to a neutral model based on random distributions. The overall average distance between the 70 species as well as the average of the top 1% of distances between species were calculated for each of the 9999 neutral matrices.

These values were used to build two distributions, which revealed whether the observed average and maximum degrees of species divergence were greater or smaller than what would be expected by chance. In addition, a species similarity analysis based on the Jaccard index was performed using all the ecological characteristics examined. All the analyses were done using the free statistical software packages PAST (v. 3.02, 2014; Hammer et al. 2001) and PopTools (v. 3.2; Hood 2010).

RESULTS AND DISCUSSION

Assemblage Structure

A total of 70 species—belonging to 19 genera and 7 tribes—were collected (Table 1, Figure 3). In terms of species richness, the dominant genus in the area was *Dichotomius* (11 species), followed by *Canthon* (9 species) and *Canthidium* (8 species). The most abundant species in the region were *O. haematopus*, *C. cupreum*, *C. aequinoctialis*, *D. parile*, and *O. conspicillatum*; they were the most commonly sampled species in both this study and some other studies conducted in the area (Castellanos et al. 1999). It is particularly interesting to note that *S. leander* and *G. lemoinei* were present; they are the only two species found on river beaches (Figure 3; Noriega 2002).

Table 1. List of the species of dung beetles (Scarabaeinae) collected at the CIEM - Tinigua National Park, Meta Department, Colombia. Code Spp: species code

Tribe	Species	Code Spp.
Ateuchini	*Ateuchus murrayi* (Harold, 1868)	*Ate mur*
	Ateuchus pygidialis (Harold, 1939)	*Ate pyg*
	Ateuchus cf. *scatimoides* (Balthasar, 1939)	*Ate sca*
	Eutrichillum cf. *hirsutum* (Boucomont, 1928)	*Eut hir*
	Uroxys bidentis Howden & Young, 1981	*Uro bid*
	Uroxys micros Bates, 1887	*Uro mic*
	Uroxys sp. 1	*Uro sp1*
	Uroxys sp. 2	*Uro sp2*
Coprini	*Canthidium euchalceum* Balthasar, 1939	*Can euc*
	Canthidium funebre Balthasar, 1939	*Can fun*
	Canthidium gerstaeckeri Harold, 1867	*Can ger*
	Canthidium onitoides (Perty, 1830)	*Can oni*
	Canthidium ruficolle (Germar, 1824)	*Can ruf*
	Canthidium splendidum Preudhomme de Borre, 1886	*Can spl*
	Canthidium cf. *centrale* Boucomont, 1928	*Can cen*
	Canthidium cf. *cupreum* (Blanchard, 1845)	*Can cup*
	Dichotomius belus (Harold, 1880)	*Dic bel*
	Dichotomius boreus (Olivier, 1789)	*Dic bor*
	Dichotomius compressicollis (Luederwaldt, 1929)	*Dic com*
	Dichotomius deyrollei (Harold, 1869)	*Dic dey*
	Dichotomius mamillatus (Felsche, 1901)	*Dic mam*
	Dichotomius ohausi (Luederwaldt, 1923)	*Dic oha*

Tribe	Species	Code Spp.
	Dichotomius podalirius (Felsche, 1901)	*Dic pod*
	Dichotomius worontzowi (Pereira, 1942)	*Dic wor*
	Dichotomius cf. *problematicus* (Luederwaldt, 1922)	*Dic prb*
	Dichotomius cf. *protectus* (Harold, 1867)	*Dic prt*
	Dichotomius aff. *inachus* (Erichson, 1847)	*Dic ina*
	Ontherus azteca Harold, 1869	*Ont azt*
	Ontherus pubens Génier, 1996	*Ont pub*
Deltochilini	*Canthon aequinoctialis* Harold, 1868	*Can aeq*
	Canthon angustatus Harold, 1867	*Can ang*
	Canthon cyanellus Harold, 1863	*Can cya*
	Canthon femoralis (Chevrolat, 1834)	*Can fem*
	Canthon fulgidus Redtenbacher, 1867	*Can ful*
	Canthon lituratus (Germar, 1813)	*Can lit*
	Canthon luteicollis Erichson, 1847	*Can lut*
	Canthon mutabilis Lucas, 1859	*Can mut*
	Canthon cf. *gutierrezi* Martínez, 1950	*Can gut*
	Deltochilum amazonicum Bates, 1887	*Del ama*
	Deltochilum orbiculare van Lansberge, 1874	*Del orc*
	Deltochilum aff. *orbignyi* (Blanchard, 1845)	*Del org*
	Deltochilum aff. *parile* Bates, 1887	*Del par*
	Scatonomus cf. *insignis* Harold, 1867	*Sca ins*
	Scybalocanthon pygidialis (Schmidt, 1922)	*Scy pyg*
	Scybalocanthon cf. *imitans* (Harold, 1868)	*Scy imi*
Demarziellini	*Bdelyrus* cf. *metaensis* Cook, 1998	*Bde met*
Oniticellini	*Eurysternus caribaeus* (Herbst, 1789)	*Eur car*
	Eurysternus contractus Génier, 2009	*Eur con*
	Eurysternus foedus Guérin-Méneville, 1844	*Eur foe*
	Eurysternus hamaticollis Balthasar, 1939	*Eur ham*
	Eurysternus hypocrita Balthasar, 1939	*Eur hyp*
	Eurysternus mexicanus Harold, 1869	*Eur mex*
	Eurysternus plebejus Harold, 1880	*Eur ple*
	Eurysternus wittmerorum Martínez, 1988	*Eur wit*
Onthophagini	*Onthophagus buculus* Mannerheim, 1829	*Ont buc*
	Onthophagus haematopus Harold, 1875	*Ont hae*
	Onthophagus rubrescens Blanchard, 1845	*Ont rub*
	Onthophagus cf. *curvicornis* (Latreille, 1811)	*Ont cur*
	Onthophagus aff. *clypeatus* Blanchard, 1846	*Ont cly*
Phanaeini	*Coprophanaeus telamon* (Erichson, 1847)	*Cop tel*
	Coprophanaeus ohausi (Felsche, 1911)	*Cop oha*
	Dendropaemon cf. *waterhousei* d´Olsoufieff, 1924	*Den wat*
	Gromphas lemoinei Waterhouse, 1891	*Gro lem*
	Oxysternon conspicillatum (Weber, 1801)	*Oxy con*
	Oxysternon silenus Castelnau, 1840	*Oxy sil*
	Phanaeus bispinus Bates, 1868	*Pha bis*
	Phanaeus cambeforti Arnaud, 1982	*Pha cam*
	Phanaeus chalcomelas (Perty, 1830)	*Pha cha*
	Sulcophanaeus faunus (Fabricius, 1775)	*Sul fau*
	Sulcophanaeus leander (Waterhouse, 1891)	*Sul lea*

