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Natural History of Ants: What We (do not) Know about Trophic and Temporal Niches of Neotropical Species

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Abstract

Our understanding of the natural history of Neotropical ants is limited, due to lack of descriptive efforts and widespread use of morphospecies in literature. Use of trophic resources and period of activity are two central niche aspects little explored for most species. This work aimed to broadly review the literature and provide empirical field data on these aspects for 23 species. The fieldwork was carried out in the Atlantic forest of southern Brazil. Trophic and temporal niches were assessed with pitfall traps and seven kinds of bait representing natural resources. Crushed insects were the preferred resource, whereas bird feces and living prey were less exploited. Most species broadly used the resources, but pronounced quantitative differences were found. *Odontomachus chelifer* (Latreille, 1802) and *Pachycondyla striata* Smith, 1858 were relatively well studied and field data matched previous accounts. They were the only species that consistently used large prey, and avoided oligosaccharides. *Wasmannia auropunctata* (Roger, 1863) differed remarkably from previous studies, using feces as its sole trophic resource. The six *Pheidole* species had no previous records and presented quantitative differences in resource use. Most species had no strong preference for period of activity. *Camponotus zenon* Forel, 1912 was nocturnal and *Crematogaster nigropilosa* Mayr, 1870, *Linepithema iniquum* (Mayr, 1870) and *Linepithema pulex* Wild, 2007 were diurnal. Complementary methods, context-dependence and descriptive studies have a central role in the understanding of ant natural history. Community assessments can contribute significantly to this knowledge if researchers also pay attention to the individual species involved.

Introduction

Ants (Hymenoptera: Formicidae) are among the most abundant groups of invertebrates in terrestrial ecosystems, presenting a wide variety of feeding habits, nesting sites, and interactions with organisms from all trophic levels (Kaspari, 2000). They are the subject of extensive and diversified research, in basic and applied science. Despite this, in all tropical regions, the biology of most species is virtually unknown, due to a combination of high richness, taxonomic uncertainty, lack of descriptive studies and widespread use of morphospecies in literature (Krell, 2004; Greene, 2005).

Two fundamental aspects that remain elusive for many tropical species are trophic and temporal niche. Ants in general are regarded as omnivorous, feeding on a combination of live prey, dead animals, seeds and plant exudates, with some notorious specialized behaviors such as fungus cultivation and pollen consumption (Kaspari, 2000; Blüthgen & Feldhaar, 2010). At genus or species level, they are sometimes classified in broad groups or guilds like "generalist predators" or simply

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"generalists" (Brandão et al., 2012). These generalizations have an important role to understand communities, but also leave out the remarkable variation among species in nature. This specific information can be assessed from indirect sources such as body ratios of stable isotopes (Blüthgen et al., 2003) and remains found in nests (Lattke, 1990), and direct observation such as interaction with plant resources (Byk & Del-Claro, 2010) and items carried to nests (Medeiros & Oliveira, 2009; Raimundo et al., 2009). Every approach has its focus and limitations, and adds a piece to the puzzle that is the niche of a species.

In turn, studies on temporal niche of ants are common in open areas and/or temperate habitats, where the fluctuations in abiotic factors could have a stronger effect on ant activity. This variation is often linked with temporal niche partitioning and coexistence of competing species (Lessard et al., 2009; Anjos et al., 2016). Less information is available for tropical forests (e.g. Medeiros & Oliveira, 2009; Raimundo et al., 2009; Feitosa et al., 2016). Inside a forest, less variation would be expected, because daily changes in temperature, humidity and wind are smaller. However, temporal niche could still be affected by the existing fluctuations or by competitive pressure.

In view of the importance of both use of trophic resources and period of activity, and considering the lack of information available for most Neotropical species, this work aims to quantify use of trophic resources and period of activity of ground-dwelling ants from a Neotropical forest. An extensive literature review was performed to assess how much is known about these individual species and compare results from the viewpoint of complementarity of methods and ecological context-dependence. These case studies highlight that descriptive studies are still fundamental for tropical faunas. In this sense, broader ecological assessments can give a significant contribution, if researchers also pay attention to the individual species involved.

Methods

Study area and sample design

Fieldwork was carried out in Desterro Conservation Unit, Florianópolis, south Brazil (27º31'38'' S, 48º30'15'' W, altitude ca. 250 m), between December 2015 and January 2016. Average annual temperature and precipitation is 20.5 ºC and 140 mm per month (data from meteorological station of EPAGRI/CIRAM). Vegetation consists of secondary Atlantic forest *sensu stricto* (= ombrophilous dense forest) with at least 60 years of relatively undisturbed regeneration. This work was conducted in accordance with Brazilian laws, under authorization SISBIO number 51173-1.

The sampling was based on the recent design of Houadria et al. (2015) to assess community patterns on resource use and daily activity, but here its suitability to understand individual species is explored. Four plots with 4 x 4 sample points (16 per plot) were set up, with distances from 30 to 50 m between plots. Distance between sample points was 10 m. The baits were set up in transparent plastic boxes with diameter of 10 cm and ground-level slits that allowed the entrance of ants, and retrieved after 90 minutes. All individuals were collected from the baits in laboratory and stored in ethanol 70% for subsequent sorting.

Seven baits were offered as proxies for common resources available to ants (Table 1; see Supplementary Material for details on bait display and rationale for their choice). In each round, only one bait was offered per sample point, and bait types were mixed among points, with a similar number of points receiving each type (8-9 per round). Fourteen baiting rounds were performed, with only one period sampled each day, at daytime (around 13:00-15:30) or nighttime (around 21:00 – 23:30). In total, 896 baits were applied in the 64 sample points, with all seven baits being offered in each sample point two times (one at day and one at night). This design is suitable to assess multidimensional trophic niches, which are inferred from how often ants use each resource. Hence, "preferences" means simply relative high use of certain resources. Distance between each colony and the bait does not change from one resource to another, and the use of one resource does not affect the other. Thus, it differs from a typical cafeteria experiment, which is designed to assess preferences through choices among different resources offered at the same time (Krebs, 1999).

An independent community assessment was performed with three rounds of pitfall trapping, alternated with bait rounds. The plastic cups were 6 cm wide and contained propylene glycol 50% and a small amount of neutral detergent. Cups were buried previously and replaced after each round to avoid the digging-in effect. Pitfalls stayed opened for 10 hours during the day and 9 hours during the night (due to short summer nights), then an extra 3-hour nocturnal round was performed. One nocturnal and one diurnal pitfall round were performed in sequence, separated by intervals to avoid dusk and dawn times.

Specimen processing and identification

For each sample point, at least one individual per morphospecies was mounted. They were identified to genus level with Baccaro et al. (2015) and to species level with taxonomic revisions, and comparison to identified specimens in collections and Antweb images (AntWeb, 2016). The taxonomic sources used were: *Crematogaster* – Longino (2003); *Cyphomyrmex* – Kempf (1965) and Snealling and Longino (1992); *Gnamptogenys* – Lattke (1995); *Hylomyrma* – Kempf (1973); *Linepithema* – Wild (2007); *Odontomachus* and *Pachycondyla* – Fernández (2008); *Pheidole* – Wilson (2003); *Wasmannia* – Longino and Fernández (2007). *Camponotus* and *Strumigenys* were identified just by comparison with collections. The identifications were partially confirmed by taxonomists of the Laboratory of Ant Systematics and Biology, Federal University of Paraná, Brazil (see Acknowledgements). Vouchers were deposited at the Laboratory of Ant Biology, Federal University of Santa Catarina, Brazil, and at the Ecological Networks research group, Technical University of Darmstadt, Germany.

