No evidence for discovery-dominance tradeoffs in *Pheidole* (Hymenoptera: Formicidae) assemblages

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Abstract

Understanding ant community structure is of great interest among ant ecologists, since these insects stand out for their diversity, especially in the tropics, where they show high co-occurrence levels in many habitats. Discovery-dominance tradeoff is considered an important mechanism acting on ant community structure in many habitats, ensuring species co-occurrence by a temporal share of resources. We investigate the occurrence of this structuring mechanism in a *Pheidole* (Hymenoptera: Formicidae) assemblage at Atlantic Rainforest remains in south Brazil. If the discovery-dominance tradeoff is structuring this ant community, we expect that some species should be better to found food sources quickly, whereas other species arrive later and dominate food sources for their own consumption. We established 55 sampling locations at two sites, settling one sardine bait in each sampling unit to take note on the resource use by ants in a three-hour experiment. There was no distinction among species in terms of their ability to found or dominate food sources, which suggests that the discovery-dominance tradeoff is not structuring this assemblage. The low levels of aggression between ant species could avoid the establishment of dominance hierarchies, whereas territoriality could be acting to ensure resource partitioning. Also important is the fact that tradeoffs can vary with spatial scale, which can be assessed in further studies.

Introduction

Ants are important components of terrestrial ecosystems worldwide, particularly in the tropics, where they account for a substantial portion of the animal biomass (Fittkau & Klinge 1973) and show considerable species diversity (Economo et al. 2018). Most ant species are food generalists to some degree (Kaspari 2001; Brandão et al. 2009), because of the marked differences in brood and adult nutritional requirements (Blüthgen & Feldaar 2010). Therefore, if several ant species co-occur and share common resources, one would expect that they might show some level of competition. However, the role of competition in ant community structure is far from settled

(Parr & Gibb 2010), although having traditionally been considered as a "hallmark" of ant communities (Hölldobler & Wilson 1990). Several authors demonstrated that many ant assemblages are organized into dominance hierarchies, in which some species (dominants) are better competitors for food sources than others (subordinates) (Fellers 1987; Blüthgen & Fiedler 2004; Feener et al. 2008; Parr 2008; Arnan et al. 2012; Bertelsmeier et al. 2015b; Ennis & Philpott 2017; Yitbarek & Philpott 2019), yet a more critical view has become prevalent in recent years, and the role of competition has been questioned (Cerdá et al. 2013).

The establishment and use of dominance hierarchies itself is being criticized, which adds many concerns about the supremacy of competition in ant communities (Stuble et al. 2017). Ant species are considered as dominant, in the context of those hierarchies, either by the outcomes of pairwise interactions with other species, where the winners are considered dominants (behavioural dominance), or by a large recruitment of workers on food sources, preventing other species to use this resource (numerical dominants) (Davidson 1998). These features are not necessarily correlated and little is known about how they relate with other life history traits, so dominance may become subjective and hard to ascertain in most ant communities (Blüthgen & Stork 2007). Additionally, dominance hierarchies can change on daily and seasonal basis, and no ultimate hierarchical outcomes can be expected (Stuble et al. 2017).

Regardless of the uncertainty about the prevalence of competition in ant assemblage rules, if dominance hierarchies are true, something is necessary to balance the partitioning of resources, since otherwise dominant species would eliminate subordinate ones, resulting in poorer communities (Hölldobler & Wilson 1990; Feener et al. 2008). A few such mechanisms have been proposed and their applicability tested in a number of ant assemblies (Stuble et al. 2013), such as the dominance-thermal tolerance (Cerdá et al. 1998; Roeder et al. 2018) and the discovery-dominance (Fellers 1987) tradeoffs. Also reported are the effects of parasitism (Feener 2000), predation (Gotelli 1996), daily and seasonal resource partitioning (Fellers 1989), divergences on dietary requirements (Roeder et al. 2018), habitat complexity (Sarty et al. 2006) and disturbances (Cerdá et al. 2013). Finally, more neglected are the contribution of neutral interactions in ant assembling rules (Stuble et al. 2017).

