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Effect of dominant parabiotic Ant-Garden ants on the understory and ground-dwelling ant assemblage in the Amazon rainforest

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ABSTRACT. 1. *Camponotus femoratus* (Fabricius, 1804) and *Crematogaster levior* Longino, 2003 are Amazonian ants that jointly live in a parabiotic association in arboreal nests that are known as Ant-Gardens (AGs). Both species are locally abundant and aggressive, which forage on the ground and on the vegetation.

2. We evaluated, with extensive sampling, the effect of *Ca. femoratus* and *Cr. levior* on the ground and the understory dwelling of ant assemblages in the southern Amazon using pit-fall traps, beating-tray sampling, and baiting.

3. We found that *Ca. femoratus* and *Cr. levior* caused a decrease in both the abundance and the species richness of the ground ants, changing the assemblage composition, and causing a nestedness pattern. Yet, AG ants seem to not promote significant changes in the assemblage of ants in the understory, with the exception of canopy openness and region, indicating a spatial resource partitioning.

4. Our results showed that the frequency of these parabiotic AG ant pairs can modify the regional assemblage of the ground-dwelling ants. As ants are ecological engineers and interact with numerous organisms in tropical habitats, the effect of the parabiotic ants can be extended to other organisms that inhabit the gaps along succession.

Key words. Beta-diversity, community, competition, dominance, formicidae, neotropical, parabiosis, partition of diversity.

Introduction

Different ant assemblages can be found in a single site, while using different environments, as in the case of arboreal and epigeic ants (Brühl *et al*., 1998; Frizzo *et al*., 2012; Campbel *et al*., 2015). These independent sub-communities were observed in studies conducted in the Amazon (Ryder Wilkie *et al*., 2010; Vicente *et al*., 2016). Nevertheless, these studies mostly discuss the factors that affect the ant community structure, which are focused only on the ground-dwelling communities (Dáttilo *et al*., 2012; Baccaro *et al*., 2013; Solar *et al*., 2016). Most studies have considered that the agonistic interspecific interactions are one of the main factors that affect the structuring of ant communities, in which the dominant ant's foraging strategy and territory are the main factors that shape the community both spatially and temporally (Hölldobler & Lumsden, 1980; Stuble *et al*., 2012; Cerdá *et al*., 2013). Moreover, studies have also demonstrated that other factors may be more important or that the competition can vary according to the habitat characteristics (Gibb & Hochuli, 2004; Parr, 2008; Gibb & Johansson, 2011; Baccaro *et al*., 2012). Despite the number of studies demonstrating the effects of dominant ants on the epigeic (Parr, 2008; Baccaro *et al*., 2012) or arboreal ant assemblages that form mosaics (Dejean *et al*., 2015a, 2018), few studies have investigated the effects of a given dominant species on both the vertical strata at the same time.

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Furthermore, a parabiotic association was observed in Ant-Gardens (AG) between *Camponotus femoratus* (Fabricius, 1804) and *Crematogaster levior* Longino, 2003 can act as an ideal study model to investigate the effects of the dominant species in both strata. In such AGs, the two ant species share their nest, the foraging trail (known as parabiosis) (Swain, 1980), and plant as well as protect the mutualistic epiphytes that feed the ants and offer support to the nest (Orivel & Leroy, 2011). Both ant species are widely distributed in the Amazon and numerically dominant across all vertical strata of the vegetation and on the ground (Ryder-Wilkie *et al*., 2010; Dáttilo & Izzo, 2012; Souza *et al*., 2016). Particularly, *Ca. femoratus* is fairly well known for its aggressiveness towards herbivores, other ants, and even researchers (Wilson, 1987; Davidson, 1988; Vantaux *et al*., 2007, Vicente & Izzo, 2017). Therefore, the parabiotic association is very pervasive that it was proposed that *Cr. levior* lost its chemical defence by taking advantage of the aggressiveness and defensiveness of *Ca. femoratus* (Longino 2003). Furthermore, in the forest gaps where AGs occur, several nests can be observed from approximately 30 cm above the ground and to the canopy (Vicente *et al*., 2020).

Hence, we investigated whether the frequency of occurrence of parabiotic AG ants, *Ca. femoratus* and *Cr. levior*, can be a factor in structuring the ant community of a tropical rainforest in the Southern Amazon. To assess this, we evaluated whether the frequency and richness of ants decreased with the increase of the local number of AG nests. In addition, by using diversity partitioning methods, we disentangled the effects of the parabiotic AGs into two diversity components: (i) the modification of the community by decreasing the number of specific species (nestedness effect) or (ii) the replacement of specific ant species by other species in the community (turnover effect).

Materials and methods

Study area

This study was performed across five Brazilian Research Programs in Biodiversity sites (PPBio – Fig. 1) that are located in the Amazon in three municipalities in the north of the Mato Grosso state. The ant assemblage was sampled in four of these research sites, called modules, which had plot sets of 250 m in length that were installed at a minimum distance of 1 km apart (Costa & Magnusson, 2010). Three modules were located in the Claudia municipality (MCLA) that were installed in close proximity (MI-MIII: 7 km in a straight line, MI-MII: 19 km, and MII-MIII: 26 km), in a large forest path that is intersected by highways and surrounded by plantations, which consisted of Module I (11°34'S, 55°17'W), Module II (11°25'S, 55°18'W), and Module III (11°39'S, 55°16'W). The other module was installed in the Parque Estadual do Cristalino (PEC), a continuous pristine forest in the Novo Mundo municipality (9°28'S, 55°50'W), which is approximately 220 km further from the other three. Additionally, a dominance experiment was performed on the São Nicolau Farm (SNF) that is located in the Cotriguaçu municipality in the state of Mato Grosso (9°49'S, 58°16'W).