Analysis

For analysis and literature review of trophic niche, all species with at least 10 bait records were included, and for daily activity all species with at least 6 records on baits and pitfalls. The systematic literature review included the following sources: search for species names in Google Scholar; original descriptions; taxonomic revisions and references therein; references found in AntWiki (AntWiki, 2016). In case of species subject to name changes, older versions were also considered. Taxonomic history and current nomenclature of species were checked with AntCat (Bolton, 2016). Distribution records were retrieved from AntMaps (Janicki et al., 2016). A representative, species-specific, literature on trophic and temporal niche for these species was gathered. Artificial breeding diets for laboratory colonies were not included, and use of generic baits (e.g. tuna, cookies) was considered just when relevant to discuss trophic niche.

Data is shown as proportions of records in each bait type/period relative to the total records for that species. For bait use, day and night records were not pooled. Records for the pitfall replicas of each period were pooled for every point. Differences were tested with two-tailed exact multinomial and binomial goodness-to-fit tests against a hypothesis of no preference, that is, equal proportions expected for each bait (1/7 or 0.14) or period (1/2 or 0.5). Tests were run in R 3.3.0 (R Core Team, 2016). Exact tests are the most appropriate for nominal variables with small sample sizes (McDonald, 2014), but are limited nonetheless. A non-significant result could mean either low sample size or very generalist diet/activity. Species with low number of records and non-significant results are discussed more briefly, since their results may not quantitatively represent their trophic niche.

Results

Seventy-six morphospecies were collected. It was possible to name 46 species, of which 23 had at least 6 records and 15 at least 10 (Table 2; see Supplementary Material for records of the remaining identified species).

A similar number of species was recorded in most bait types, but they differed greatly in the number of records and individuals attracted (Table 1). Crushed insects not only attracted ants more often, but also triggered larger recruitments. Seeds were extensively used by many species, but no specialized granivory was detected. Crickets attracted less species and were the resource less exploited overall. Feces and termites also presented a lower number of records and small recruitments compared to other resources.

Almost all common species (= frequent in pitfalls and/or in sample points) were well represented in baits (Table 2, Supplementary Material). The only species conspicuously absent was *Pachycondyla harpax* (Fabricius, 1804) and, to a lesser extent, *Cyphomyrmex rimosus* (Spinola, 1851) and *Hylomyrma reitteri* (Mayr, 1887).

The use of trophic resources is discussed in the following sections (Fig 1). Literature review, results and discussion are presented for every individual species or genus. Period of activity is presented afterwards, for all species combined (Fig 2). General aspects are explored in a final Discussion section.

Gnamptogenys striatula Mayr, 1884 (Ectatomminae)

This species (or species complex – Arias, 2008; G. P. Camacho, UFPR, personal communication) is a rare example of a Neotropical ant extensively studied in the laboratory, covering many aspects of its biology (e.g. Giraud et al., 2000; Kaptein et al., 2005). However, the only information available about its trophic niche in the wild comes from Lattke (1990), who reports remnants of several insect orders inside nests, and posteriorly called it "a generalist epigeic forager of humid forests" (Lattke, 1995). A recent account recorded it rarely on experimental vertebrate carcasses left to rot in a forest, predating the larvae and pupae of necrophagous insects (Paula et al., 2016).

In accordance with this short background, the species was observed using termites frequently, but crushed insects, feces and sucrose were important as well (Fig 1). Hence, the species will scavenge and consume sugar when given the opportunity (but notice the lower use of melezitose, discussed in the next section). The relatively high use of feces, a less preferred resource overall, is a noteworthy feature that differentiates *G. striatula* from most other species of this study, particularly the two "generalist predators" discussed next.

Odontomachus chelifer (Latreille, 1802) and *Pachycondyla striata* Smith, 1858 (Ponerinae)

These two widespread species radically differ in morphology, but are similar in many aspects, therefore is appropriate to discuss both together. They are one of the most conspicuous elements of the southern Atlantic forest ground fauna, due to their abundance, solitary foraging mode and large size. Also, they are two of the most well-known species included in this study, and several account showed a multitude of functional roles and a broad trophic niche for them. Observation of nest entrances showed that 80-90% of the items carried by *Pa. striata* were arthropod parts, mostly termites and other ants, the remaining consisting of plant material (Giannotti & Machado, 1991; Medeiros & Oliveira, 2009). Through direct observation, Medeiros and Oliveira (2009) also showed that scavenging accounts for more than 80% of its foraging behavior. On the other hand, Fowler (1980) reported *O. chelifer* preferences for certain termite species in laboratory, and qualitatively stated that in the field prey consisted almost entirely of termites. In the Atlantic forest, all items carried to nests were arthropods, mainly termites, but other animal groups accounted for 60% of them (Raimundo et al., 2009). Scavenging was also cited in this study, although not quantified. Both *O. chelifer* and *Pa. striata* were recorded on experimental carcasses predating the larvae and pupae of necrophagous insects (Paula et al., 2016).

Other important items used by the two species are seeds with elaiosomes and other fallen diaspores rich in proteins and lipids, frequently collected from the ground in the Atlantic forest (Pizo & Oliveira, 2000; Passos & Oliveira, 2002, 2004). Field records on use of liquid sugars are scant and qualitative. *Odontomachus chelifer* was not observed using extra-floral nectaries (EFNs) by Raimundo et al. (2009), while there is one record for *Pa. striata* (in Cerrado, the Brazilian savannah – Byk & Del-Claro, 2010).

The results presented here are mostly consistent with this broader picture (Fig 1). Both species used more frequently dead insects, sucrose and large prey. In fact, they were the only two species consistently recorded on crickets. The low frequency in termite baits is unexpected and probably represents a methodological artifact. These large solitary foragers were observed quickly collecting termites (even glued ones) and leaving the baits in a few minutes, contrary to ants of smaller species that were recruited to them. In cricket baits, however, the two species spent more time, trying to carry out the tied cricket or dismembering it. Smaller ants frequently took advantage of this to grab the remains or lick spilled hemolymph. This largely contributed to the richness found in this bait (Table 1) and could happen in nature, whenever predators kill prey too large to carry them out at once.

Besides predation, scavenging was a common behavior, and *P. striata* in particular would prioritize it whenever possible, in accordance with what was observed by Medeiros and Oliveira (2009). This could be result of their morphology, because the triangular mandibles may be more suited to chop large carcasses than the trap-jaws of *O. chelifer*. In addition, it could be an effect of competition. The two species were never found at the same bait, and co-occurred in just 10 of the 62 points where they were recorded (Table 2). The two were previously reported to avoid each other, but, when agonistic interactions occur, *Pa. striata* usually is the winner, and can steal the food or kill (and eat) *O. chelifer* (Medeiros & Oliveira, 2009; Raimundo et al., 2009). Thus, *Pa. striata* could displace *O. chelifer* and maintain control of a valuable resource such as dead arthropods through tandem recruitment (Medeiros & Oliveira, 2009; Silva-Melo & Giannotti, 2012), while cooperative foraging behavior was not observed in *O. chelifer* (Raimundo et al., 2009). Effectively, the average numbers of workers per bait was smaller for the latter species (*O. chelifer* = 1.4 ± 0.9; *Pa. striata* = 2.5 ± 2; Mann-Whitney, z = -2.27, p = 0.02).

