OXFORD

Community and Ecosystem Ecology

Co-occurrence Patterns in a Subtropical Ant Community Revealed by Complementary Sampling Methodologies

Priscila E. Hanisch,[1,4,] Andrew V. Suarez,[2] Pablo L. Tubaro,[1] and Carolina I. Paris[3]

[1]Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' MACN-CONICET, Buenos Aires, Argentina, [2]Department of Animal Biology and Department of Entomology, University of Illinois, Urbana, IL, [3]Departamento Ecología, Genética y Evolución, Universidad de Buenos Aires, Buenos Aires, Argentina, and [4]Corresponding author, e-mail: hanisch.priscila@gmail.com

Abstract

Ants are abundant and ecologically dominant insects in most terrestrial communities. In subtropical ecosystems, there is a high turnover of species from the canopy to the top layers of the soil. Additionally, ant communities are often influenced by inter-specific competition. Collectively, these two processes (abiotic filtering and competition) make ants ideal for studies of community structure. We examined composition, co-occurrence, and species interactions in a sub-tropical forest ant community to examine how ground-foraging ant species partition microhabitats. We used four methods: pitfall traps, litter samples, surface baits, and subterranean baits. Surface baiting was employed at three different time periods to examine how foraging activity and species interactions at baits varied with time of day and temperature. Each method sampled a particular assemblage of the 97 total ant species. Pitfall traps shared ~50% of species with surface baits and litter samples. Subterranean baits had the fewest total species but included some uncommonly sampled ants. The majority of interactions between species at baits were neutral, but a few agonistic interactions were also observed when bait occupancy was highest. Species co-occurrence patterns suggest that this ant community may not be heavily influenced by interspecific competition. Our results reinforce the advantages of applying complementary sampling techniques to examine ant community structure, and suggest that competition and dominance is best considered in the context of resource type, foraging strategy and time of sampling. Finally, we discuss the lack of two conspicuous Neotropical groups in our samples, leaf-cutting ant and army ants.

Key words: ant ecology, Atlantic Forest, ecological dominance, competition, Iguazú National Park

Tropical forests host some of the highest levels of terrestrial biodiversity. Many ecological and evolutionary mechanisms have been proposed to explain the origin and maintenance of their diversity (Willig et al. 2003, Ricklefs 2004, Mittelbach et al. 2007, Harrison and Cornell 2008, Kozak and Wiens 2012, Graham et al. 2014). One ecological factor commonly thought to promote diversity is habitat heterogeneity (Stein et al. 2014). The vertical structure of tropical forests, provides extensive variation in temperature, moisture and nest sites that may promote the coexistence of many species. Ecological research often highlights patterns of diversity between the ground and canopy (e.g., Yanoviak and Kaspari 2000, Weiser et al. 2010). However, there is also substantial variation in microhabitats near the surface where species may specialize by foraging or nesting on the ground, in the litter, or in top layers of soil (e.g., Wilkie et al. 2010, Jacquemin et al. 2016).

Ants are an abundant and ecologically diverse group of insects in most terrestrial communities, particularly in tropical ecosystems where they may exceed the combined mass of all vertebrates (Hölldobler and Wilson 1990). Ant diversity and distribution varies spatially and temporally due to a variety of abiotic and biotic factors (Yanoviak and Kaspari 2000, Jacquemin et al. 2016). While most studies focus on variation in these characters among populations or across broad geographic regions, factors such as temperature, humidity, and light availability can also vary substantially at very small (e.g., cm) spatial scales (Baudier et al. 2015, Spicer et al. 2017) and throughout the day (Andersen 1983). Subsequently, there can be high turnover or vertical stratification of ant species from the canopy to the top layers of the soil even within relatively small sample areas (Brühl et al. 1998, Yanoviak and Kaspari 2000, Wilkie et al. 2010).

Estimates of ant community composition and structure are highly sensitive to sampling methodology and effort (Agosti and Alonso 2000). Moreover, the effectiveness of each method will depend on biotic and abiotic factors such as the type of vegetation, soil, and climate (Bestelmeyer et al. 2000). In addition to affinities for different abiotic environments, body size can influence the microhabitat used by ants (Farji-Brener et al. 2004, Wills et al. 2018). Most common standardized ant-capture methodologies include pitfalls trap (for ground surface-active ants), Berlesse funnels or Winkler samples (for

ants inhabiting leaf litter), and surface baiting (for ground-foraging ants) (Agosti and Alonso 2000). More recently, techniques have also been developed to sample subterranean species (Wilkie et al. 2007, Schmidt and Solar 2010, Pacheco and Vasconcelos 2012, Jacquemin et al. 2016). The application of complementary ant-sampling techniques not only maximizes diversity estimates (Agosti and Alonso 2000, Wong and Guérard 2017), but also it provides insight into the foraging and nesting biology of species. Similarly, studies that complement passive sampling (e.g., pitfall trap and litter samples) with baiting can provide insight into how foraging activity and dominance at resources relates to relative abundance across the landscape (Andersen 1992, Cerdá et al. 1997, LeBrun 2005, Adler et al. 2007).