Experimental setup

The ant inventory was conducted across 24 plots at MCLA (MI: 10, MII: six, and MIII: eight plots, respectively) during the rainy season from November 2009 to February 2010 as well as 10 plots at PEC between November 2012 and the beginning of May 2013, totalling 34 plots (Vicente *et al*., 2016). In each plot, the ants were sampled at every 25 m on the ground and in the understory, resulting in 20 samples per plot with 10 on the ground and low vegetation, respectively, totalling 680 samples of 340 on the ground and in the understory, respectively. The sampling of the ground-dwelling ant assemblage was performed by using a single pitfall trap that was installed in each sample point and remained active for 48 hours. The pitfalls consisted of plastic containers containing water and detergent of 500 ml with a 14 cm radius that were installed at ground level. We sampled the ants foraging in the understory once between 9 am to 3 pm at four points around each pitfall using the beating-tray method. At each point, the vegetation within 1 m^2, which had over 1–3 m in height, was shaken to provide 4 m^2 of vegetation per sample. Below the shaken vegetation, we installed an entomological umbrella that was approximately 1 m above the ground. All invertebrates that fell into the entomological umbrella were collected (Vicente *et al*., 2016).

In addition, ants and light incidence are known to be related (Dáttilo & Izzo, 2012). Thus, we measured the canopy openness across all sampling points with a concave spherical densiometer as a proxy to the relative availability of light input (Baudry *et al*., 2014). In the centre of each forest gap, we recorded four measurements across the cardinal directions to calculate an average availability of light (Baudry *et al*., 2014). Furthermore, to reduce the possibility of a correlative effect between the frequency of AGs ants and the differences in frequency as well as the number of species and the composition of ant assemblage, we performed a bioassay in the sites harbouring AGs to observe the percentage of bait dominance by the parabiotic AG ants. In this experiment, we placed 80 baits of 40 sardines (protein) and 40 alimentary glucose pieces (carbohydrate) in the understory between 1 and 1.7 m for accurate viewing as well as on the ground with 40 baits in each stratum. Considering that Amazonian ants can find resources almost 6 m away (Baccaro & Ferraz, 2013) and the proximity of other nests in the area, all the baits were placed approximately 2 m further from the tree harbouring an AG. Next, we placed the equivalent of approximately 5 g (a teaspoon) of the bait on a paper card of 15 × 15 cm. Soon after placing the bait, two trained researchers observed, within 10 min, the time of discovery and the identity of the species on the bait. After 45 min, we returned to the baits and recorded for another 5 min the species that dominated the bait, while taking into account the worker number and the behavioural dominance through the conflicts and exclusion of other ants. This resulted in a total of 1 h of observation per bait. The workers in each bait were counted individually from 1 to 10. From then on, estimates were made in the groups of approximately 20, 50, or more than 50 individuals. Both in the case of the discovery of the bait and in the dominance, at least one worker was gently collected for further identification with minimal bait disturbance. We did not observe any ants escaping while we performed this procedure.

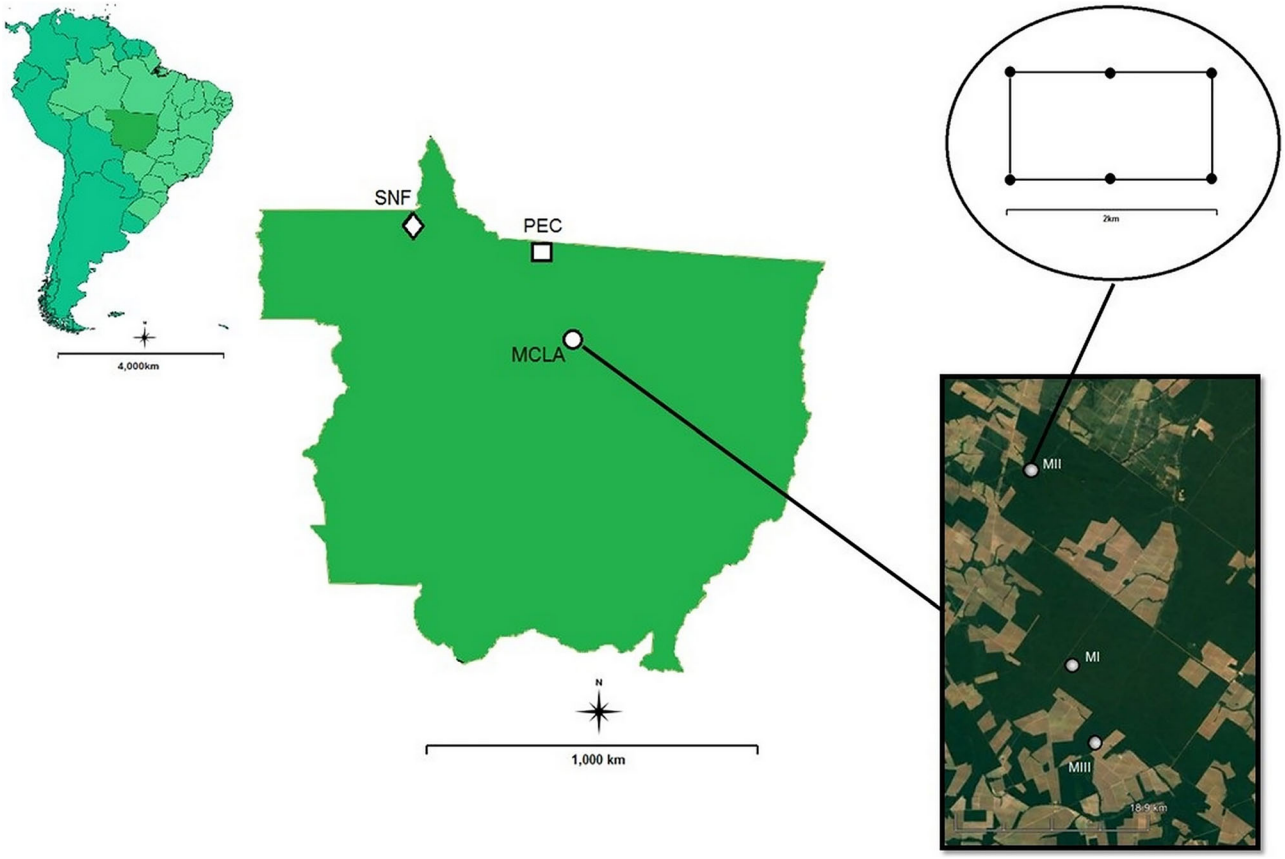

Figure 1. Location map of South America (a) highlighting the three locations in Mato Grosso State (b), Brazil, where the ant assemblages were sampled. Ants were sampled with beating-tray method in the understory and with pitfall trap on the ground in the Parque Estadual do Cristalino (PEC – white square) and in the modules of Claudia (MCLA – white circle). The MCLA (c) follows the configuration shown on the satellite image (c) and MCLA (MI, MII and MIII) and PEC follow the RAPELD design (d). São Nicolau farm (SNF – white rhombus) was where the bioassay was made (b). Software: QGSIS v.2.14.8 [Color figure can be viewed at wileyonlinelibrary.com]