One of the least common species was *S. faunus*: it never came to baited pitfall traps, even those baited with carrion (rotten fish, squid, calamari, and chicken). The only two individuals that were collected (one male and one female) were captured in a mist net intended for birds. It is also interesting to note that individuals of the genus *Ontherus* (*O. azteca* and *O. pubens*) occurred in low numbers. Genier (1996) says that some species of this genus have very specific habitat restrictions and resource preferences that may explain these low numbers. For instance, in the study area, there are ant and termite nests that could serve as microhabitats for these two species (Kistner 1982, Krikken 2008, Krell & Phillips 2010, Vårdal & Forshage 2010, Maruyama 2012), which may explain why *O. azteca* was frequently observed in interception traps. Other species that also occurred in low numbers were *Scatonomus* cf. *insignis*, *Bdelyrus* cf. *metaensis*, and *Eutrichilum* cf. *hirsutum*; little information is available on the ecology, behavior, and habitat preferences of these three genera (Pereira 1954, Martínez 1967, Vulcano & Pereira 1973, Ratcliffe 1980, Cook 1998, Medina et al. 2001, Solis et al. 2011).

Table 2. Different numbers of Scarabaeinae found in five biogeographical regions in Colombia (Ama: Amazon, And: Andean, Car: Carribean, Cho: Choco – Pacific, Ori: Orinoquia – Plain grasslands and Guy: Guayana) and at the CIEM - Tinigua National Park, Meta Department, Colombia

Region	Department	Locality	Altitude (m.a.s.l.)	Genera/ Species	Reference
Ama	Amazonas	Leticia	80	15/60	Howden & Nealis (1975)
	Caquetá	PNN Serranía de Chiribiquete	300	14/61	Pulido et al. (2003)
And	Caldas	Cuenca Río La Miel	160, 2600 - 2750	12/55	Arango & Montes (2009)
	Tolima	Mariquita	690	13/30	Fuentes & Camero (2006)
Car	Atlántico	Barranquilla	0 - 500	17/35	Solís et al. (2011)
	Magdalena	PNN Sierra Nevada de Santa Marta	50 - 940	15/29	Martínez et al. (2009)
Cho	Choco	Salero	115	13/23	Neita et al. (2003)
	Choco	Lloro	90	13/19	Neita & Escobar (2011)
Ori	Meta	Puerto Colombia	200	14/32	Amézquita et al. (1999)
	Guaviare	San José del Guaviare, RN Nukak	200 - 360	14/48	Escobar (2000)
Guy	Meta	CIEM	350	19/70	(this work)

Figure 3. Dorsal view of a sample of dung beetle species in the CIEM - Tinigua National Park, Meta Department, Colombia. a) *Onthophagus haematopus* (♀), b) *Eurysternus plebejus* (♂), c) *Canthidium funebre* (♀), d) *Scybalocanthon pygidialis* (♀), e) *Canthon luteicollis* (♀), f) *Canthon aequinoctialis* (♂), g) *Canthon fulgidus* (♂), h) *Eurysternus caribaeus* (♀), i) *Phanaeus chalcomelas* (♂), j) *Dichotomius belus* (♂), k) *Gromphas lemoinei* (♂), l) *Eurysternus hamaticollis* (♂), m) *Coprophanaeus telamon* (♂), n) *Oxysternon conspicillatum* (♂), o) *Sulcophanaeus leander* (♂), p) *Deltochilum orbignyi* (♀), q) *Sulcophanaeus faunus* (♂). Bar scale = 1 cm.