One of the main hypotheses of coexistence tested to date, the discovery-dominance tradeoff, posits that subordinate species ensure their survival by discovering food sources at faster rates, being able to use these resources before arrival of dominant species (Fellers 1987). To find

resources at faster rates, an ant colony needs to optimize the number of scout workers (Pearce-Duvet et al. 2011) that search for food, as opposed to the colonies of dominant species that invest more in recruiters (Fellers 1987). This tradeoff was tested in several situations, including in intraspecific interactions (Jordan & Blüthgen 2007), between invasive species (Bertelsmeier et al. 2015b) and within guilds (Fellers 1987). Although much studies demonstrate the importance of this mechanism in warranting ant species coexistence (Lebrun & Feener 2007; Feener et al. 2008; Bertelsmeier et al. 2015b; Camarota et al. 2016), some authors questioned its ubiquity (Jordan & Blüthgen 2007; Parr & Gibb 2012), and others stress factors that can modified the outcome of discovery-dominance tradeoffs, such as parasitism (Feener 2000; Parr & Gibb 2012).

In order to access the role of discovery-dominance tradeoff in a phylogenetic restricted assembly, we evaluated the occurrence of this mechanism between species of the worldwide-distributed genus *Pheidole* Westwood (1839). By focusing on interactions within the same genus, we avoid confounding factors related to deeper evolutionary divergences, as occurs when considering higher taxonomic levels (Siepielski & McPeek 2010). The high abundance and diversity at the study area, coupled with the generalist habitat shown by most of these species (Brandão et al. 2009) makes them a good model system to investigate mechanisms of species coexistence. If discovery-dominance tradeoff explain the coexistence of *Pheidole* species, we expect to observe some species more frequently at the beginning of bait experimentation (subordinates), whereas dominant species should arrive later, expelling subordinates and controlling baits.

Material and Methods

We carried out field experiments in two neighboring urban forest fragments located in the campus of the Universidade Federal do Paraná in Curitiba, Paraná, southern Brazil (Site A; 25º26’45.9”S; 049º13’55.5”W and site B; 25°26'52.06"S; 49°14'19.24"W) . The vegetation in this region is classified as mixed ombrophylous forest (Reginato et al. 2008), which is part of the Atlantic Forest biome (Leite e Klein 1990; IBGE 2012). The climate in the study region is subtropical humid with temperate summers, categorized as Cfb according Köppen’s system (Alvares 2013).

Experiments were carried out between February and April of 2018, during the summer, always in the morning. We established 55 sampling locations (25 and 30 on sites A and B, respectively), which were visited on 11 different dates over the course of the study. Each sampling station consisted of a 2-mL mixture of sardine and wheat flour kept within a syringe that had its end cut off so that approximately the same surface area of the bait was presented to the foraging ants. The syringe in turn was placed on a Petri dish (9 cm in diameter), which prevented ants from having access to the bait from below, thus potentially underestimating their presence at the baits and hampering direct observation. Each experiment lasted for 3 h, such that each bait was checked every 20 min. We estimated the number of major and minor at the baits and recorded which subcaste manipulated or carried food (division of labor), positive interactions between workers (e.g. trophallaxis or social grooming), and aggressive interactions with other species. For later species identification, we collected one individual per subcaste and morphospecies at each sampling unit and deposited them in micro tubes filled with 95% ethanol. Vouchers specimens were deposited at the "Coleção Entomológica Padre Jesus Santiago Moure", Zoology Department - UFPR. Variation in ant abundance over time in each experiment was visualized using GGPLOT2 (Wickham 2009) in R 3.5-0 (R Core Team 2018).