Both species used sucrose frequently. They were never observed foraging on trees or low vegetation in this study, which fits previous accounts (Fowler, 1980; Medeiros & Oliveira 2009), so it is unlikely that they commonly use nectar as food source. This behavior also should limit honeydew use by them. Effectively, the difference between use of sucrose and melezitose is remarkable here. Ants differ in their sugar preferences/tolerances, and melezitose is highly attractive to some species, and less so for others (Völkl et al., 1999; Blüthgen & Fiedler, 2004). In some insects, weak or negative effect of melezitose on fitness was observed (Zoebelein, 1956; Chen & Fadamiro, 2006), and some evidence points out to reduced suitability of aphid oligosaccharides for predators (Wäckers, 2000). The low number of records for these ant species, even when melezitose was readily available, suggests a physiological constraint to the use of complex sugars. While some congeneric species are known to visit EFNs or tend hemipterans (e.g. *O. troglodytes* – Lachaud & Dejean, 1991), the main source of sugars for these ground foragers in the Atlantic forest is more likely to be fallen fruits rich on mono- and disaccharides.

***Wasmannia auropunctata* (Roger, 1863) (Myrmicinae)**

This tiny species is native to the Neotropics, but infamous as an unpleasant guest worldwide. It is an exotic invader on many continents and islands, and also an indoor exotic species in colder places (Wetterer & Porter, 2003). A large body of knowledge describes how *W. auropunctata* dominate habitats and displace other ants, which often happens

Table 1 – Baits used to represent natural resources in this work, with total number of species (S), records (BA) and average number of individuals ± S.D. (IN) recorded.

Bait	Resource represented	S	BA	IN
Living crickets	Larger and highly mobile prey	26	107	4 ± 8
Living termites	Smaller and slower prey	31	203	4 ± 15
Crushed insects	Dead arthropods	33	422	14 ± 38
Chicken feces	Bird droppings	32	215	3 ± 5
Seeds mixture	Seeds of diverse sizes and shapes, without elaiosomes	32	344	7 ± 10
Melezitose	Oligossacharides produced by sap-sucking insects	34	327	6 ± 9
Sucrose	Dissacharides present in extra-floral nectar and fleshy fruits	34	366	7 ± 15

when the species is introduced or, within its native range, in crops and other open/disturbed areas. The species is portrayed feeding virtually on everything: scavenging; preying on small and large arthropods; collecting diversified plant parts; visiting extra-floral nectaries and tending honeydew-producing insects (Creighton, 1950; Kusnezov, 1952; Smith, 1954; Smith, 1965; Fabres & Brown, 1978; Clark et al., 1982; Deyrup et al., 2000; Wetterer & Porter, 2003; Longino & Fernández, 2007). Some of these authors suggest that honeydew is their main resource, such as Clark et al. (1982).

A comparatively small amount of information suggests that, inside forests within its native range, the species is not nearly as dominant (Majer & Delabie, 1999; Longino & Fernández, 2007). Very little is known about *W. auropunctata* habits in this context. Using generic baits, Orivel et al. (2009) showed a steep decline in bait use and nest density within a gradient from open areas to undisturbed forest. In Atlantic forest, ca. 1400 km north of the present study site, Santana et al. (2013) qualitatively showed it interacting with seven non-myrmecophorous diaspores on the ground.

In light of this literature record, it was really surprising to find the species to be a strict specialist in feces (Fig 1). In fact, it was the only species in this study that used a single resource. It was a comparatively frequent species (Table 2), but appeared always in low numbers and was not collected in pitfalls. This result differs from the widespread use of fleshy diaspores found in Santana et al. (2013), and also from the use of baits in Orivel et al. (2009). The latter authors suggested that abiotic factors play a role in the ecological shift of *W. auropunctata* from open to forest areas. A physiological constraint related to environmental conditions (e.g. temperature) could explain why the species has a limited role inside forests, and why, in a higher latitude, it shifts to a resource less preferred by other species. This intriguing behavior will be explored further and shows that there are open questions related to this important species, particularly outside the invasive context.

Table 2 – Species analyzed in this work. BA = total records in baits. PF = total records in pitfalls. PT = total records in sample points, considering both methods.

Species	BA	PF	PT
Camponotus lespesii Forel, 1886	9	1	4
Camponotus zenon Forel, 1912	14	0	10
Crematogaster nigropilosa Mayr, 1870	5	1	5
Cyphomyrmex rimosus (Spinola, 1851)	6	10	15
Gnamptogenys striatula Mayr, 1884	47	26	26
Hylomyrma reitteri (Mayr, 1887)	8	10	13
Linepithema iniquum (Mayr, 1870)	10	0	7
Linepithema micans (Forel, 1908)	16	1	6
Linepithema pulex Wild, 2007	14	1	5
Odontomachus chelifer (Latreille, 1802)	42	12	25
Pachycondyla harpax (Fabricius, 1804)	1	11	10
Pachycondyla striata Smith, 1858	88	58	47
Pheidole angusta Forel, 1908	6	1	4
Pheidole aper Forel, 1912	27	10	10
Pheidole avia Forel, 1908	9	2	5
Pheidole lucretii Santschi, 1923	50	10	13
Pheidole nesiota Wilson, 2003	89	14	19
Pheidole risii Forel, 1892	21	4	5
Pheidole sarcina Forel, 1912	51	13	12
Pheidole sigillata Wilson, 2003	91	25	35
Strumigenys denticulata Mayr, 1887	0	6	6
Wasmannia auropunctata (Roger, 1863)	19	0	16
Wasmannia affinis Santschi, 1929	20	3	6

Wasmannia affinis Santschi, 1929 (Myrmicinae)

As a small genus (11 species) with one outstandingly famous representative, it is not unexpected to find very little information on the other *Wasmannia* (Longino & Fernández, 2007). That is the case for *W. affinis*, which has a geographic distribution apparently restricted to Atlantic forests of south and southwest Brazil. The single record about its feeding habits comes from Bieber et al. (2013), who reported it as the ant species most frequently interacting with fallen fruits of *Psychotria suterella* (Rubiaceae).

The results for this species were very distinct from *W. auropunctata* (Fig 1). *Wasmannia affinis* had a smaller incidence in the community, but used a broader range of resources. Feces were not particularly important, and having more records on termites, seeds and melezitose would make it unique among species of this work, although it was not possible to statistically confirm this pattern.

Pheidole (Myrmicinae)

With over a thousand species described (Bolton, 2016), *Pheidole* usually is the most rich, frequent and abundant genus on the ground of tropical and subtropical forests. This was also the case here, with 17 species, eight of them fitting previously described species. After the literature review, all the previous knowledge on these species can be summarized in Wilson's (2003) words: "Biology: unknown". Not surprising at all, taking into account its complicated taxonomic history that only recently began to be solved (Wilson, 2003; Longino 2009). However, identification is a time-consuming task, depends on the infrequently collected major workers, and it is still common to find new species, which could be the case for five morphospecies in the present work (A. C. Ferreira, UFPR, personal communication; see Supplementary Material).