If species richness in this area is compared with that in other parts of Colombia, the area around the CIEM is one of the most species rich in the country (Noriega et al. 2015; Table 2). Given the high number of species it shares with neighboring biogeographical regions (n=56; 79.8%) and its low number of endemic species (n=4; 5.7%) compared to other areas of the country (Escobar 2000), faunal composition in this area is likely greatly determined by species contributions distributed in the entire country (n=8; 11.4%), in surrounding regions (Andes, Amazonia, and Orinoquia) and less influenced by local speciation (i.e., inside the Guayana region, agreeing with the proposed by Hernandez et al. 1992) (Figure 4).

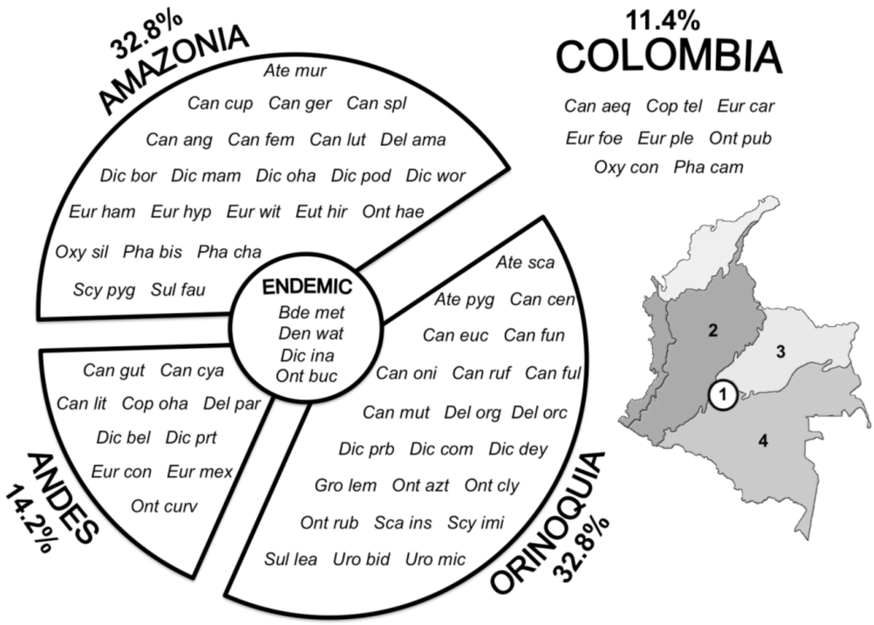

Figure 4. Composition of dung beetle species assemblage at the CIEM - Tinigua National Park, Meta Department, Colombia, in terms of the species biogeographical origin: Endemic (1), Andes (2), Orinoquia (3), Amazonia (4) or present throughout the entire country.

Spatial Coexistence Mechanisms

Taxonomic richness was highest in MF, which harbored 17 genera, 53 total species (75.7%), and 41 unique species (58.6%). Next was FF with 12 genera, 28 total species (40%), and 15 unique species (21.4%). Last were the RB with just 2 genera, 2 total species (2.9%), and 1 unique species (*S. leander*). There are no species that were present in all the CIEM's main habitats. However, MF and FF shared 13 species (18.6%), and FF and the RBs shared just one species (*G. lemoinei*) (Figure 5).

Vertical partitioning of forest habitat appears to be another important spatial coexistence mechanism. Given the results obtained from the linear transect of elevated traps (Noriega 2011) placed at heights of 3, 6, 9, and 15 m in MF, it is clear that some species are using different strata within the forest (floor - 0 m vs. arboreal level – 6 m) and are especially abundant between 6 and 9 m (Noriega unpub. data). Of the 70 species found in this area, 10

(14.7%; *B.* cf. *metaensis*, *C. funebre*, *C. gerstaeckeri*, *C.* cf. *cupreum*, *C. aequinoctialis*, *C. fulgidus*, *C. luteicollis*, *O. buculus*, *O. haematopus* and *S. pygidialis*) came to the elevated traps.

In particular, *B.* cf. *metaensis* was collected exclusively in one such trap, and *C. fulgidus* was by far more common in traps located 6 m above the ground than in ground-level pitfall traps. Other species like *C. splendidum*, *C. angustatus*, and *O. conspicillatum* were found perching on leaves in the forest but never occurred in the elevated traps (Noriega unpub. data). It is recommended to install elevated traps in the canopy and studying this as yet unexamined stratum of the forest; it is possible that some species use the canopy microhabitat.

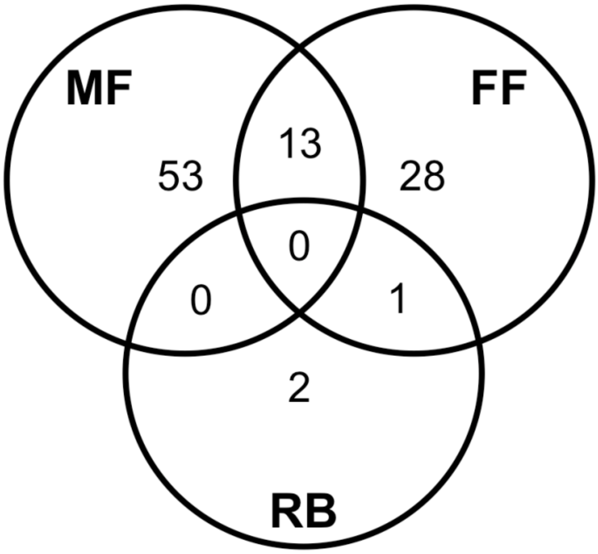

Figure 5. Shared and unique species in the three main habitats (MF=Mature mainland forest, FF=Flooded lowland forest and RB=River beaches) of the CIEM - Tinigua National Park, Meta Department, Colombia.