Ants engage in a variety of ecological interactions, including mutualism, competition, parasitism and predation (Rico-Gray and Oliveira 2007, Lach et al. 2010), and play a major role in ecosystem functioning (Folgarait 1998, Del Toro et al. 2012). Interspecific competition is often evoked as a key process in structuring ant community (e.g., Hölldobler and Wilson 1990, Cerdá et al. 2013). Competition is mainly suggested by the presence of ant mosaics or the observation of agonistic behavior among individuals or colonies (Ribas and Schoereder 2002). Under the framework of competition, Wilson (1971) suggested that ant assemblages are structured into dominance hierarchies with regard to speed of resource discovery and fighting ability. However, dominance may not be a major factor in community structure if aggressive interspecific encounters are uncommon (Stuble et al. 2017).

The main objective of this work was to describe ant community structure and patterns of co-occurrence in the southern-most extent of the Atlantic Forest, a region of high conservation priority. We use this data, in part, to test the hypotheses that 1) different sampling methodologies are needed to sample ground-foraging ant community assembly due to variation in microhabitat preference and 2) if competition is an important mechanism, species will be less likely to co-occur in samples than expected by chance. We assessed ant occurrence and foraging using four methodologies that sample different microhabitats: pitfall traps, litter samples, surface baiting, and subterranean baiting. Furthermore, we examined temporal variation in ant activity and species interactions by sampling with surface baits at three different times throughout the day. We discuss our results from the perspectives of the necessity of using complementary sampling methodologies for determining information about community attributes, how foraging strategies of dominant ant species and abiotic factors may influence community structure, and how sampling methodologies influence our perception of ecological dominance in ants.

Materials and Methods

Study Site

Research was conducted in semi-deciduous subtropical forest in Iguazú National Park (INP), located in the northwestern of the Misiones Province, Argentina (25°40′48.54″S, 54°27′15.09″W). This park was created in 1934 to protect 67,000 ha of the Atlantic Forest. The topography of this region is undulating with elevations up to 380 m as a result of erosion from a network of rivers belonging to Paraná drainage (Devoto and Rothkugel 1936, Srur et al. 2007). The dominant soils are red and loamy, belonging to Alfisols and Ultisols, locally known as 'Tierra colorada' (Red soil). Heterogeneity in local environmental conditions, particularly of soil properties, has resulted in recognition of 18 different plant communities including forests with and without understory, gallery forests, bamboo forests, and palm forests (*Euterpe edulis*) Mart. (Arecales: Arecaceae) (Srur et al. 2007). The climate is subtropical humid without a defined dry season with mean monthly temperatures ranging from 15°C (June–August) to 26°C (December–February), annual rainfall between 1,800 and 2,000 mm, and humidity between 70 and 90%.

Ant Sampling and Identification

We surveyed ants during the summer months of 2008 (pitfall and litter sampling), 2009 (subterranean baiting) and 2011 (surface baiting). Each year we sampled along six transects; two in each of three different zones of the park: Macuco, Yacaratiá, and Garganta del Diablo (Supp. Fig. S1). In 2008, transects were 100 m and we placed a pitfall trap and collected a litter sample every 20 m. Litter samples consisted of sifting 1 m² of litter. Arthropods were collected with mini-Winkler extractors over a 48 h period. Pitfall traps were placed 1–2 m away from litter sites and consisted of an 8 cm diameter and 12 cm deep plastic cup. This size allowed the capture of the largest ant species at the site, *Dinoponera australis* Emery (Hymenoptera: Formicidae), with a body length of 2.5 cm. Pitfall traps remained closed for 5 d to minimize 'digging-in' effects which could result in biased sampling due to species that either avoid or are drawn to small disturbances in the soil (Greenslade 1973). Once opened, traps were partially filled with a solution of 70% ethanol and a drop of detergent, and remained open for 72 h.