Results

We recorded 12 *Pheidole* species across our two sampling locations (Table 1). Two morphospecies were indistinguishable in the field, so to avoid any under or overestimation of worker numbers at each sampling unit we combined their data under a unique species cluster, the *P. sospes* complex. *Pheidole* species visited 48 out of 55 sampling units during our field experiments. A single species was present at 47% of the experiments, two species at 24% and three species at 16% of the experiments. The most frequent species was *P. sospes* complex (f= 45.45%), followed by *P.* aff. *hetschkoi* (32.73%) and *P. risii* (20%) (Table 1).

Minor workers conducted most of the food manipulation and transport. The most commonly recorded positive interaction was social grooming/trophallaxis, as we were not able to confidently distinguish those behaviors in the field (Table 1). Three species did not exhibit negative interactions (*P.* aff. *burculenta*, *P.* aff. *susannae* and *P.* aff. *tijucana*), whereas the remaining nine species showed some aggressive behavior, either against a different *Pheidole*

species or any other ant that eventually occurred at the baits, such as *Camponotus rufipes* Fabricius (1775), *Gnamptogenys striatula* Mayr (1884), *Odontomachus chelifer* Latreille (1802) or *Solenopsis* spp. Although the majority of species showed some negative interactions, these occur in just 20.7% of records (Table 2).

We did not find any correspondence between the relative abundance of different *Pheidole* species and their temporal variation at baits (Figure 1). In general, most species stay on sampling units throughout the entire duration of the experiments. Even rarely recorded species, like *P*. aff. *tijucana* and *P*. aff. *susannae*, that occurred just at one sampling unit, remained at those baits for the entire experiments (Table 3).

Discussion

Despite the relatively high number of co-occurring *Pheidole* species at our sampling locations, we did not found any evidence for discovery-dominance tradeoffs structuring these assemblages. In particular, we could not identify any species that preferentially occurred at beginning or the end of the experiments, a necessary pattern if these tradeoffs were true. Interestingly, a recent meta-analysis suggests that the tradeoff might be context dependent and greatly restricted to some ant assemblages affected by parasitism (Parr & Gibb 2012). Parasites of ants, such as phorid flies, ideally attack ecologically dominant species, which are efficient in finding and recruiting to food sources. In the presence of flies, these ants reduce their activity, and the interactions with the remaining species are consistent with the discovery-dominance tradeoff (LeBrun & Feener 2007). Although we did not assess the occurrence of parasitism in our study, important behavioral characteristics found in our results could explain the lack of the discovery-dominance tradeoff signature.

Since levels of aggressiveness between pairwise species interactions are the basis for dominance hierarchies (Savolainen & Vepsäläinen 1988), the low frequency of agonistic behaviors between *Pheidole* species observed at our experimentation is inconsistent with such hierarchies in our study. Aggressiveness is a trait constantly referred to in ant interactions, but a more comprehensive look at this topic revealed that agonistic behaviors need not to be a rule in interspecific encounters, even among dominant and highly invasive ants (Bertelsmeier et al. 2015a). Neutral interactions between coexisting species at baits experiments represent a great portion of the observed outcomes (Stuble et al. 2017; Gray et al. 2018), yet they are mainly

neglected, with emphasis in studies granted preferentially to true agonistics behaviors (Stuble et al. 2017). Before engaging on a dispute to ensure access of a limited resource, a suite of fighting costs need to be evaluated (Briffa & Elwood 2004; Briffa & Sneddon 2007). Rivals need to assess their own fighting ability, their opponent's status and the value of the resource to decide whether entering or not in conflict (Vieira & Peixoto 2013; Briffa & Lane 2017). All these aspects are more complex when considering social insects, especially ants, which in many cases forage collectively and recruit a great worker force to retrieve food items to their nests. Hence, other ways of resource partitioning, such as exploitative competition, seem to be preferred to avoid direct interference and the costs associated (Gordon 1996).