Even if often labeled as "generalists", the little we know about *Pheidole* species shows a diversity of habits and functional roles (Wilson, 2003), which is expected for such a large genus. In accordance with this, differences were found among the six species with at least 10 records (Fig 1). *Pheidole lucretii* Santschi, 1923*, Pheidole nesiota* Wilson, 2003*,* and *Pheidole sigillata* (Wilson, 2003) had similar

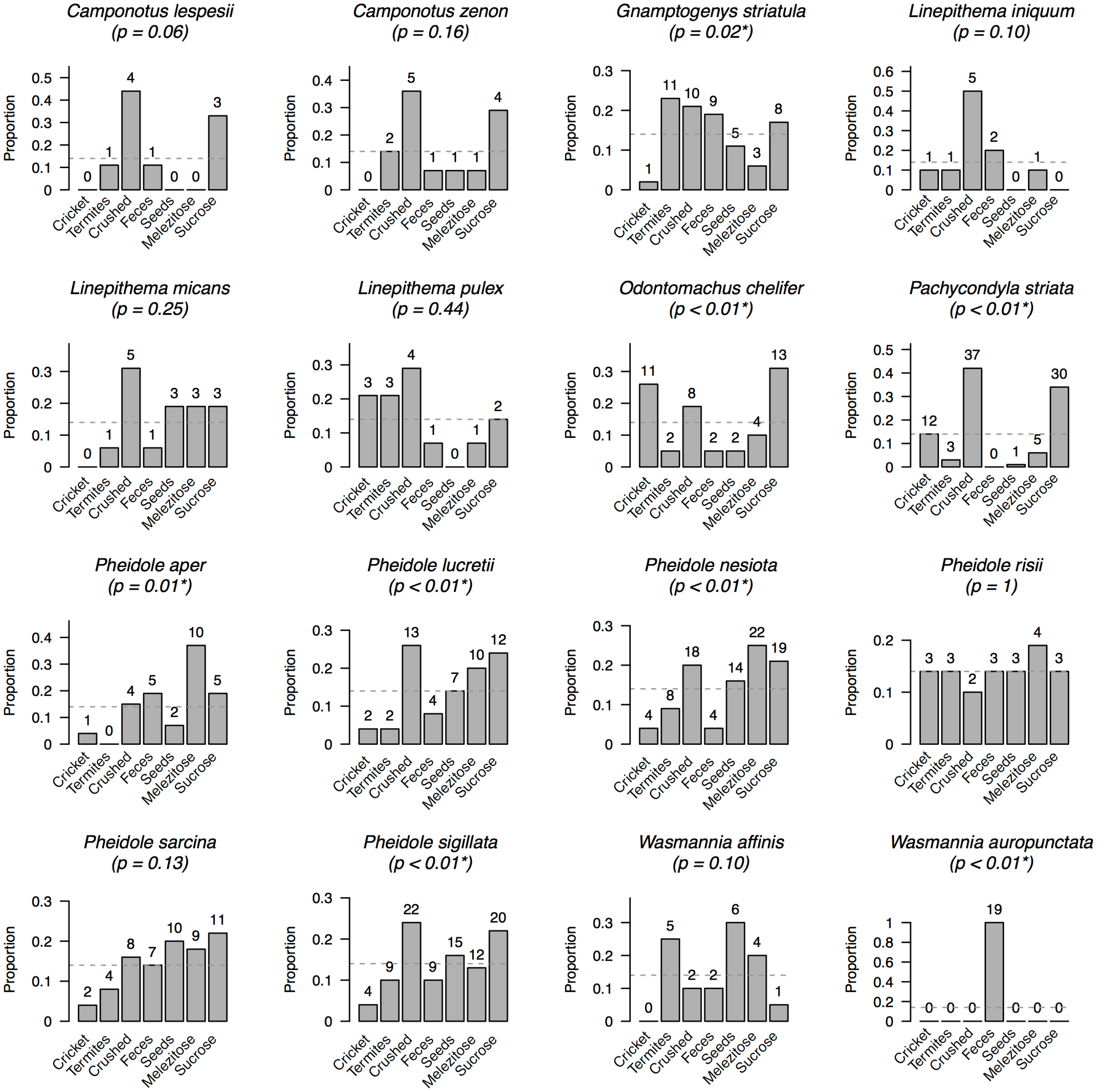

Fig 1 – Use of trophic resources by ant species in southern Brazil. Values above bars are numbers of records. The expected proportions in case of no preference for baits (= 0.14). Asterisks indicate statistical significant differences.

patterns and broadly used the most attractive resources. *Pheidole sarcina* Forel, 1912 included more seeds and feces than the others. *Pheidole aper* Forel, 1912 occupies a distinct niche, being the only species in this study that distinctively used more melezitose over other resources. Since honeydew is the only reliable source of this sugar in nature, interaction with sap-sucking insects should be important for this species. Finally, there is *Pheidole risii* Forel, 1892, the very definition of a generalist, which used all resources indiscriminately. The higher occurrence on living baits set it apart from its congeneric species.

Several mechanisms are proposed to explain the coexistence of dozens of ant species in a community, through a complex interplay of habitat structure, interspecific interactions and species traits (Cerdá et al., 2013). Behavioral adaptations might be the main factor allowing coexistence among *Ph. lucretii*, *Ph. nesiota* and *Ph. sigillata*. But overall, the results also suggest that species-specific multidimensional trophic niches, presenting quantitative rather than qualitative differences, could play a role in coexistence, even among related species of the same "generalist" group.

Linepithema (Dolichoderinae)

The case of *Linepithema* is similar to *Wasmannia*. Besides the invasive and extensively studied *Linepithema humile* (Mayr, 1868), little is known about most species of the genus (Wild, 2007). *Linepithema micans* (Forel, 1908) is common in south Brazilian vineyards, strongly associated with sap-sucking insects (Morandi Filho et al., 2015). This species certainly suffers from a misdiagnosed past, and Nondillo et al. (2013) suggest that many previous records of *L. humile* in infested vineyards should be *L. micans* instead. More is known about *Linepithema iniquum* (Mayr, 1870), mainly because it also appears as an exotic indoor species in North America and Europe. A few instances of honeydew and extra-floral nectaries use exist in the literature (Wheeler, 1929; Wild, 2007; Schmid et al., 2010) and Smith (1929) described it collecting arthropods, although without specifying if that meant scavenging or predation. Wild (2007) describes it as a primary arboreal ant, but clearly it also forages on the ground (Table 2). Finally, *Linepithema pulex* Wild, 2007 is one of the smallest and less-known representatives of the genus. It was recorded occasionally on experimental carcasses, predating the larvae and pupae of necrophagous insects (Paula et al., 2016).

None of these species showed statistically significant preferences, due to low number of records and use of several resources (Fig 1). *L. micans* and *L. pulex* seem to use resources more broadly than *L. iniquum*, which might descend to the ground mostly to scavenge animal resources. The small *L. pulex* may have stronger carnivorous tendencies and, in fact, twice they were able to recruit a few dozens of workers and predate crickets just by themselves, a remarkable feat considering its size.