Ant identification

The sampled ants were identified using a dichotomous key for the subfamilies and the genera that were reported in the study by Baccaro *et al*. (2015). The specimens were separated into morphospecies and identified to the specific level using known taxonomic keys. All the identified species were compared with the specimens that were deposited at the Laboratório de Ecologia de Comunidades from the Centro de Biodiversidade da Universidade Federal de Mato Grosso (UFMT) and with the ant collection from the Laboratório de Sistemática, Evolução e Biologia de Hymenoptera from the Museu de Zoologia da Universidade de São Paulo (MZSP). In addition, specialists were consulted to confirm the identification of species (see Acknowledgments section). Vouchers were also deposited in the aforementioned biological collections.

Data analysis

To analyse the effect of AG ants on the frequency as well as the number of species and composition of the ant community, each plot was considered as a sample unit. The ant frequency of each plot was obtained by the sum of the frequencies of each species per sample. We opted for this sample-based measure because true ant abundance cannot be independently measured in biodiversity estimates since ants are social insects (Gotelli *et al*., 2011). Hence, the sampled abundance of the workers using the sample method may strongly be related to the proximity to the nest (Gotelli *et al*., 2011), where the number of workers in a colony can greatly vary between species (Baccaro *et al*., 2015). Due to the aforementioned reasons, a sample-based measurement in terms of frequency is commonly used in ant studies (Ryder Wilkie *et al*., 2010; Dáttilo & Izzo, 2012; Baccaro *et al*., 2013). Based on the same principle, the variable "*frequency of parabiotic AG ants*" was also created. Since both, *Ca. femoratus* and *Cr. levior*, almost always occur in the same nest and are present in the nest clusters of the parabiotic colony, the collection of any of them in a single sample implies the existence of an AG nearby. Hence, the frequency of AGs ants per plot was independent of the stratum of which they were collected from and can represent the extension of the dominant effect in the assemblage.

To evaluate the frequency of the parabiotic AGs ants' effect in the frequency and richness of the ground and understory ant species along the Amazon forest, generalised linear mixed-effect models (GLMM) with a Poisson distribution (Bolker, 2008) were used. We checked for any overdispersion by analysing the residual deviance and the degrees of freedom across all the GLMM that were employed to fit with the data (goodness-of-fit $P > 0.05$). As all models were overdispersed, we conducted the GLMMs using a negative binomial distribution. In these analyses, we used the frequency of ants and the number of ant species in the strata assemblage as dependent variables, while the frequency of AG ants and the canopy openness acted as fixed factors and the geographical region nested to module was considered a random factor.

The composition dissimilarity between samples or sites is a classical measuring method, called the beta diversity that was coined by Whittaker (1960). Many discussions aiming at proposing a measure of beta diversity independent of alpha diversity were conducted, regardless of the richness of the species (Baselga & Leprieur, 2015). From these discussions, it was shown that beta diversity is formed by two antithetical components with two different biological significances, including the turnover (substitution species across sites) and the nestedness-resultant (poorest sites as sub-samples of the richest sites) (Baselga & Leprieur, 2015). Thus, the total beta diversity, turnover, and the nestedness-resultant components of the ant assemblage were calculated between the plot pairs based on a binary matrix with the presence and absence dates with Sorensen dissimilarity as well as their turnover component, the Simpson dissimilarity index (Baselga & Leprieur, 2015). Next, the dissimilarity matrices were used in the multiple regression on distance mMatrices (MRM of 10 000 permutations), with the frequency of the parabiotic AG ants, geographical region, and the canopy openness as factors to evaluate the effect of *Ca. femoratus* and *Cr. levior* on ant communities. MRM is a flexible method as it accepts several types of data as categorical, continuous, counts, and presence–absence using a permutation test of significance for the regression coefficients and R^2 values (Goslee & Urban, 2019; Lichstein, 2007). The partial regression coefficients (hereafter b) of an MRM model provided a measure of the rate of change in the partition of the ant community similarity in the variables of interest. For this reason, it was used in ecological studies with different approaches (Walter *et al*., 2017; Busse *et al*., 2018; Tourinho *et al*., 2020).

All these investigations were performed both for the assemblage of ground-dwelling ants and the assemblage of understory ants. We previously found that the frequency, richness, and composition of ant assemblages were different across vertical strata (Vicente *et al*., 2016). Therefore, we decided to conduct the analyses per strata. Since the foraging activity of the parabiotic AG ants, and the ant assemblage, could be structured to the same causal factors (Dáttilo & Izzo, 2012; Vicente & Izzo, 2017), we added the canopy openness in all the analyses as an independent variable.

An analysis of indicator species (IndVal) was performed with the sampled ants in the understory, using the beating-tray methodology, and on the ground, using the pitfall traps, to determine the species of ants being affected by the presence of the parabiotic AG ants that occurred at more than one point or by the absence of an indicator, which did not occur at any point, as well as the strata its species represents. The IndVal is considered a robust method that compares the distribution of a single species at a time between the habitat categories or types of community, while assuming a species to be a group indicator with high abundance and occurs frequently in the group (Legendre & Legendre, 2012). The significance of the IndVal of each species was calculated by a randomisation procedure with 999 permutations. As IndVal only permits the use of categorical data as an independent variable, the frequency of the identified species by IndVal as an indicator of the presence or absence of the AGs ants was used in a linear regression relative to the average canopy openness per plot.