In 2009, transects were 200 m long and every 20 m we placed a pair of subterranean baits at a depth of 12 cm where Wilkie et al. (2007) found the highest ant richness. Subterranean baits (Schmidt and Solar 2010) consisted of a plastic container 3 cm diameter × 5 cm deep with four equidistant holes and a plastic platform inside the container over which one of two baits (tuna or honey) was placed. The bottom of the container was filled with soapy water to kill the ants (Supp. Fig. S2A) This type of device is also known as Subterranean pitfall trap (Pacheco and Vasconcelos 2012, Wong and Guénard 2017). Subterranean baits were collected after 72 h.

In 2011, we placed a bait station on the surface every 20 m along 200 m transects (10 baits per transect). Bait stations consisted of a plastic box 8 cm in diameter and 5 cm deep with four equidistant slots of 2 × 5 cm at the sides. A box was used (instead of a bait card) to prevent the baits from getting stolen and from getting wet during light rains. We also drilled twenty to twenty-five 2-mm holes on the roof of each box to prevent condensation. In each box, we placed three baits: tuna, honey and cracked corn flakes (Supp. Fig. S2B). Baits were distributed along each transect at three different times of day: 0830, 1200 and 1600 hours. After placement, baits were inspected after 15, 30, and 45 min. At each visit, we recorded which species were present and collected voucher individuals for species identification. We avoided collecting the first individuals that appeared at the bait to allow worker recruitment or subsequent visits for species in case of solitary foragers. To prevent earlier baits from influencing recruitment to baits placed later in the day, we sampled the three different time points on three different days and determined the order of sampling randomly for each transect. We recorded the temperature at each inspection lapse (*n* = 54 observations [six transects, three times of day, three observations per bait]). Transects were located at least 50 m away from major trails.

Collected ants were placed in 96% ethanol and identified to species when possible using available bibliography (Kempf 1962, 1965; Brown 1976, Kugler and Brown 1982; MacKay 1996; Wild 2005, 2007; Lattke et al. 2007; Longino and Fernández 2007; Jiménez et al. 2008; MacKay and Mackay 2010; Dash 2011; Ortíz Sepúlveda 2012; Boudinot et al. 2013; Lenhart et al. 2013; Fernandes et al. 2014; Ronque et al. 2015). All individuals collected were deposited in the Museo Nacional de Ciencias Naturales 'Bernardino Rivadavia'. Images, Cytochrome c oxidase subunit I (COI) sequences, DNA barcode BINs (Barcode Index

Numbers) codes and deposit numbers of voucher individuals of this study, in addition to other ant species collected in INP can be found at dx.doi.org/10.5883/DS-AOI16ALL (Hanisch et al. 2017).

Data Analysis

While sampling occurred during different years, all methods were employed in the same season (January 18–March 4 of years 2008, 2009, and 2011) when weather conditions were similar (Supp. Fig. S3). While ant activity does vary seasonally in many habitats, there is often little year-to-year variation in ant composition when sampling at the same season and using the same sampling methods, with the exception of rare or hard to detect species (Longino and Colwell 1997, Jacquemin et al. 2016). Therefore, we feel confident that differences in species composition among sampling regimes are due to methodology, and not stochastic annual variation (see discussion for additional information). To compare species composition across sampling methodologies we constructed a matrix containing the presence/absence of each species for all sampling methods. We used non-metric multidimensional scaling (NMDS) based on the Jaccard index to evaluate the similarity of ant species composition between the four collecting methods. We performed a nonparametric analysis of similarity (ANOSIM) (Clarke 1993) to test if species composition differed between the sampling methodologies. Analysis were performed with PC-ORD v.5 (McCune and Mefford 1999) and PAST v.3.04 (Hammer et al. 2001).

To compare species richness across sampling methodologies we performed occurrence-based rarefaction curves for incidence data. An occurrence by species incidence matrix was produced for all sampling methodologies using EstimateS v.9.1 (Colwell 2013). For baiting where multiple surveys were done in the same location (surface baits sampled at three different times and subterranean baits with two different baits), samples were combined for each specific baiting location.