Camponotus (Formicinae)

Camponotus is the only ant genus that currently rivals *Pheidole* in richness (Bolton, 2016), but still lacks comprehensive revisions at genus level. Accordingly, the biology of most tropical species remains unknown, such as the two recorded here. *Camponotus lespesii* Forel, 1886 is widespread in the Neotropics. Byk and Del-Claro (2010) recorded it qualitatively visiting extra-floral nectaries and Paula et al. (2016) observed it on experimental carcasses, predating the larvae and pupae of necrophagous insects and feeding on the carcass itself. Conversely, *Camponotus zenon* Forel, 1912 has its distribution apparently restricted to southernmost Brazil and nothing is known about its biology.

The number of records was low for both species, precluding clear statistical results, even if their resource use was restricted (Fig 1; *Ca. lespesii* is included only 9 records due to its marginally significant result). The few records for both species were quite similar, both concentrated on crushed insects and sucrose.

Daily activity

In this work, most species have not displayed strong tendencies to be active at a particular time (Fig 2). In south Brazil, summer is both the warmest and wettest season, and any temporal preference that is linked to abiotic factors should be at its lowest. Still, some species showed preferences. Three species were exclusively, or almost exclusively, diurnal (*Crematogaster nigropilosa* Mayr, 1870, *L. iniquum* and *L. pulex*) and one nocturnal (*Ca. zenon*). *Gnamptogenys striatula* showed a moderate, statistically significant, preference for the night, and *Ph. nesiota* for the day. Not much previous information on daily activity for individual species was found. The ones with information available are discussed below.

A single account of "mainly diurnal activity" exists for *Ca. lespesii* (Byk & Del-Claro, 2010). In this work, performed in the Brazilian savannah, most *Camponotus* species were qualitatively classified as diurnals. This is rather distinct from the Atlantic forest, where *Ca. lespesii* had more records at night (and *Ca. zenon* displayed a truly nocturnal behavior). For *Cr. nigropilosa* in Costa Rica, Longino (2003) says "foragers may be found day or night". However, in south Brazil the species seems to be a diurnal specialist. For *W. auropunctata*, the lack of preference was the same as previously observed in the invasive context (Clark et al., 1982).

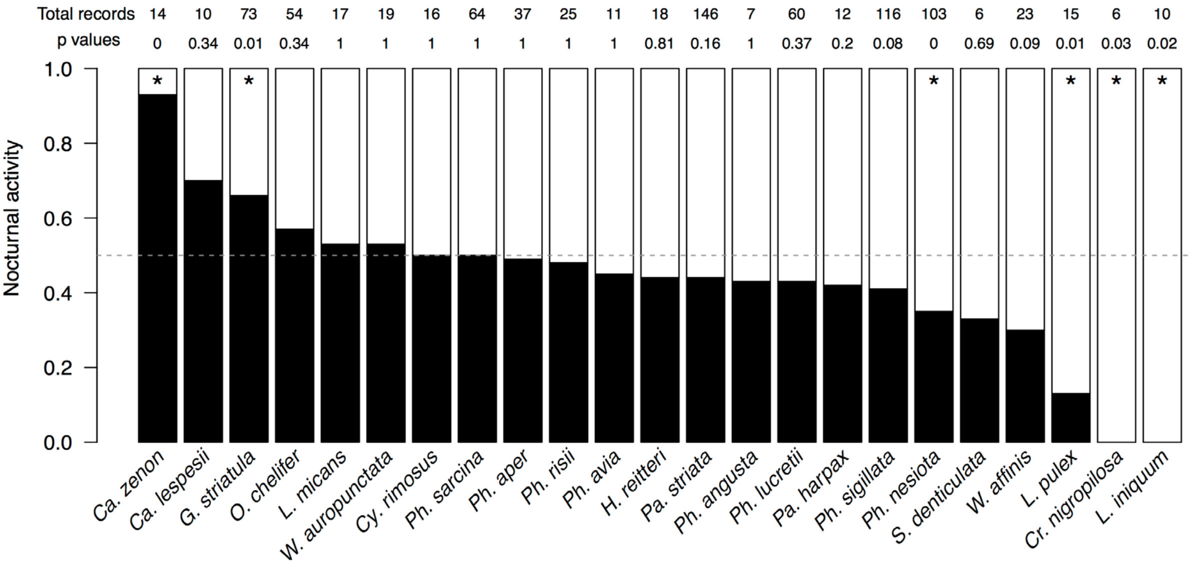

Fig 2 – Daily activity of ant species in southern Brazil. The dashed line shows expected proportions in case of no preference for period (= 0.5). Asterisks indicate statistical significant differences.

The studies in the Atlantic forest with *O. chelifer* and *Pa. striata* also assessed their period of activity (Medeiros & Oliveira, 2009; Raimundo et al., 2009). In these studies, *O. chelifer* showed a strong preference for nocturnal activity, and the inverse was found for *Pa. striata*. However, this clear pattern was not repeated in the present study. There was a slight inclination towards the same trends, but far lower than compared to the equivalent season in these studies. A response to variable weather conditions, community context or distinct behavioral adaptations to coexistence could generate such discrepancies. The interaction between these species inside and across communities is still an interesting and open topic for a detailed study.

Discussion

The life history of a species involves many aspects and is the result of a complex set of external variables and species traits. To fully understand one single history is not a trivial task. Methodology plays a key role on this, and results must be interpreted in the light of the advantages and caveats associated to every approach (Birkhofer et al., 2017). Since the bait method used in this study relies on proxies to broadly access resource use, the possibility of artificial, non-representative results must be considered. However, the results were consistent with previous accounts for two well-studied species (*O. chelifer* and *Pa. striata*), excluding the use of termites explained before. The unusual result for *W. auropunctata* is unlikely to be an artifact. The species proved to be relatively frequent in the community and, if it maintained its generalist habits, at least some records on other baits would have been expected. Also, this method does not evaluate extensively the natural variations for each resource, therefore is less suitable for detecting specialized behaviors, but focuses instead on the oft-neglected generalist species, which represent most of the community. The ants rarely recorded in baits were also uncommon in pitfalls, and many present known specialized behaviors or forage mainly on vegetation or inside leaf-litter (Table 2 and Supplementary Material). *Pachycondyla harpax* is the most notorious absence, and this could be due to a preference for specific termite species (García-Pérez et al., 1997), or also an artifact, as for the other two large Ponerinae. Finally, ants may be driven to more limited resources, instead of the ones they used more frequently. This may be particularly true for nitrogen-deprived arboreal ants (Kaspari & Yanoviak, 2001), and could be the reason behind the lack of melezitose use by *L. iniquum*. However, the two *Camponotus* species, which forage both on vegetation and ground, used sucrose and crushed insects similarly. Therefore, this deviation might be less relevant for ground-dwelling ants. In short, although with potential bias that must be considered, this bait method seems to appropriately assess the trophic niche of most species in the site and season in question, and the data it yields is useful to understand individual species.

Many methods to assess resource use cannot discriminate well between hunting and scavenging (e.g. nest excavation, observation of foragers on a nest entrance, barcoding of gut content, stable isotopes). On the other hand, this bait method assesses what species prefer to use, but not what they have available in the community. Carcasses are a rich and easy to gather resource, but in their absence ants have to fight their prey. Even taking this into account, and in light of the previous accounts (Medeiros & Oliveira, 2009; Raimundo et al., 2009), it is likely that resource use plays a role in the coexistence of the more scavenger *Pa. striata* and the more predator *O. chelifer*. This reduces niche overlap and may lead to distinct functional roles. On the other hand, species frequent on crushed insects, but not in living baits, probably are restricted to scavenging, independent of resource availability. That was the case for most *Linepithema*, *Pheidole* and *Camponotus*.