In the bioassay, we used a combination of parameters to consider the bait that was dominated by one species (i) if it was the only species on the bait, (ii) if the species had a number of workers that were 25% more than the non-dominant species, or (iii) if the dominant species behaved aggressively by biting or spraying formic acid and causing the subordinate specie to abandon the bait (Parr, 2008; Baccaro *et al*., 2012). With recording the number of each species arriving first at the bait and the number of baits dominated by each species, we calculated the percentage and summarised the results.

All the analyses and graphs were generated by the R statistical software v.4.0.0 (R Core Team, 2019) using the packages: betapart (partition of beta diversity – Baselga & Orme, 2012), ecodist (MRM – Goslee & Urban 2019), effects (GLMM graphics – Fox & Hong, 2009), ggplot2 (MRM graphics – Wickham, 2016), gglat (MRM graphics – Rudis *et al*., 2017), ggplot2 (MRM graphics – Tang *et al*., 2016), glmmTMB (GLMM – Brooks *et al*. 2017), indicspecies (IndVal – De

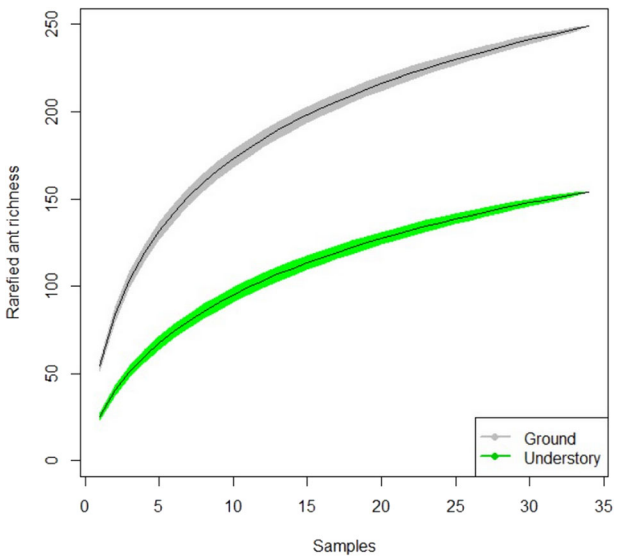

Figure 2. Rarefied species curve comparison for the ants sampled with beating-tray and pitfall-trap by stratum, showing the number of species expected. The coloured area around the curve is the confidence interval of 95%. [Color figure can be viewed at wileyonlinelibrary.com]

Cáceres & Jansen, 2015), lme4 (GLMM – Bates *et al*., 2016), and vegan (Oksanen *et al*., 2016).

Results

A total of 4359 occurrences and 325 species of ants were registered across all sample plots (Supporting information Table S1, Fig. 2). The ground samples had 3071 occurrences of 251 ant species. The most frequent species on the ground were *Pheidole transversostriata* (202 samples, 59.41% of ground samples), *Ectatomma lugens* (154 samples, 45.29%), *Pachycondyla crassinoda* (125 samples, 36.76%), *Trachymyrmex* TJI01 (92 samples, 27.06%), and *Crematogaster tenuicula* (89 samples, 26.18%). In the understory, the frequency was of 1,287 records of 159 ant species, in which the most frequent species in the understory were *Ochetomyrmex semipolitus* (92 samples, 27.06% of understory samples), *Crematogaster tenuicula* (85 samples, 25%), *Crematogaster brasiliensis* (67 samples, 19.71%), *Ectatomma tuberculatum* (57 samples, 16.76%), and *Solenopsis* TJI01 (43 samples, 12.65%). The parabiotic AG ants, *Ca. femoratus* and *Cr. levior*, were found in 20 of the 34 plots in both the litter/soil and the understory. On the ground, *Ca. femoratus* were recorded in 24 pitfall traps that were distributed in 15 plots (PEC = 4; MCLA = 11), while *Cr. levior* was found in 11 pitfall traps of 7 plots (PEC = 3; MCLA = 4). In the understory, *Ca. femoratus* were less frequent and only recorded in 14 beating-tray samples that were distributed in eight plots