Temporal Coexistence Mechanisms

The wet season was more taxonomically rich (17 genera; 57 total species, 81.4%, 60.2% in contrast; 32 unique species, 45.7%) than the dry season (13 genera; 38 total species, 54.3%, 39.8% in contrast; 13 unique species, 18.6%; Figure 6). Twenty-five species (35.7%) occurred during both seasons. However, sampling during the transition season was incomplete, and it is certain that there are no species that were present throughout the entire year at the CIEM. It is noteworthy that five of the eight species of the genus *Eurysternus* were present during both seasons. In general, the arrival of the rainy season produces an increase in resources in the forest that favors the coexistence of a greater number of species; the opposite occurs during the dry season, as it was registered in other studies (Montes de Oca & Halffter 1995, Morelli et al. 2002, Vernes et al. 2005).

As for dial activity, slightly more species were out during the day (14 genera; 40 total species, 57.1%, 52.4% in contrast; 31 unique species, 44.3%) than at night (13 genera, 39 total species, 55.7%, 47.6% in contrast; 30 unique species, 42.9%; Figure 6). Nine species (12.9%) occurred both during the day and at night hours. However, no species was active all day (24 hours), and most had very short windows of activity during the crepuscular hours—for instance, *S. leander* is active for less than an hour at dusk and dawn (Noriega 2002b). These differences in periods of activity decrease the competition for limited resources in dung beetles (Hanski & Cambefort 1991, Estrada et al. 1993, Giller & Doube 1994, Montes de Oca & Halffter 1995, Hernández 2002, Krell-Westerwalbesloh et al. 2004).

This crepuscular peak in activity is probably related to the fact that mammals, and especially primates, produce much more dung at dawn and during the early morning, as it has been registered for *L. lagotricha* in this locality, after one hour of rest (P. Stevenson pers. comm.). During the middle of the day (12–2 pm) and after the middle of the night (12–2 am), species number and activity are lower (Noriega unpub. data). In addition, it is possible that some species prefer resources in a specific state of decay or freshness (e.g., fresh vs. old; Hanski 1980b); such preferences have yet to be studied in this area.

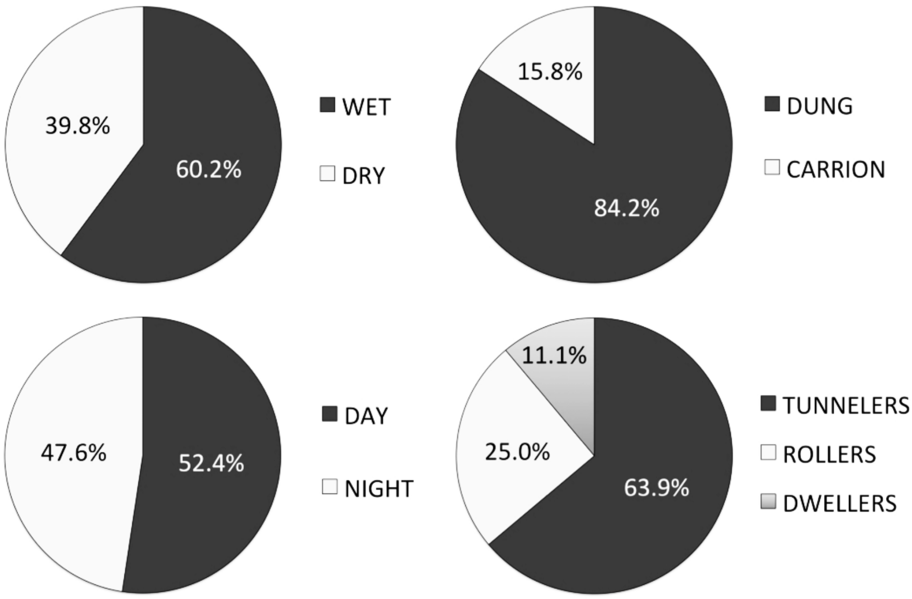

Figure 6. Structure of the dung beetle assemblage found at the CIEM - Tinigua National Park, Meta Department, Colombia. Four different categories of niche partitioning were examined: season (wet vs dry), resource preference (dung vs carrion), dial activity (day vs night) and resource-relocation behavior (tunnelers vs rollers vs dwellers).