Sugar consumption is more frequently studied through observation of interactions with EFNs or hemipterans in plants, due to their role as main attractors in ant-plant interactions (Rosumek et al., 2009). Interactions of ground foragers with plant diaspores are assumed to be more associated with lipid-rich elaiosomes that mimic animal prey (Hughes et al., 1994; Giladi, 2006). However, the use of fallen fruits simply as sugar sources might be overlooked. This could partially explain the pronounced lack of use of carbohydrate resources by the "poneroid" clade observed by Lanan (2014). Few species in the present work were not attracted by sucrose, and some of them probably climb vegetation in search for EFNs (e.g. *Camponotus*). However, fallen fruits might be an occasional but disputed resource for species restricted to the ground. Preference for melezitose was less common, and it was conspicuously avoided by some species. Among physiological constrains that could reduce suitability of certain sugars to a species, particularly insect-synthesized oligosaccharides, are low gustatory perception, digestibility and nutritional value (Boevé & Wäckers, 2003). These constraints could be another source of niche partitioning among ant species.

Other fundamental aspect underlying the results of this work is the context-dependence of the patterns and processes studied in ecology, including the interaction between organisms and resources (Agrawal et al., 2007). The few well-studied species told different stories in a distinct context, like the trophic niche of *W. auropunctata* and daily activity of *Pa. striata* and *O. chelifer*. It is likely that the other, less-known species would exhibit such variation in different contexts, influenced by biotic interactions, abiotic factors and evolutionary history of the community.

Taking into account the lack of knowledge about most species, the complementary results given by different methodologies, and the variation under distinct contexts, it is clear that descriptive studies are still very much needed for tropical species, even if these studies are often relegated to second plane in modern science practice and funding (Greene, 2005). In this way, studies at community or larger scales could bring a considerable amount of information for individual species, above all when they are virtually unknown. This could be achieved first by spending time and effort on the taxonomic stage, and avoid use of morphospecies whenever possible. Second, researches should learn about their species to point out relevant findings, and prevent these to end up buried in a datasheet cell or the supplementary material. The large scale, pattern-driven enterprise is clearly important for the advancement of knowledge, but such basic aspects of natural sciences still are important. Claims for this "old-fashioned" natural history are not new (Jordan, 1916). A century later they remain valid, because we still have a lot to describe.

Supplementary Material

http://periodicos.uefs.br/index.php/sociobiology/rt/suppFiles/1623/0

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References

Agrawal, A.A., Ackerly, D.D., Adler, F., Arnold, A.E., Cáceres, C., Doak, D.F., Post, E., Hudson, P.J., Maron, J., Mooney, K.A. (2007). Filling key gaps in population and community ecology. Frontiers in Ecology and the Environment, 5: 145-152. doi: 10.1890/1540-9295(2007)5

Anjos, D.V., Caserio, B., Rezende, F.T., Ribeiro, S.P., Del-Claro, K., Fagundes, R. (2016). Extrafloral-nectaries and interspecific aggressiveness regulate day/night turnover of ant species foraging for nectar on *Bionia coriacea*. Austral Ecology, 42: 317-328. doi: 10.1111/aec.12446.

AntWeb. (2016). http://www.antweb.org/. (accessed date: 15 March, 2016)

AntWiki. (2016). http://www.antwiki.org/. (accessed date: 10 November, 2016)

Arias, T.M. (2008). Subfamilia Ectatomminae. In Jiménez, E., Fernández, F., Arias, T.M., Lozano-Zambrano, F.H. (Eds.), Sistemática, biogeografía y conservación de las hormigas cazadoras de Colombia (pp. 53-107). Bogotá: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.

Baccaro, F.B., Feitosa, R.M., Fernández, F., Fernandes, I.O., Izzo, T.J., de Souza, J.L.P., Solar, R.R.C. (2015). Guia para os gêneros de formigas do Brasil. Manaus: Editora INPA. doi: 10.5281/zenodo.32912.

Baker, H.G., Baker, I., Hodges, S.A. (1998). Sugar composition of nectars and fruits consumed by birds and bats in the Tropics and Subtropics. Biotropica, 30: 559-586. doi: 10.1111/j.1744-7429.1998.tb00097.x.

Bieber, A.G.D., Silva, P.S.D., Oliveira, P.S. (2013). Attractiveness of fallen fleshy fruits to ants depends on previous handling by frugivores. Écoscience, 20: 85-89. doi: 10.2980/20-1-3573.

Birkhofer, K., Bylund, H., Dalin, P., Ferlian, O., Gagic, V., Hambäck, P.A., Klapwijk, M., Mestre, l., Roubinet, E., Schroeder, M., Stenberg, J.A., Porcel, M., Björkman, C., Jonsson, M. (2017). Methods to identify the prey of invertebrate predators in terrestrial field studies. Ecology and Evolution, 7: 1942-53. doi: 10.1002/ece3.2791.

Blüthgen, N., Feldhaar, H. (2010). Food and shelter: How resources influence ant ecology. In Lach, L., Parr, C.L., Abbott, K.L. (Eds.), Ant Ecology (pp. 115–136). Oxford: Oxford University Press.

Blüthgen, N., Fiedler, K. (2004). Preferences for sugars and amino acids and their conditionality in a diverse nectar-feeding ant community. Journal of Animal Ecology, 73: 155-166. doi: 10.1111/j.1365-2656.2004.00789.x.

Blüthgen, N., Gebauer, G., Fiedler, K. (2003). Disentangling a rainforest food web using stable isotopes: dietary diversity in a species-rich ant community. Oecologia, 137: 426-435. doi: 10.1007/s00442-003-1347-8.

Boevé, J.L., Wäckers, F.L. (2003). Gustatory perception and metabolic utilization of sugars by *Myrmica rubra* ant workers. Oecologia, 136: 508-514. doi: 10.1007/s00442-003-1249-9.

Bolton, B. (2016). An online catalog of the ants of the world. http://antcat.org/. (accessed date: 28 March 2017).

Brandão, C.R.F., Silva, R.R., Delabie, J.H.C. (2012). Neotropical ants (Hymenoptera) functional groups: Nutritional and applied implications. In Panizzi, A.R., Parra, J.R.P. (Eds.), Insect Bioecology and Nutrition for Integrated Pest Management (pp. 213-236). Boca Raton: CRC Press.

Byk, J., Del-Claro, K. (2010). Nectar- and pollen-gathering *Cephalotes* ants provide no protection against herbivory: a new manipulative experiment to test ant protective capabilities. Acta Ethologica, 13: 33-38. doi: 10.1007/s10211-010-0071-8.

Cerdá, X., Arnan, X., Retana, J. (2013). Is competition a significant hallmark of ant (Hymenoptera: Formicidae) ecology? Myrmecological News, 18: 131-147.

Chen, L., Fadamiro, H.Y. (2006). Comparing the effects of five naturally occurring monosaccharide and oligosaccharide sugars on longevity and carbohydrate nutrient levels of a parasitic phorid fly, *Pseudacteon tricuspis*. Physiological Entomology, 31: 46-56. doi: 10.1111/j.1365-3032.2005.00484.x.