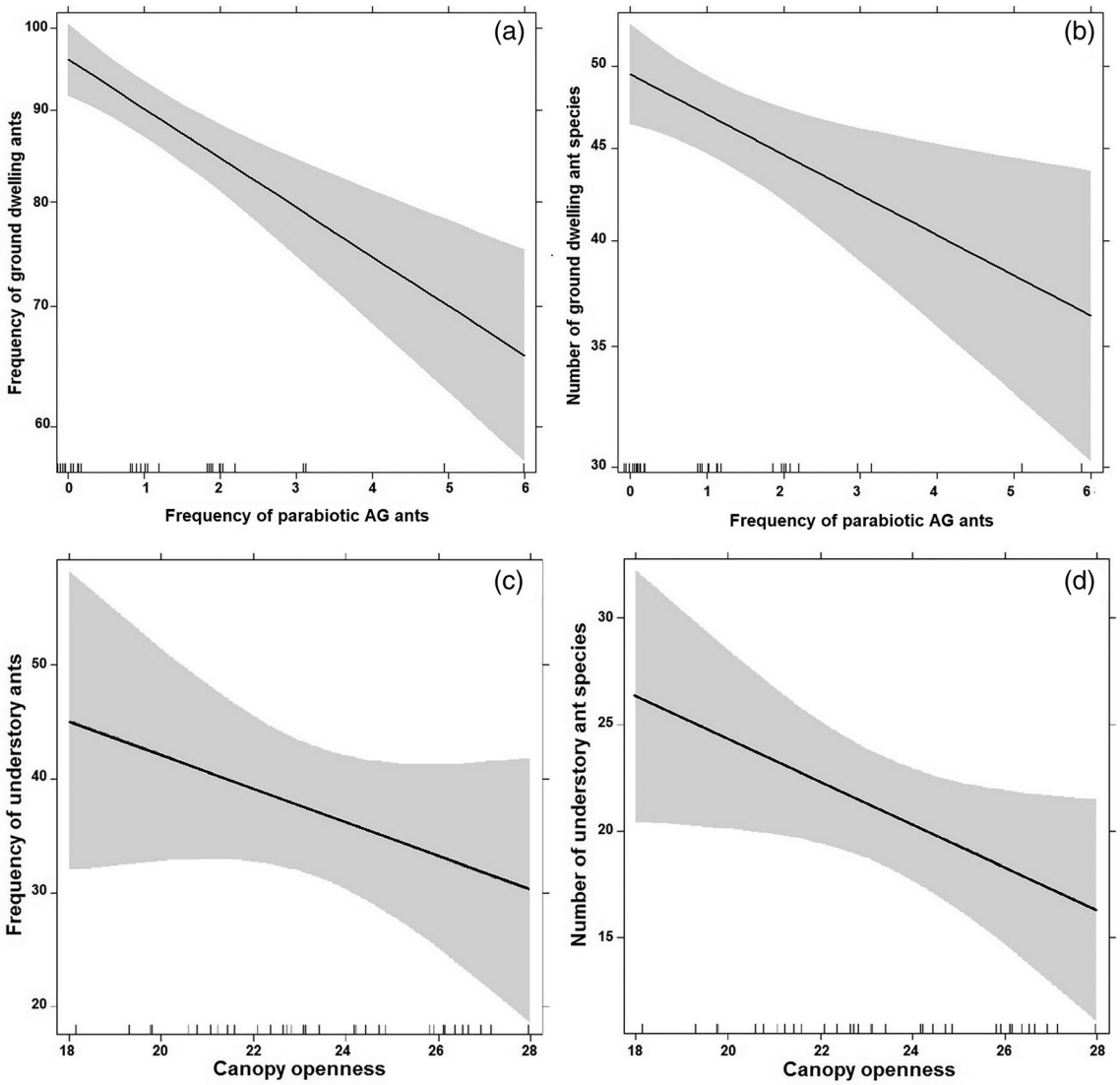

Figure 3. The GLMM models of the relation of the local frequency (a) and species number (b) of ground ants sampled with pitfall-traps and the number of frequencies of Ant-Garden ants per site. Below, the models of the local frequency (c) and species number (d) of understory ants related to canopy openness. The grey shade represents 95% confidence interval.

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(PEC = 3; MCLA = 5), while *Cr. levior* had a similar pattern in terms of the ground samples and was sampled in 12 beating-tray samples of seven plots (PEC = 3; MCLA = 4).

In addition, the frequency of parabiotic AG ants decreased the total frequency (GLMM: $Z_{2,34} = -2.638$, $P = 0.008$; Fig. 3a) and the number of ground-dwelling ant species per plot ($Z_{2,34} = -2.769$, $P = 0.006$; Fig. 3b). The mean frequency was 86 registers per plot of the ground-dwelling ants in plots where the AGs was found (±20.61 SD), whereas in the plots where the AGs were absent, 94.07 (±16.54 SD) registers were observed. Moreover, the mean number of the ground-dwelling ant species in the plots where the AGs were found and not found was 45.7 (±8.56 SD) and 48 (±7.90 SD), respectively. These parameters of the understory ants assemblage were not affected by the parabiotic AG ants (Table 1), while the canopy openness decreased the understory ant frequency (GLMM: $Z_{2,34} = -1.184$, $P = 0.236$) and richness ($Z_{2,34} = -2.946$, $P = 0.003$ Fig. 3(d)). The mean frequency of the understory ants was 38.45 registers per plot (±14.28 SD) where the parabiotic AG ants were present and 35.14 (±18.26 SD) where AGs were absent. Finally, the mean number of the species was 22.35 (±7.27 SD) where the parabiotic AG ants were present and 18.93 (±7.36 SD) where the AGs were not present. Furthermore, the analysis of the composition of the ground-dwelling ant assemblage demonstrated that the frequency of parabiotic AG ants in the site affected the total beta diversity (MRM: b = 0.007, $P = 0.04$; Fig. 4a) and the nestedness component of the ground-dwelling ant assemblage (b = 0.009, $P = 0.021$; Fig. 4b). Most of the evaluated parameters of the ground and understory ant composition were structured by the geographic distance and by the canopy openness (Table 1).

A total of 29 species indicated the presence or absence of the AG ants in both strata of the understory and the ground (Table 2), in which the frequency of these species was not affected by canopy openness. Moreover, the influence of the AG ants in the composition of the ground-dwelling ants can be observed by the changes in the frequency of the 26 ant species when the AG ants were absent (19 species) or present (7 species, Table 2) in the plots. Additionally, the indicator species of the AG absence, which were more frequent in soil samples, were *Pheidole transversostriata*, *Pachycondyla crassinoda*, *Solenopsis* TJI06, *Pheidole nitella*, and *Nylanderia* TJI02. In addition, the more frequent indicators of the ground species of the AG presence were *Megalomyrmex* aff. *wallacei*, *Pheidole* INPA14, *Pheidole bufo*, and *Gnamptogenys moelleri*. Only three understory ant species were found related to the occurrence of AGs, in which *Ochetomyrmex semipolitus* and *Neoponera unidentata* indicated the presence of AGs ants, whereas only *Crematogaster wardi* indicated the absence of AGs (Table 2).