Resource Coexistence Mechanisms

More species were found on dung (19 genera; 63 total species, 90%, 84.2% in contrast; 58 unique species, 82.9%) than on carrion (7 genera; 12 total species, 17.1%, 15.8% in contrast; 7 unique species, 10%; Figure 6). Five species (7.1%) occurred on both resources (*C. aequinoctialis*, *C. telamon*, *D. amazonicum*, *E. caribaeus* and *E. plebejus*), which show that they are generalists in terms of their food preferences. The differences in the spatial distributions and abundances of these two resources have a clear effect on the number of species associated with each. The high richness and abundance of dung beetles in this area is supported by the high diversity and density of mammals. Castellanos et al. (1999) estimated that woolly monkey populations in this area might produce 400–600 fecal deposits/km^2 per day. However, this study found that a large number of species use carrion, a result that contrasts with those of other studies in Colombia (Howden & Nealis 1975, Bustos-Gómez & Lopera 2003, Pardo et al. 2004, Esparza-Leon & Amat-García 2007, Murillo et al. 2010, Delgado-Gomez et al. 2012) and in other regions (Hanski 1983, Klein 1989, Hill 1996, Boonrotpong et al. 2004, Larsen et al. 2006, Damborsky et al. 2008, Almeida & Louzada 2009, Davis et al. 2010, Barragan et al. 2011). The exploitation of carrion could be related to the Neotropical absence of large mammals (Halffter & Matthews 1971, Louzada & Lopes 1997), which can produce large quantities of excrement; consequently, some species of dung beetles may have turned to other available resources.

In addition, some studies in Colombia (Santos-Heredia et al. 2010) and in other regions (Howden & Young 1982, Estrada & Coates 1991, Gill 1991, Estrada et al. 1993) suggest that dung beetles might be highly specialized in the type of mammal excrement (carnivorous, herbivorous or omnivorous) they use. Another study conducted in this area (Noriega 2012) compared species preferences for excrement produced by two different primates (*A. seniculus* and *L. lagotricha*); it found that some beetle species were more attracted to the dung produced by one primate and not to that produced by the other. It is also important to note that most of the baits used in this study were small in size (20–30 g), and it is possible that some species could be more attracted to smaller or larger baits (Gill 1991). For instance, based on data obtained in other areas and from the literature (Edmonds & Zidek 2010), it is proposed that *S. faunus* is not attracted to small baits but rather prefers large carcasses in highly conserved forests.

Furthermore, numerous records show that some dung beetles use other, very specific resources that are completely different from vertebrate dung and carrion, such as invertebrate feces, flowers, fungi, fruits, eggs, and diplopods, among others (Young 1980, Monteith & Storey 1981, Howden & Young 1982, Gill 1991, Navarrete & Galindo 1997, Cano 1998, Pfrommer & Krell 2004, Noriega & Calle 2008, Halffter & Halffter 2009). The fact that these species exploit such a wide range of non-fecal resources raises the question as to whether this group of insects should even be called “dung beetles” at all.

Guild-Resource Relocation Coexistence Mechanisms

In terms of the dung beetle guilds that show resource relocation behavior, the paracoprids (T) were the most common (14 genera; 46 species, 63.9%), followed by the telecoprids (R) (4 genera; 16 species, 25.0%) and the endocoprids (D) (1 genus, *Eurysternus*; 8 species, 11.6%; Figure 6). Some additional resource relocation behaviors were observed at the CIEM, such as pellet- or fragment-pushing, but they were exhibited by very few species and not commonly.

If beetle size (small, medium and large) is examined in tandem, it is possible to gain a better idea of how effectively relocation behavior limits direct competition and partitions species in this area. Indeed, the results indicate that, in some categories like medium and small rollers and large, medium, and small dwellers, there were no more than three species sharing the resource (Table 3). No kleptoparasitism was directly observed in the field in this area, but since this behavior is very common at other localities (Cambefort 1991, Gill 1991, Rougon & Rougon 1991), it seems highly probable that it occurred between small and large species.

Table 3. Matrix of beetle species belonging to different resource-relocation guilds (tunnelers, rollers and dwellers) and of different sizes (large, medium and small) found at CIEM - Tinigua National Park, Meta Department, Colombia

	TUNNELERS		ROLLERS		DWELLERS
LARGE (> 18 mm)	*Cop tel* *Cop oha* *Dic bor* *Dic mam* *Dic pod*	*Dic wor* *Oxy con* *Sul fau* *Sul lea*	*Del ama* *Del orc* *Del org*		*Eur con* *Eur ham* *Eur hyp*
MEDIUM (10 – 18 mm)	*Can cen* *Can ful* *Den wat* *Dic bel* *Dic com* *Dic dey* *Dic ina* *Dic oha* *Dic prt*	*Dic prb* *Gro lem* *Ont pub* *Ont azt* *Oxy sil* *Pha bis* *Pha cam* *Pha cha*	*Can aeq*		*Eur car* *Eur foe*
SMALL (< 10 mm)	*Ate mur* *Ate pyg* *Ate sca* *Can cup* *Can euc* *Can fun* *Can ger* *Can lut* *Can oni* *Can ruf* *Can spl*	*Eut hir* *Ont buc* *Ont cly* *Ont cur* *Ont hae* *Ont rub* *Uro bid* *Uro mic* *Uro sp1* *Uro sp2* *Bde met*	*Can ang* *Can cya* *Can fem* *Can gut* *Can lit*	*Can mut* *Del par* *Sca ins* *Scy pyg* *Scy imi*	*Eur mex* *Eur ple* *Eur wit*

Ecological Segregation of Species

The five components retained in the principal coordinates analysis accounted for 71% of the interspecific variability in species niche characteristics. The first component (Table 4) accounted for 27.76% of the niche information (species that were found in MF, active during wet season, with nocturnal activity and they use carrion resources).