Coupled with the low number of agonistic interactions between ant species at baits, we recorded only one species in nearly half of our experiments, which suggests that other mechanisms are involved in structuring of this community. Many ant species protect their nesting structures and the surrounding foraging area against conspecifics or other ant species, resulting in defined territories that are fiercely protected (Cerdá et al. 2013, Adams 2016). The territory establishment ensures the domination of food sources inside the protected area and, as demonstrated for other systems, competitors often avoid fighting against the territory owner (Haering & Fox 1987; Gordon 1996; Adams 2016). In addition, ant territories are arranged in nonrandom patterns, resembling mosaics with free spaces between contiguous protected areas (Adams 2016), which could be occupied by subordinate species that do not represent a threat to the dominant ones (Andersen 2008). If the assembly of *Pheidole* species investigated here is structured on some degree of territoriality, this fact can explain why so many sampling units were visited by just one species, and the presence of so many species in relative low frequency (eight out of 12 species occurred in less than 10% of the sampling units). Even when two or more species were present on a sampling unit, one of them occur at almost the entire experimentation time, not being replaced by coexisting species that were present nearly ever in low numbers, behaving like insinuating species (Andersen 2008; Tschá & Pie 2018).

Once established, an ant colony would hardly be removed definitively, since the queen and brood are fiercely protected by the nesting structure itself and the presence of the worker force (Andersen 2008), and mortality of workers is not detrimental for the colony maintenance as a whole if it occurs at lower rates than egg laying by the queen. On the other hand, the founding stage of a colony is the most crucial in terms of probability of success. At this moment, queens are

unprotected and completely exposed to predators and any kind of stochastic danger, resulting in high queen mortality (Hölldobler & Wilson 1990). Consequently, the interactions within and between ant species that occur at the founding stage have important implications for the community structure, driving the spatial arrangement of ant nests (Andersen 2008; Billick et al. 2014) and consequently the competitive pressures along the entire life cycle of each colony, due to the role of territoriality early discussed (Adams 2016).

The territoriality context suggests that the first ants arriving at baits were those that nest closely to the sampling units, being able to recruit workers and monopolize food sources at faster rates (Albrecht & Gotelli, 2001). The implication is that the crucial stage for resource assurance is the discovery event, a fact recently suggested for a Neotropical arboreal ant community (Camarota et al. 2018). This differs from the two step view whereby the resource use by ants is partitioned between a food search phase, where a portion of species are competitively inferior, followed by a latter moment of competition displacement and species turnover where other ants take greater success, the so called discovery-dominance tradeoff (Fellers 1987). Beyond territoriality, recent efforts on disentangle dietary preferences in co-occurring ants suggest that we need to know more about the dietary role in niche partitioning for ants in general (Rosumek 2017). While being considered as highly generalists species in general (Brandão et al. 2009), *Pheidole* species appear do display some degrees of food preference, which could have large contributions to food partitioning and coexistence patterns between this very abundant and diverse ant lineage (Rosumek 2017). Recently, Tschá & Pie (2018) investigate the role of several morphological, behavioural and physiological traits in underlying mechanisms of ecological dominance in Atlantic Rainforest *Pheidole* assemblages. Although expecting the occurrence of some kind of tradeoffs between performance in those traits and ecological dominance, the authors found that for many traits dominant species also show better performances, as in relation to walking speed and environmental tolerance (Tschá & Pie 2018), whereas subordinates where the worst in these aspects. These results call attention to a possible secondary role of evolutionary tradeoffs in structuring *Pheidole* assemblages at the Atlantic Rainforest.

Patterns of co-occurrence in ant communities are usually interpreted almost exclusively around the predictions of competitive interactions within and between species (Hölldobler & Wilson 1990). Recently, the debate about what allows so many ant species to coexist in the same

habitat is being revisited by a more critic view of the competition status as the hallmark of ant community structure (Cerdá et al. 2013; Stuble et al. 2017). We show here that a classical mechanism of co-occurrence, the discovery-dominance tradeoff (Fellers 1987), fails to account for *Pheidole* species co-occurrence in assemblages of two Atlantic Forest remains in South Brazil. Although the spatial distribution of ant nests and territoriality can help to explain co-occurrence in these assemblages (Andersen 2008), a deeper understanding of ant dietary preferences (Kaspari 2001; Rosumek 2017) and the colony founding stage (Billick et al. 2014) is needed, as well approaches to investigate co-occurrence patterns along distinct broader spatial scales (Kneitel & Chase 2004).