In the bait experiment, the greater majority of the baits were discovered by the parabiotic ants ($N = 52$; 65%; Table 3) *Crematogaster levior* ($N = 29$; 36.25%) and *Camponotus femoratus* ($N = 23$; 28.75%). *Cr. levior* arrived first at 17 baits on the ground and 12 in the understory, while *Ca. femoratus* arrived at 9 baits on the ground and 14 in the understory. In terms of dominance, the parabiotic ants dominated 66 baits (82.5%), in which *Ca. femoratus* dominated 38 baits (47.5%) with 18 on the ground and 20 in the understory (Table 4), while *Cr. levior* dominated 28 baits (35%) with 15 on the ground and 13 in the understory. In many of these baits that were dominated by parabiotic ant species, we observed that the dominant species had more than 10 times the number of non-dominant worker species. We also observed that this dominance, regardless of the stratum, was linked to the species' food preference, with *Ca. femoratus* dominating approximately two and a half times the protein baits ($N = 27$) and *Cr. levior* dominating approximately two and a half times the carbohydrate baits ($N = 20$). In the baits dominated by one parabiotic ant species, no conflicts were observed between *Ca. femoratus* and *Cr. levior*. However, *Ca. femoratus* exhibited very aggressive behaviour when ants of other species arrived at the dominated bait, in which the behaviour consisted of curving the gaster between their legs, while seeming to squirt formic acid and biting, which sometimes immobilised the intruder ants. *Cr. levior* has only displayed the behaviour of repeatedly clapping its jaws, which is likely simulating a bite to chase away the other ants.

Table 1. Interrelations among the assemblage parameters with frequency of parabiotic AG ants, canopy openness and region.

Assemblage parameter	Analyse	Factor	Ground	Understory
Frequency	GLMM	AG	**$Z_{2,34} = -2.638$, $P = 0.008$**	$Z_{2,34} = -1.184$, $P = 0.236$
		Canopy	$Z_{2,34} = 1.230$, $P = 0.219$	**$Z_{2,34} = -2.026$, $P = 0.042$**
Species number	GLMM	AG	**$Z_{2,34} = -2.769$, $P = 0.006$**	$Z_{2,34} = -1.209$, $P = 0.227$
		Canopy	$Z_{2,34} = 1.065$, $P = 0.287$	**$Z_{2,34} = -2.946$, $P = 0.003$**
Total beta	MMR	AG	**$b = 0.007$, $P = 0.04$**	$b = -0.00005$, $P = 0.990$
		Canopy	$b = 0.028$, $P = 0.109$	$b = -0.002$, $P = 0.364$
		Region	**$b = 0.179$, $P = 0.00001$**	**$b = 0.013$, $P = 0.00001$**
Nestedness	MMR	AG	**$b = 0.009$, $P = 0.021$**	$b = -0.002$, $P = 0.358$
		Canopy	$b = -0.0004$, $P = 0.774$	$b = 0.002$, $P = 0.136$
		Region	**$b = -0.016$, $P = 0.014$**	$b = 0.006$, $P = 0.448$
Turnover	MMR	AG	$b = -0.002$, $P = 0.497$	$b = 0.002$, $P = 0.694$
		Canopy	$b = 0.003$, $P = 0.170$	$b = -0.005$, $P = 0.164$
		Region	**$b = 0.195$, $P = 0.0001$**	**$b = 0.122$, $P = 0.00001$**

Statistical significance is indicated in bold.