The second component included the 20.57% of the niche (species that were found in FF, active during dry season, with nocturnal activity and with paracoprid behavior). These two components alone accounted for nearly the 50% of the ecological divergence between species. The third, fourth, and fifth components, which explained the 22.9% of the variability, are described in Table 4. Based on these five components, the average degree of divergence between species was 0.363 (the maximum theoretical value is 1, and the maximum observed Euclidean distance was 0.723).

Table 4. Analysis of the principal coordinates matrix for all the species sampled at CIEM - Tinigua National Park, Meta Department, Colombia. The signs + and – indicates respectively, the positive and negative relationships that exist between the binomial variables (0-1), which describe the species niche characteristics and the five principal coordinates components

	Comp 1	Comp 2	Comp 3	Comp 4	Comp 5
MF	+	-			-
FF	-	+	-	-	
RB					
Dry	-	+	-	-	-
Wet	+	-		+	-
Day	-	-	+	-	
Night	+	+	-	+	
Dung	-			+	+
Carrion	+		-	-	
Tunneler		+	+	-	+
Roller			-		+
Dweller					-
Floor	-			-	+
Arboreal				+	+
Autovalue	3.90	2.89	1.49	0.94	0.79
% variance	27.76	20.57	10.60	6.71	5.59

This observed average value was significantly greater than the average of the neutral distribution (P=0.050; Figure 7). This result means that the 70 species sampled were slightly more segregated than expected by chance based on a neutral model of ecological segregation. In contrast, average maximum divergence was significantly smaller (p=0.036; Figure 7) than expected by chance (neutral model: average maximum value of 0.970). This result indicates that there are no extreme ecological positions within the niche space of the group of species and therefore not observed degrees of ecological segregation that did not have representation in the 70 species registered.

On average, species were more ecologically segregated than expected by chance, but species with extreme ecological niches were not detected, which generated maximum values of interspecific divergence within the niche space available for the 70 species.

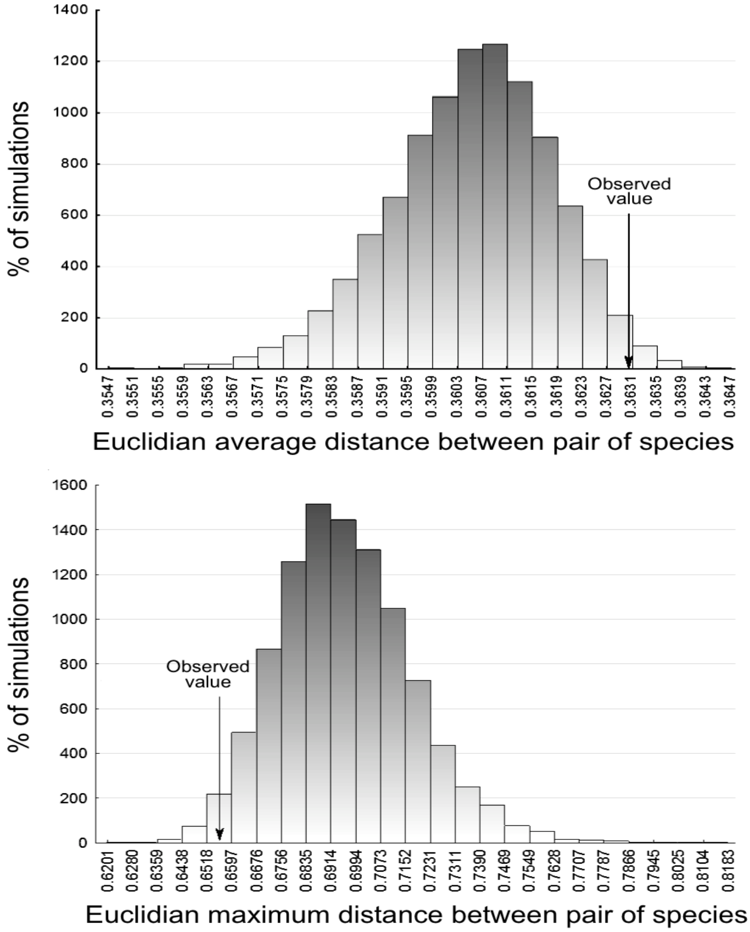

Figure 7. Euclidian average and maximum distance between pair of species sampled at the CIEM - Tinigua National Park, Meta Department, Colombia.

The analysis of similarity using Jaccard index shows that there are 20 different groups of species or single species with a 75% of similarity (25% of dissimilarity) that do not use and share the niche in the same way (Figure 8).

Relative to the high level of species richness in this area, the degree of interspecific niche overlap is low, meaning that few species interact directly in the same space, at the same time, and on the same resource (Figure 9). Indeed, this assertion is supported by the presence of all of the coexistence mechanisms described above.