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Table 1. General behavior information's, frequency at baits, number of majors and minors of the twelve species recorded at our sampling sites.

Species	**N major records[1]**	**N minor records[1]**	**Frequency at baits (%)**	**Manipulation**	**Transport**	**Positive interaction**
P. sospes complex	15	1544	45.45	Minor	Minor	AG/T[2]
P. aff. *burculenta*	0	4	1.82	none	Minor	No
P. aff. *hetschkoi*	1	699	32.73	Minor	Minor	AG/T
P. aff. *rosae*	0	209	7.27	Minor	Minor	AG/T
P. aff. *susannae*	211	900	1.82	Minor and Major	Minor	AG/T
P. aff. *tijucana*	3	109	1.82	Minor	Minor	AG/T
P. longiseta	24	345	3.64	Minor	Minor	AG/T
P. nesiota	35	197	7.27	Minor and Major	Minor	AG/T
P. aff. *lucretii*	218	3833	18.18	Minor and Major	Minor and Major	AG/T
P. risii	0	831	20	Minor	Minor	AG/T
P. sp.1	4	335	1.82	Minor	Minor	No
P. sp.2	0	16	1.82	Minor	Minor	No

[1]The number of majors and minors workers at each bait in each time lag, this measure do not correspond to abundance, since it is likely that the same individuals were present in the same Petri dish over the entire experiment range.

[2]AG= Allogrooming or T= Trophallaxis.

Table 2. Proportion of negative interactions shown by species in relation to the number of coexisting *Pheidole* species at each sampling unit. Values are number (%) of negative interactions recorded for each species.

Species	**Negative interactions**				**Total records[1]**
	No		**Yes**		
	Co-occurring *Pheidole* species		**Co-occurring *Pheidole* species**		
	1[2]	**2**	**1[2]**	**2**	
P. sospes complex	40(25.8)	90(58.1)	5(3.2)	20(12.9)	**155**
P. aff. *burculenta*	0	4(100)	0	0	**4**
P. aff. *hetschkoi*	44(41.9)	33(31.4)	13(12.4)	15(14.3)	**105**
P. aff. *rosae*	0	9(45)	0	11(55)	**20**
P. aff. *susannae*	9(100)	0	0	0	**9**
P. aff. *tijucana*	0	9(100)	0	0	**9**
P. longiseta	0	9(69.2)	0	4(30.8)	**13**
P. nesiota	14(66.7)	4(19.1)	1(4.8)	2(9.5)	**21**
P. aff. *lucretii*	26(37.1)	23(32.9)	9(12.9)	12(17.1)	**70**
P. risii	17(27.9)	40(65.6)	0	4(6.6)	**61**
P. sp.1	0	8(88.9)	0	1(11.1)	**9**
P. sp.2	0	4(57.1)	0	3(42.9)	**7**
Total records[1]	**150(31.1)**	**233(48.2)**	**28(5.8)**	**72(14.9)**	**483**

[1]Total number of sampling units multiplied by time intervals a species was recorded.

[2]Negative interactions with other than *Pheidole* ant species.

Table 3. Number of time intervals a species remain at one bait. Values are number (%) of baits that each species remain for each quantity of time intervals, that range for 1 (20 min) to 9 (180 min, the entire experimentation time). Also showed are the number of baits (N baits) a species was present.