Clark, D.B., Guayasamin, C., Pazmino, O., Donoso, C., de Villacis, Y.P. (1982). The tramp ant *Wasmannia auropunctata*: Autecology and effects on ant diversity and distribution on Santa Cruz Island, Galapagos. Biotropica, 14: 196-207. doi: 10.2307/2388026.

Creighton, W.S. (1950). The ants of North America. Bulletin of the Museum of Comparative Zoology at Harvard College, 104: 1-585.

Deyrup, M., Davis, L., Cover, S. (2000). Exotic ants in Florida. Transactions of the American Entomological Society, 126: 293-326.

Egerton, F.N. (2013). History of ecological sciences, part 47: Ernst Haeckel's ecology. The Bulletin of the Ecological Society of America, 94: 222-244. doi: 10.1890/0012-9623-94.3.222.

Fabres, G., Brown, W.L. (1978). The recent introduction of the pest ant *Wasmannia auropunctata* into New Caledonia. Australian Journal of Entomology, 17: 139-142.

Feitosa, R.M., Silva, R.R., Aguiar, A.P. (2016). Diurnal flight periodicity of a Neotropical ant assemblage (Hymenoptera, Formicidae) in the Atlantic Forest. Revista Brasileira de Entomologia, 60: 241-247. doi: 10.1016/j.rbe.2016.05.006.

Fernández, F. (2008). Subfamilia Ponerinae s. str. In Jiménez, E., Fernández, F., Arias, T.M., Lozano-Zambrano, F.H. (Eds.), Sistemática, biogeografía y conservación de las hormigas cazadoras de Colombia (pp. 123–218). Bogotá: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.

Fowler, H.G. (1980). Populations, prey capture and sharing, and foraging of the Paraguayan Ponerine *Odontomachus chelifer* Latreille. Journal of Natural History, 14: 79-84.

García-Pérez, J., Blanco-Piñón, A., Mercado-Hernández, R., Badii, M. (1997). El comportamiento depredador de *Pachycondyla harpax* Fabr. sobre *Gnathamitermes tubiformans* Buckley en condiciones de cautiverio. Southwestern Entomologist, 22: 345-353.

Giannotti, E., Machado, V.L.L. (1991). Notes on the foraging of two species of ponerine ants: food resources and daily activity (Hymenoptera, Formicidae). Bioikos, 5: 7–17.

Giladi, I. (2006). Choosing benefits or partners: a review of the evidence for the evolution of myrmecochory. Oikos. 112: 481-492. doi: 10.1111/j.0030-1299.2006.14258.x.

Giraud, T., Blatrix, R., Poteaux, C., Solignac, M., Jaisson, P. (2000). Population structure and mating biology of the polygynous ponerine ant *Gnamptogenys striatula* in Brazil. Molecular Ecology, 9: 1835-1841. doi: 10.1046/j.1365-294x.2000.01085.x.

Greene, H. (2005). Organisms in nature as a central focus for biology. Trends in Ecology and Evolution, 20: 23-27. doi: 10.1016/j.tree.2004.11.005.

Heath, R.J.; Rock, C.O. (2002). The Claisen condensation in biology. Natural Product Reports, 19: 581-596. doi: 10.1039/b110221b.

Houadria, M., Salas-Lopez, A., Orivel, J., Blüthgen, N., Menzel, F. (2015). Dietary and temporal niche differentiation in tropical ants — Can they explain local ant coexistence? Biotropica, 47: 208-217. doi: 10.1111/btp.12184.

Hughes, L., Westoby, M., Jurado, E. (1994). Convergence of elaiosomes and insect prey: evidence from ant foraging behaviour and fatty acid composition. Functional Ecology, 8: 358-365.

Janicki, J., Narula, N., Ziegler, M., Guénard, B., Economo, E.P. (2016). Visualizing and interacting with large-volume biodiversity data using client–server web-mapping applications: The design and implementation of antmaps.org. Ecological Informatics, 32: 185-193. doi: 10.1016/j.ecoinf.2016.02.006.

Jordan, D.S. (1916). Plea for old-fashioned natural history. Bulletin of the Scripps Institution for Biological Research of the University of Calofornia, 1: 3-6.

Kaptein, N., Billen, J., Gobin, B. (2005). Larval begging for food enhances reproductive options in the ponerine ant *Gnamptogenys striatula*. Animal Behaviour, 69: 293-299. doi: 10.1016/j.anbehav.2004.04.012.

Kaspari, M. (2000). A primer on ant ecology. In Agosti, D., Majer, J.D., Alonso, L.E., Schultz, T.R. (Eds.), Ants: standard methods for measuring and monitoring biodiversity (pp. 9-24). Washington: Smithsonian Institution Press.

Kaspari, M., Yanoviak, S.P. (2001). Bait use in tropical litter and canopy ants – Evidence of differences in nutrient limitation. Biotropica, 33: 207-211.

Kempf, W.W. (1965). A revision of the Neotropical fungus-growing ants of the genus *Cyphomyrmex* Mayr. Part II: Group of *rimosus* (Spinola) (Hym. Formicidae). Studia Entomologica, 8: 161-200.

Kempf, W.W. (1973). A revision of the Neotropical myrmicine ant genus *Hylomyrma* Forel (Hymenoptera: Formicidae). Studia Entomologica, 16: 225-260.

Krebs, C.J. (1999). Ecological methodology. 2nd ed. Menlo Park: Benjamin/Cummings, 620 p.

Krell, F.T. (2004). Parataxonomy vs. taxonomy in biodiversity studies – pitfalls and applicability of "morphospecies" sorting. Biodiversity and Conservation, 13: 795-812. doi: 10.1023/B:BIOC.0000011727.53780.63.

Kusnezov, N. (1952). El género *Wasmannia* en la Argentina (Hymenoptera, Formicidae). Acta Zoologica Lilloana, 10: 173-182.

Lachaud, J.P., Dejean, A. (1991). Food sharing in *Odontomachus troglodytes* (Santschi): a behavioral intermediate stage in the evolution of social food exchange in ants. Anales de Biología, 17: 53-61.

Lanan, M. (2014). Spatiotemporal resource distribution and foraging strategies of ants (Hymenoptera: Formicidae). Myrmecological News, 20: 53-70.

Lattke, J.E. (1990). Revisión del género *Gnamptogenys* Roger en Venezuela (Hymenoptera: Formicidae). Acta Terramaris, 2: 1-47.

Lattke, J.E. (1995). Revision of the ant genus *Gnamptogenys* in the New World (Hymenoptera: Formicidae). Journal of Hymenoptera Research, 4: 137-193.

Lessard, J.P., Dunn, R.R., Sanders, N.J. (2009). Temperature-mediated coexistence in temperate forest ant communities. Insectes Sociaux, 56: 149–156. doi: 10.1007/s00040-009-0006-4.

Longino, J.T. (2003). The *Crematogaster* (Hymenoptera, Formicidae, Myrmicinae) of Costa Rica. Zootaxa, 151: 1-150.

Longino J.T. (2009). Additions to the taxonomy of New World *Pheidole* (Hymenoptera: Formicidae). Zootaxa, 2181: 1-90.

Longino, J.T., Fernández, F. (2007). Taxonomic review of the genus *Wasmannia*. Memoirs of the American Entomological Institute, 80: 271–289.

Majer, J.D., Delabie, J.H.C. (1999). Impact of tree isolation on arboreal and ground ant communities in cleared pasture in the Atlantic rain forest region of Bahia, Brazil. Insectes Sociaux, 46: 281-290. doi: 10.1007/s000400050147.