If the information of food relocation guilds and categories of size (Table 3) is added with the coexistence scheme of niche segregation structure (Figure 9) there were very few species sharing the same space, time and resource decreasing radically the interspecific competition. In addition, it is important to notice that at least there is one species using the available resource in each “niche-space” in the coexistence scheme (Figure 9).

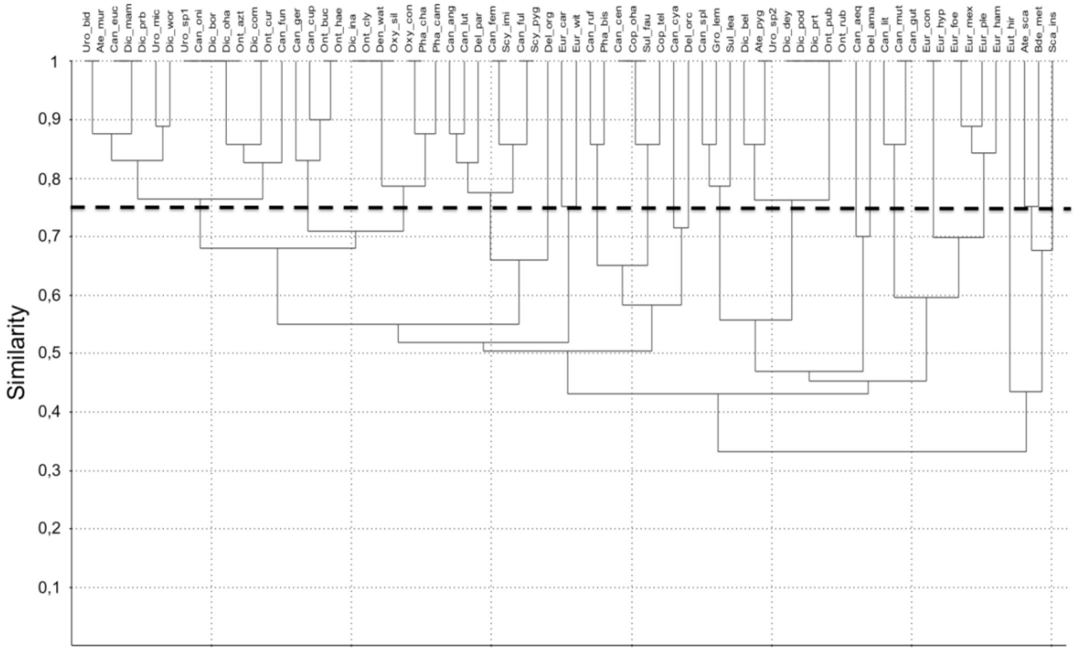

Figure 8. Jaccard index of similarity (dashed line=75%) for the species sampled at the CIEM - Tinigua National Park, Meta Department, Colombia.

All these mechanisms are the result of interactions between historical and ecological factors (Davis & Scholtz 2001) and promote the coexistence of different species by limiting the effect of the factors that are primarily responsible for high levels of interspecific competition (Hanski 1980a, b, Giller & Doube 1989, Lumaret et al. 1992, Finn & Gittings 2003, Hutton & Giller 2004).

"Rare Species" and Sampling Recommendations

Over the course of the sampling process, some species appeared to be rare because of their low abundances. However, when a new habitat or microhabitat was sampled, a new bait or trap type was used, or sampling was conducted at a new time of the year, it was discovered that that these "rare" species were not rare at all, instead, their presence was underestimated as a result of sampling inaccuracy. For example, this was the case for *C. fulgidus*, which rarely occurred in ground-level pitfall traps but was common in 6 m elevation traps, for *S. faunus*, which was collected when mist nets were used, and for *S. leander*, which was only found on river beaches.

These examples of "rare" species reveal how imprecise sampling can be and underscore the necessity of using a sampling approach that includes a wide variety of trap types, a wide range of bait types and sizes, and all possible habitats and microhabitats; that is carried out over the entire year; and that incorporates more natural history studies.