	Number of time intervals									
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**N total[1]**
P. sospes complex	1(4)	2(8)	2(8)	2(8)	1(4)	3(12)	4(16)	4(16)	6(24)	**25**
P. aff. *burculenta*	0	0	0	1(100)	0	0	0	0	0	**1**
P. aff. *hetschkoi*	2(11.1)	2(11.1)	0	1(5.6)	2(11.1)	1(5.6)	4(22.2)	3(16.7)	3(16.7)	**18**
P. aff. *rosae*	0	1(25)	0	1(25)	1(25)	0	0	0	1(25)	**4**
P. aff. *susannae*	0	0	0	0	0	0	0	0	1(100)	**1**
P. aff. *tijucana*	0	0	0	0	0	0	0	0	1(100)	**1**
P. longiseta	0	0	0	1(50)	0	0	0	0	1(50)	**2**
P. nesiota	0	1(25)	0	1(25)	0	0	1(25)	1(25)	0	**4**
P. aff. *lucretii*	0	1(10)	1(10)	0	0	0	3(30)	1(10)	4(40)	**10**
P. risii	2(18.2)	0	1(9)	2(18.2)	0	0	1(9.1)	4(36.4)	1(9.1)	**11**
P. sp.1	0	0	0	0	0	0	0	0	1(100)	**1**
P. sp.2	0	0	0	0	0	0	1(100)	0	0	**1**
N total[1]	**5(6.3)**	**7(8.9)**	**4(5.1)**	**9(11.4)**	**4(5.1)**	**4(5.1)**	**14(17.7)**	**13(16.5)**	**19(24.1)**	**79**

[1]Total of sampling units that each species was record (these numbers are greater than 55 because some species coexist with other at the same sampling point).

Figure 1. Species frequency (A) and relative frequency (B) along the experiment time range.

Figure 1. Species frequency (A) and relative frequency (B) along the experiment time range.

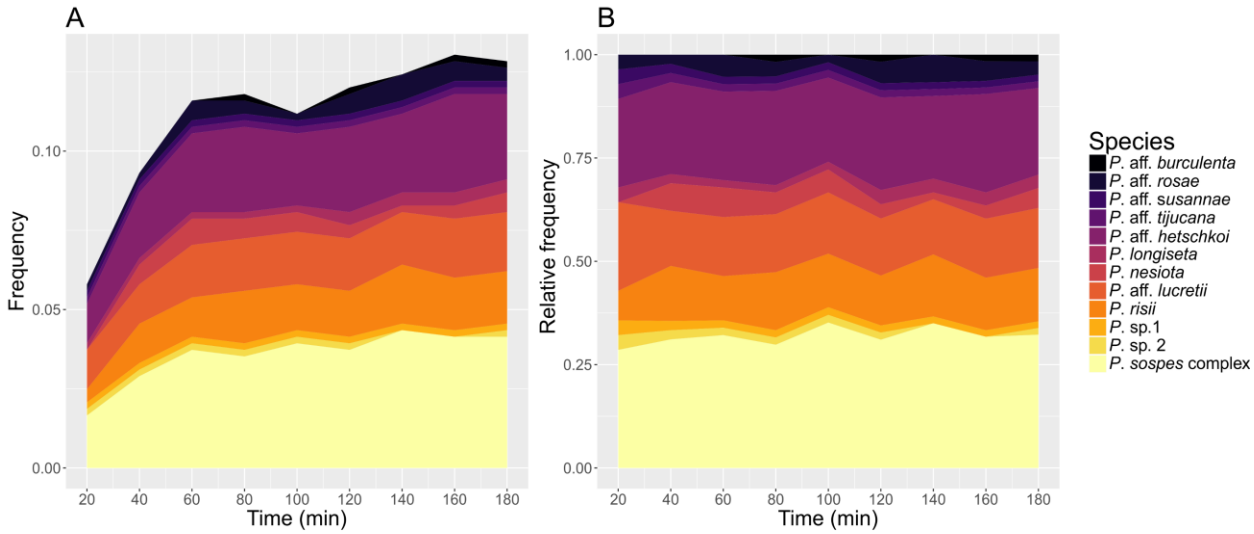

Figure 1. Species frequency (A) and relative frequency (B) along the experiment.