McDonald, J.H. (2014). Handbook of biological statistics. 3rd ed. Baltimore: Sparky House Publishing, 299 p.

Medeiros, F.N.S., Oliveira, P.S. (2009). Season-dependent foraging patterns case study of a Neotropical forest-dwelling ant (*Pachycondyla striata*; Ponerinae). In Jarau, S., Hrncir, M. (Eds.), Food exploitation by social insects: ecological, behavioral, and theoretical approaches (pp. 81-95). Boca Raton: Taylor & Francis Group.

Morandi Filho, W.J., Pacheco-da-Silva, V.C., Willink, M.C.G., Prado, E., Botton, M. (2015). A survey of mealybugs infesting South-Brazilian wine vineyards. Revista Brasileira de Entomologia, 59: 251–254. doi: 10.1016/j.rbe.2015.05.002.

Nondillo, A., Ferrari, L., Lerin, S., Bueno, O.C., Botton, M. (2014). Foraging activity and seasonal food preference of *Linepithema micans* (Hymenoptera: Formicidae), a species associated with the spread of *Eurhizococcus brasiliensis* (Hemiptera: Margarodidae). Journal of Economic Entomology, 107: 1385–1391. doi: 10.1603/EC13392.

Nondillo, A., Sganzerla, V.M.A., Bueno, O.C., Botton, M. (2013). Interaction between *Linepithema micans* (Hymenoptera: Formicidae) and *Eurhizococcus brasiliensis* (Hemiptera: Margarodidae) in vineyards. Environmental Entomology, 42: 460-466. doi: 10.1603/EN13004.

Oliveira, R.F., Silva, R.R., Souza-Campana, D.R., Nakano, M.A., Morini, M.S.C. (2015). Worker morphology of the ant *Gnamptogenys striatula* Mayr (Formicidae, Ectatomminae) in different landscapes from the Atlantic Forest domain. Revista Brasileira de Entomologia, 59: 21-27. doi: 10.1016/j.rbe.2015.02.002.

Orivel, J., Grangier, J., Foucaud, J., Le Breton, J., Andrès, F.X., Jourdan, H., Delabie, J.H.C., Fournier, D., Cerdan, P., Facon, B. (2009). Ecologically heterogeneous populations of the invasive ant *Wasmannia auropunctata* within its native and introduced ranges. Ecological Entomology, 34: 504-512. doi: 10.1111/j.1365-2311.2009.01096.x.

Passos, L., Oliveira, P.S. (2002). Ants affect the distribution and performance of seedlings of *Clusia criuva*, a primarily bird-dispersed rain forest tree. Journal of Ecology, 90: 517-528. doi: 10.1046/j.1365-2745.2002.00687.x.

Passos, L., Oliveira, P.S. (2004). Interaction between ants and fruits of *Guapira opposita* (Nyctaginaceae) in a Brazilian sandy plain rainforest: ant effects on seeds and seedlings. Oecologia, 139: 376–382. doi: 10.1007/s00442-004-1531-5.

Paula, M.C., Morishita, G.M., Cavarson, C.H., Gonçalves, C.R., Tavares, P.R.A., Mendonça, A., Súarez, Y.R., Antonialli-Junior, W.F. (2016). Action of ants on vertebrate carcasses and blow flies (Calliphoridae). Journal of Medical Entomology, 1: 1–9. doi: 119. 10.1093/jme/tjw119.

Percival, M.S. (1961). Types of nectar in Angiosperms. New Phytologist, 60: 235–281.

Pizo, M.A., Oliveira, P.S. (2000). The use of fruits and seeds by ants in the Atlantic Forest of Southeast Brazil. Biotropica, 32: 851-861. doi: 10.1111/j.1744-7429.2000.tb00623.x.

R Core Team (2016). R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing. Retrieved from: https://www.R-project.org/

Raimundo, R.L.G., Freitas, A.V.L., Oliveira, P.S. (2009). Seasonal patterns in activity rhythm and foraging ecology in the Neotropical forest-dwelling ant, *Odontomachus chelifer* (Formicidae: Ponerinae). Annals of the Entomological Society of America, 102: 1151–1157. doi: 10.1603/008.102.0625.

Rosumek, F.B., Silveira, F.A.O., Neves, F. S., Barbosa, N.P.U., Diniz, L., Oki ,Y., Pezzini, F., Fernandes, G.W., Cornelissen, T. (2009). Ants on plants: a meta-analysis of the role of ants as plant biotic defenses. Oecologia, 160: 537-549. doi: 10.1007/s00442-009-1309-x.

Santana, F.D., Cazetta, E., Delabie, J.H.C. (2013). Interactions between ants and non-myrmecochorous diaspores in a tropical wet forest in southern Bahia, Brazil. Journal of Tropical Ecology, 29: 71–80. doi: 10.1017/S0266467412000715.

Schmid, S., Schmid, V.S., Kamke, R., Steiner, J., Zillikens, A. (2010). Association of three species of *Strymon* Hübner (Lycaenidae: Theclinae: Eumaeini) with bromeliads in southern Brazil. Journal of Research on the Lepidoptera, 42: 50–55.

Smith, M.R. (1929). Two introduced ants not previously known to occur in the United States. Journal of Economic Entomology, 22: 241–243.

Smith, M.R. (1954). Ants of the Bimini Island Group, Bahamas, British West Indies (Hymenoptera, Formicidae). American Museum Novitates, 1671: 1–16.

Smith, M.R. (1965). House-infesting ants of the Eastern United States: Their recognition, biology and economic importance. Washington: United States Department of Agriculture, 105 p.

Snealling, R.R., Longino, J.T. (1992). Revisionary notes on the Fungus-growing Ants of the genus *Cyphomyrmex, rimosus* group (Hymenoptera: Formicidae: Attini). In Quintero, D., Aiello, A. (Eds.), Insects of Panama and Mesoamerica: selected studies (pp. 479–494). Oxford: Oxford University Press.

Völkl, W., Woodring, J., Fischer, M., Lorenz, M.W., Hoffmann, K.H. (1999). Ant-aphid mutualisms: the impact of honeydew production and honeydew sugar composition on ant preferences. Oecologia, 118: 483–491. doi: 10.1007/s004420050751.

Wäckers, F.L. (2000). Do oligosaccharides reduce the suitability of honeydew for predators and parasitoids? A further facet to the function of insect-synthesized honeydew sugars. Oikos, 90: 197-201. doi: 10.1034/j.1600-0706.2000.900124.x.

Wetterer, J.K., Porter, S.D. (2003). The little fire ant, *Wasmannia auropunctata*: distribution, impact, and control. Sociobiology, 42: 1-42.

Wheeler, W. M. (1929). Two Neotropical ants established in the United States. Psyche, 36: 89–90.

Wild, A.L. (2007). Taxonomic revision of the ant genus *Linepithema* (Hymenoptera: Formicidae). Berkeley: University of California Press, 151 p.

Wilson, E.O. (2003). *Pheidole* in the New World: a dominant, hyperdiverse ant genus. Cambridge, Mass: Harvard University Press, 794 p.

Zoebelein, G. (1956). Der Honigtau als Nahrung der Insekten: Teil I. Zeitschrift für Angewandte Entomologie, 38: 369-416.