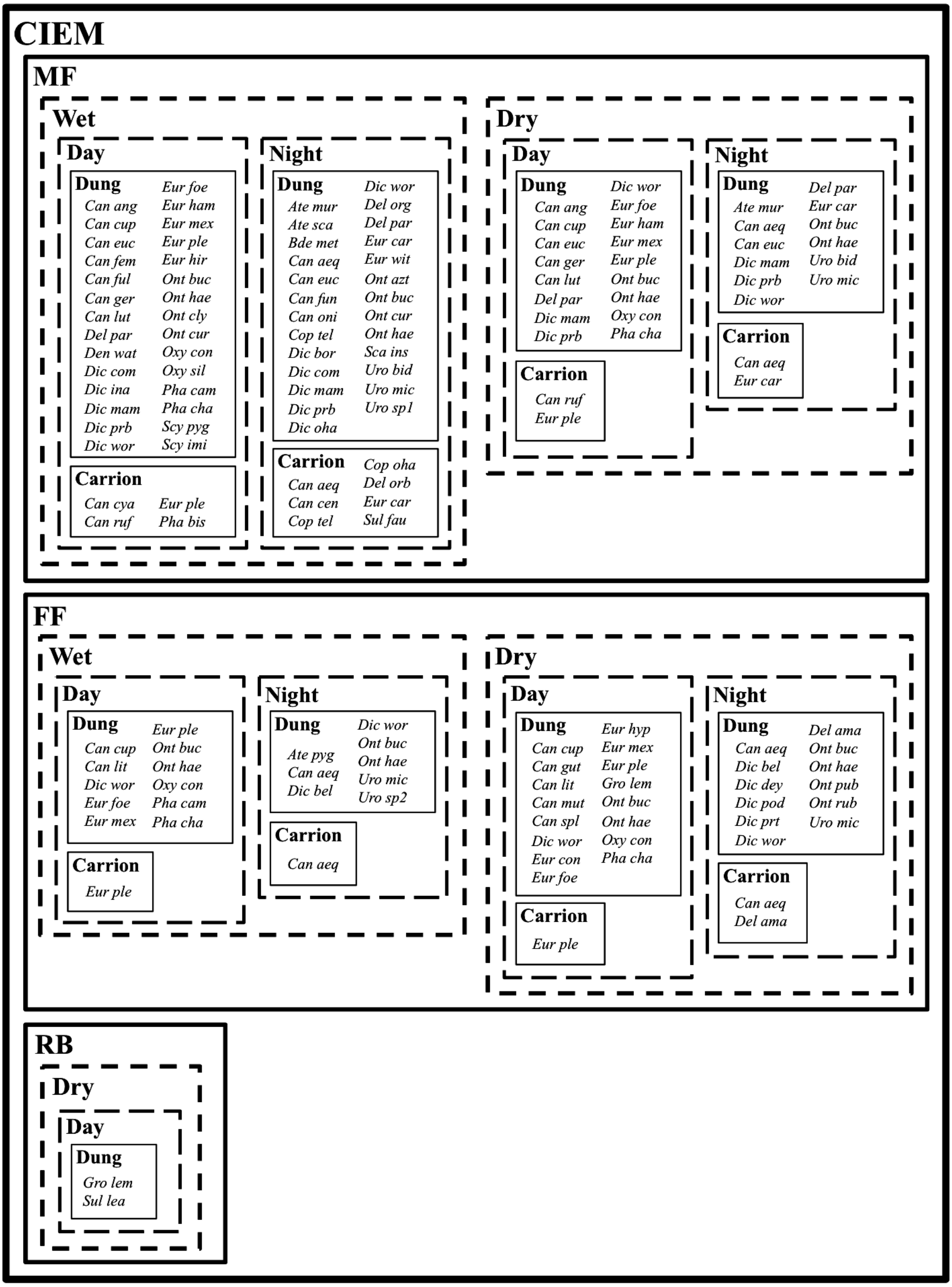

Figure 9. Coexistence scheme of the principal aspects of the niche segregation structure of the dung beetles assemblage at the CIEM - Tinigua National Park, Meta Department, Colombia.

Finally, to more thoroughly characterize assemblage composition, exhaustive sampling should take place over a full year and other kinds of traps should be used (Newton & Peck 1975, Moron & Terrón 1984, Noriega 2011). Furthermore, more specialized baits should be utilized; these baits could include invertebrate feces, such as from earthworms (Matthews 1965, Howden & Young 1981), dead spirobolid millipedes (Bernon 1981, Cano 1998, Brühl & Krell 2003), excrement from vertebrates found in the area (Martinez 1952, Young 1981a, Janzen 1983, Gill 1991, Estrada et al. 1993), rotten fungi (Navarrete & Galindo 1997), and other rare resources (Young 1980, Howden & Young 1981, Monteith & Storey 1981, Gill 1991, Villalobos et al. 1998, Pfrommer & Krell 2004).

In addition, it may be important to sample certain specific microhabitats, such as bromeliads (Pereira et al. 1960, Huijbregts 1984, Cook 1998), caves (Zunino & Halffter 1988), mammal burrows (Zunino & Halffter 2007), ant nests (particularly made by the genera *Acromymex*, *Atta*, *Pheidole*, and *Solenopsis*), and termite nests (Vaz-de-Mello et al. 1998, Navarrete 2001). Lastly, the close (e.g., phoretic) relationships that some beetle species may have with mammals such as sloths should not be forgotten (Ratcliffe 1980, Young 1981b).

ACKNOWLEDGMENTS

To the Japanese-Colombian cooperative agreement between the University of Los Andes and the University of Myiagi. To the National Park Unit for granting the permits to carry out research in Tinigua National Park. To Carlos Arturo Mejia, Ivan Jimenez, Daniel Cadena, Alejandra Vega, Libia Carolina, Juan Cristobal Calle and Ramiro Montealegre for their help in the field samplings. To Fernando Vaz-de-Mello, David Edmonds, Bruce Gill, Francois Genier and Alejandro Lopera for their help in identifying the specimens. To Luis M. Carrascal and Daniel Monroy for their important and valuable contributions and their help with the statistical analyses in this paper. To Edison Torrado-Leon from Naturavision (www.naturavision.com) for his significant support and collaboration in taking the photos of the species. Ricardo Botero Trujillo made comments and suggestions that improved the manuscript. To Pablo Stevenson for providing valuable information and references. To David Morris and Jessica Pearce-Duvet for kindly checking the English version of the manuscript.

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