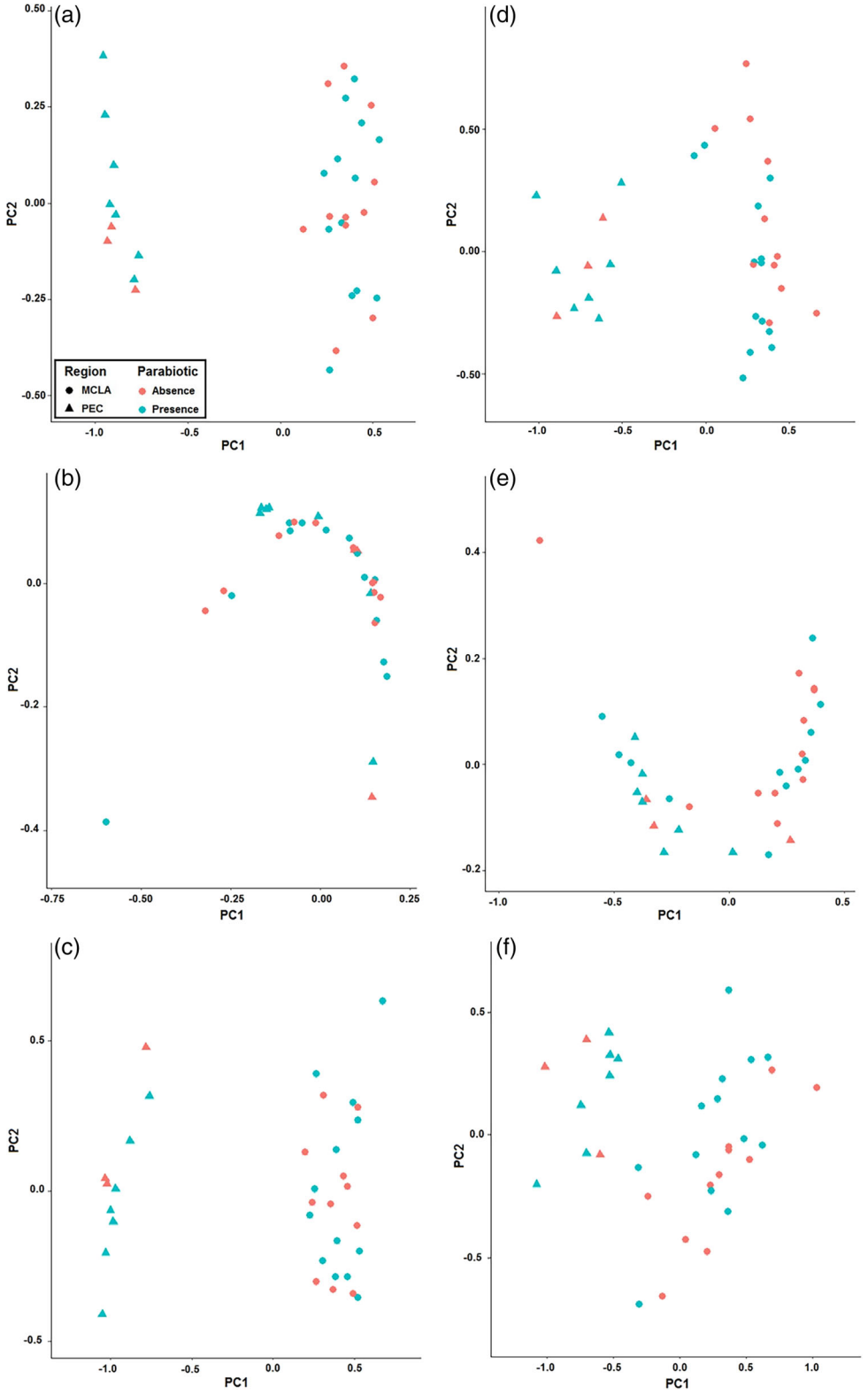

Figure 4. The ground (a–c) and understory (d–f) ant assemblages are represented by the total composition (a, d) and the components Nestedness-resultant (b, e) and turnover (c, f). The circles represent plots of Module of Claudia (MCLA) and of Parque Estadual do Cristalino, in which the blue points representing plots where parabiotic AG ants are present and the red points plots where parabiotic AG ants are absent. [Color figure can be viewed at wileyonlinelibrary.com]

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Table 2. List of ground-dwellings (pitfall trap samples) and vegetation (beating-tray methods) ant species that indicate the presence or absence of AG ants.

Taxa	IndVal Stat	Vertical Strata	Parabiotic AG ants	Frequency in the strata (FS)	Percent of the strata samples (FS*100/340)
Trachymyrmex aff. *bughioni*	0.679	Ground	Absence	58	17.06
Pachycondyla crassinoda	0.659	Ground	Absence	125	36.76
Pheidole nitella	0.648	Ground	Absence	70	20.59
Pheidole TJI41	0.622	Ground	Absence	40	11.76
Pheidole transversostriata	0.603	Ground	Absence	202	59.41
Pheidole TJI49	0.600	Ground	Absence	12	3.53
Solenopsis TJI06	0.577	Ground	Absence	70	20.59
Pheidole TJI21	0.566	Ground	Absence	56	16.47
Odontomachus aff. *meinerti*	0.562	Ground	Absence	12	3.53
Apterostigma urichii	0.561	Ground	Absence	43	12.65
Atta cephalotes	0.557	Ground	Absence	35	10.29
Pheidole TJI22	0.551	Ground	Absence	14	4.12
Neoponera apicalis	0.550	Ground	Absence	53	15.59
Nylanderia TJI02	0.537	Ground	Absence	70	20.59
Pheidole INPA019	0.519	Ground	Absence	11	3.23
Pheidole TJI35	0.505	Ground	Absence	31	9.12
Trachymyrmex INPA03	0.474	Ground	Absence	13	3.82
Acromyrmex hystrix	0.463	Ground	Absence	4	1.18
Myrmicocrypta sp02	0.425	Ground	Absence	6	1.76
Gnamptogenys moelleri	0.635	Ground	Presence	23	6.76
Pheidole INPA014	0.555	Ground	Presence	34	10
Megalomyrmex aff. *wallacei*	0.552	Ground	Presence	48	14.12
Pheidole bufo	0.542	Ground	Presence	25	7.35
Camponotus ager	0.540	Ground	Presence	12	3.53
Pheidole TJI17	0.536	Ground	Presence	19	5.59
Mycocepurus smithii	0.500	Ground	Presence	4	1.18
Ochetomyrmex semipolitus	0.4286	Arboreal	Absence	92	27.06
Neoponera unidentata	0.656	Arboreal	Absence	32	9.41
Crematogaster wardi	0.561	Arboreal	Presence	16	2.77

Discussion

Although studies have been conducted on AGs (Davidson, 1988; Vantaux *et al*., 2007; Vicente *et al*., 2014), this is the first study that investigated the influence of the AG ants, *Camponotus femoratus* and *Crematogaster levior*, on the local and regional ant assemblage of the ground and vegetation habitats. In addition to the well-known aggressiveness in defending the nest and their host tree (Wilson, 1987; Vantaux *et al*., 2007; Vicente *et al*., 2014), we demonstrated that the functional role of AG ants can extend beyond the AGs and the vicinities in terms of generally arriving first at the resource and dominating it both in relation to the vegetation and on the ground by modifying the 'momentary diversity' (Andersen, 1992) at the local scale. Yet, even though the AGs are arboreal structures, *Ca. femoratus* and *Cr. levior* effectively changed the local ground but not the low vegetation ant assemblage, which would be considered as epigeic dominant species (Vasconcelos *et al*., 2003).

This aggressive behaviour of the parabiotic AG ants, which occurred in larger numbers of workers from the ground to the canopy (Vasconcelos *et al*., 2003; Ryder Wilkie *et al*., 2010), could prevent other species from having access to resources and promote a decrease in the number of nests (frequency) and even the exclusion of some competitor species (richness), as seen in our results. A similar pattern was observed in a tropical rainforest in French Guiana, where the richness and nest abundance of the ants decreased with the presence of the dominant ant, *Solenopsis saevissima* (Dejean *et al*., 2015b). Moreover, across three habitats in the South African savanna, the richness of the ant community decreased with the increase in abundance of other dominant species (Parr, 2008).

In addition to the expected effect of the geographic distance on the composition of the ant assemblage in the studied strata, the frequency of the parabiotic AG ants in a given site also affected the composition of the ground-dwelling ant assemblage and caused a nested pattern. Moreover, the permanence of some ant species, the aggressiveness of AG ants towards other species,

Table 3. Number of species workers that arrive first at the baits by stratum and order of frequency.

	Ground		Understory		Both	
Species	*N*	%	*N*	%	*N*	%
Crematogaster levior	17	21.25	12	15	29	36.25
Camponotus femoratus	9	11.25	14	17.5	23	28.75
Ectatomma edentatum	2	2.5	0	0	2	2.5
Wasmannia auropunctata	2	2.5	0	0	2	2.5
Camponotus aff *balzani*	0	0	1	1.25	1	1.25
Crematogaster aff *erecta*	0	0	1	1.25	1	1.25
Crematogaster nigropilosa	1	1.25	0	0	1	1.25
Neoponera apicalis	1	1.25	0	0	1	1.25
Ochetomyrmex neopolitus	1	1.25	0	0	1	1.25
Paraponera clavata	0	0	1	1.25	1	1.25
Pheidole aff *bufo*	1	1.25	0	0	1	1.25
Pheidole aff *radoszkowski*	1	1.25	0	0	1	1.25
Pheidole gr *flavens*	1	1.25	0	0	1	1.25
Pheidole sp1	1	1.25	0	0	1	1.25
Pheidole sp2	1	1.25	0	0	1	1.25
Solenopsis sp1	1	1.25	0	0	1	1.25
No ants	1	1.25	11	13.75	12	15
Total	40	50	40	50	80	100

and the likely species that compete for resources, were demonstrated in our bioassay. Consequently, the AGs promoted a modification in the ant assemblage by decreasing the local number of species and formed poorer sites that were subsets of the richest sites (the nestedness-resultant component). Hence, some species may be favoured by the presence of AGs or be eliminated by the parabiotic AG ants. In fact, our data showed that 19 ground-dwelling ant species indicated, and thus were favoured by, the absence of AG ants, but just seven were identified as indicators of the presence of AG ants, contributing to the nestedness pattern.

Despite the observed effect in the understory and the epigeic 'momentary diversity' of visiting the baits as well as on the ground-dwelling ant assemblage, the parabiotic ants did not change the abundance, richness, nor the composition of the ant assemblage that was active in the understory. Hence, a very low number of three species could be designated as indicators of the presence of AG. Moreover, we have frequently observed *Ca. femoratus* driving away other species of ants in the field, which was mainly in the vicinities of the extrafloral nectaries during the day (REV pers. obs.). Extrafloral nectaries are predictable resources (Rico-Gray & Oliveira, 2007) and parabiotic ants can potentially exclusively dominate and defend the plants with nectaries, driving away other ant species from these plants. Nevertheless, although nectary-bearing plants are abundant in Amazonia, the major part of the understory plant species do not have nectaries (Dáttilo *et al*., 2013). Thus, plants can be seen by the parabiotic ants as foraging sites for prey or even as arboreal bridges that link resource-rich locations to the nest (Ribas *et al*., 2003; Sarty *et al*., 2006; Powell *et al*., 2011; Yanoviak & Schnitzer, 2013).

Here, we observed the strong effect of AG ants on the access of ants to resources in the bait experiment, reinforcing the segregated pattern observed in our beating-tray samplings on the ant community. Hence, we suggest that if a dominant ant species has any effect on the diversity of their competitors, this effect should be on and in the vicinities of the resource path (nectaries, or by analogy, the baits, as reported in some studies). The competition for food can be segregating where that food is, thereby decreasing the abundance of some subdominant species, neutralising their effect on subordinated species, and masking the effect of the dominant ant on the ant assemblage (Arnan *et al*., 2011). Furthermore, the dominant species can decrease the abundance of the subordinated species, while not excluding the species from the area (Gibb & Hochuli, 2004). In certain situations, tropical ants can expand the realised food niche (Houadria & Menzel, 2020), where the nesting niche of the arboreal ant species can be aggregative (Ellwood *et al*., 2009, 2016).

The parabiotic ants, *Ca. femoratus* and *Cr. Levior*, usually inhabit areas with high light intensity, such as forest gaps (Davidson, 1988; Vicente & Izzo 2017). Thus, the natural gaps that are formed by fallen trees are a very common and predictable habitat in natural environments (Muscolo *et al*., 2014). This habitat, however, is ephemeral and shows a temporal change in the composition of plants and animals along the succession, where some species were found to inhabit open environments more frequently (at the beginning of succession), while other species replaced them during more advanced stages of the gap regeneration. Furthermore, the time of the replacement and the final composition of the area was determined by a myriad of factors (Muscolo *et al*., 2014) and by random (Hubbel, 2001), but these processes were in part responsible for the maintenance of the diversity on the regional and biome scale (Neves *et al*., 2010; Dáttilo & Izzo, 2012; Muscolo *et al*., 2014; Altman *et al*., 2016). Therefore, as demonstrated here, the presence of the parabiotic ants in a near forest gap, and not in the local microclimate changes, can modify the regional assemblage of the ground-dwelling ants by eliminating several ant species. The

Table 4. Species that dominated the baits by stratum in order of total baits dominated by the species.

	Ground		Understory		Both	
Species	*N*	%	*N*	%	*N*	%
Camponotus femoratus	18	22.5	20	25	38	47.5
Crematogaster levior	15	18.75	13	16.25	28	35
Azteca sp1	1	1.25	0	0	1	1.25
Camponotus aff *balzani*	1	1.25	0	0	1	1.25
Camponotus aff *textor*	0	0	1	1.25	1	1.25
Linepthema sp1	1	1.25	0	0	1	1.25
Pheidole sp1	1	1.25	0	0	1	1.25
Solenopsis sp1	0	1.25	1	1.25	1	1.25
Trachymyrmex sp1	1	1.25	0	0	1	1.25
No ants	2	2.5	5	6.25	7	8.75
Total	40	50	40	50	80	100

canopy openness was found to only affect the understory ant assemblage. As ants are ecological engineers and can interact with several organisms in tropical habitats (Del Toro *et al*., 2012), the effect of the parabiotic ants can be extended to other organisms that inhabit the gaps along the succession. In addition, the parabiotic ants can have a direct effect on the succession in these gaps by modifying, for example, the protection quality of the nectary-bearing plants as well as the herbivory or the other processes that occur in the gaps. Hence, more than just modifying the ant composition, the effect of these dominant species can influence the succession stages of a disturbed forest path.

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Conflict of Interest

The authors declare no conflict of interest.

Data availability statement

The data that support the findings of this study data policy are available in Programa de Pesquisa em Biodiversidade (PPBio), at https://ppbiodata.inpa.gov.br/metacatui or the corresponding author can be consulted.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 The occurrence by plot of ant species in ground-dwellings and arboreal ant assemblages of Parque Estadual do Cristalino (PEC) and in the three Modules of Claudia Municipality (MCLA).

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