To examine if species co-occurred at baits more or less than expected by chance, we generated presence/absence matrices (with bait stations as columns and ant species as rows) for each bait observation for the three sampling times (morning, midday, and afternoon). We tested for nonrandom patterns of species co-occurrence using EcoSim (Gotelli and Entsminger 2004) with 5,000 randomizations of the original matrix to generate a frequency distribution of co-occurrence indexes. We then compared the observed index to this frequency distribution using the C-Score which compares the average number of times two species co-occur together relative to what would be expected by chance among all possible pairs of species (Stone and Roberts 1990, Gotelli 2000). Our null hypothesis was the presence of a given ant species does not influence the occurrence of another species, i.e., there is no evidence for deterministic processes influencing species distribution (Ribas and Schoereder 2002, Gotelli and Entsminger 2004). For randomizations, we chose fixed rows (species) and equiprobable columns (bait stations) to keep the occurrence of ant species fixed but allowing them to occupy sites with equal probability. This assumption corresponds to a simple model of community assembly in which species colonize sites independently of one another and has the lowest probability of a type error I (Gotelli and Entsminger 2004). We also retained the degenerate matrices (those that contain missing species or empty sites).

At each bait inspection, we quantified interactions that occurred between species pairs co-occupying the surface baits. We considered an interaction neutral if species ignored or tolerated each other, and aggressive if species engaged in combat or other antagonistic behaviors (Stuble et al. 2017). At 45 min of bait occupancy, we characterized species as 'neutral' if the ratio: Number of neutral interactions/

Total number of interactions was greater than 0.5 and as 'aggressive' if this relationship was less than 0.5. The baits were considered monopolized at 45 min if a species had multiple individuals present at the bait and also prevented other species from feeding on the resource.

We compared differences on the variables (temperature, humidity and species richness at baits) across the three surface baiting periods (0830 hours, 1200 hours, 1600 hours) and baiting time (15, 30 and 45 min) using linear mixed effects models (LMMs), with transect as a random factor and observation time as fixed factor. For comparisons among baiting periods, a single value was obtained for each transect by averaging variables across the three 15-min observation intervals. Normality and homogeneity of variance was graphically inspected by dispersion of residuals. Akaike's information criterion (AIC) values were calculated to judge the quality of the models and the most parsimonious were chosen. When selected LMMs contained a significant effect, we performed a post hoc (LSD Fisher) test to determine which differences between variables were driving the overall pattern. These analyses were done using Infostat (Di Rienzo et al. 2017) coupled with an R interface, version 3.4.1 (R Core Team 2016) with the gls and lme functions of the nlme package (Pinheiro et al. 2014). Finally, to summarize the composition of the ant community at the three moments of the day we ordered the similarity between baits points using an NMDS followed by ANOSIM. This analysis was performed from a presence/absence distance matrix calculated from the Jaccard index.

Results

Complementarity of Methodology

We captured a total of 97 ant species/morphospecies from 34 genera and seven subfamilies with the four methods (Fig. 1). The subfamily Myrmicinae had the greatest number of species (56), followed by Formicinae (16), Ponerinae (13), and Dolichoderinae (5). The sampling method that collected the most species was litter extraction (52 species) followed by pitfalls traps (46 species), surface baits (41 species), and subterranean baits (30 species) (Fig. 1). This pattern is reflected in the accumulation of species relative to sample effort for pitfalls traps and litter samples compared to both bait methodologies (Fig. 2). As expected, sampling methodologies collected a particular assemblage of ants (Figs. 1 and 3) (ANOSIM, $R = 0.40$, $P < 0.001$). Only pitfall traps and surface baits had a similar species composition (ANOSIM pairwise test, $R = 0.069$, $P = 0.07$; Fig. 3), consistent with both methodologies targeting surface foraging ants. The number of shared species among methodologies ranged from 11 to 27 (Fig. 1) with *Brachymyrmex aphidicola* Forel, *Pheidole sigillata* Wilson, *Pheidole subarmata* Mayr, *Solenopsis* PEH02, *Solenopsis* PEH04, and *Wasmannia auropunctata* (Roger) (Hymenoptera: Formicidae) detected by all the methods. Several ant species were only collected by a single methodology (Fig. 1): litter extractions had the most unique species with 17, while surface baits, pitfall traps, and subterranean baits had 12, 11, and 11 unique species, respectively. NDMS ordination revealed that the sampling zones (Macuco, Yacaratía and Garganta del Diablo) had a small but significant influence on a particular composition of the ant community (ANOSIM, $R = 0.06$, $P < 0.001$).

The four most common species at surface baits (across all three time periods) were *D. australis* (occurring at 45–53% of baits), *Pachycondyla striata* Smith (Hymenoptera: Formicidae) (40–48% of baits), *Solenopsis PEH04* (10–26% of baits), and *P. subarmata* (13–18% of baits). These species were also the most common species in pitfall traps (Fig. 4). A few other species accounted for 10% or more bait discoveries in one or more day times, these include *Pheidole*
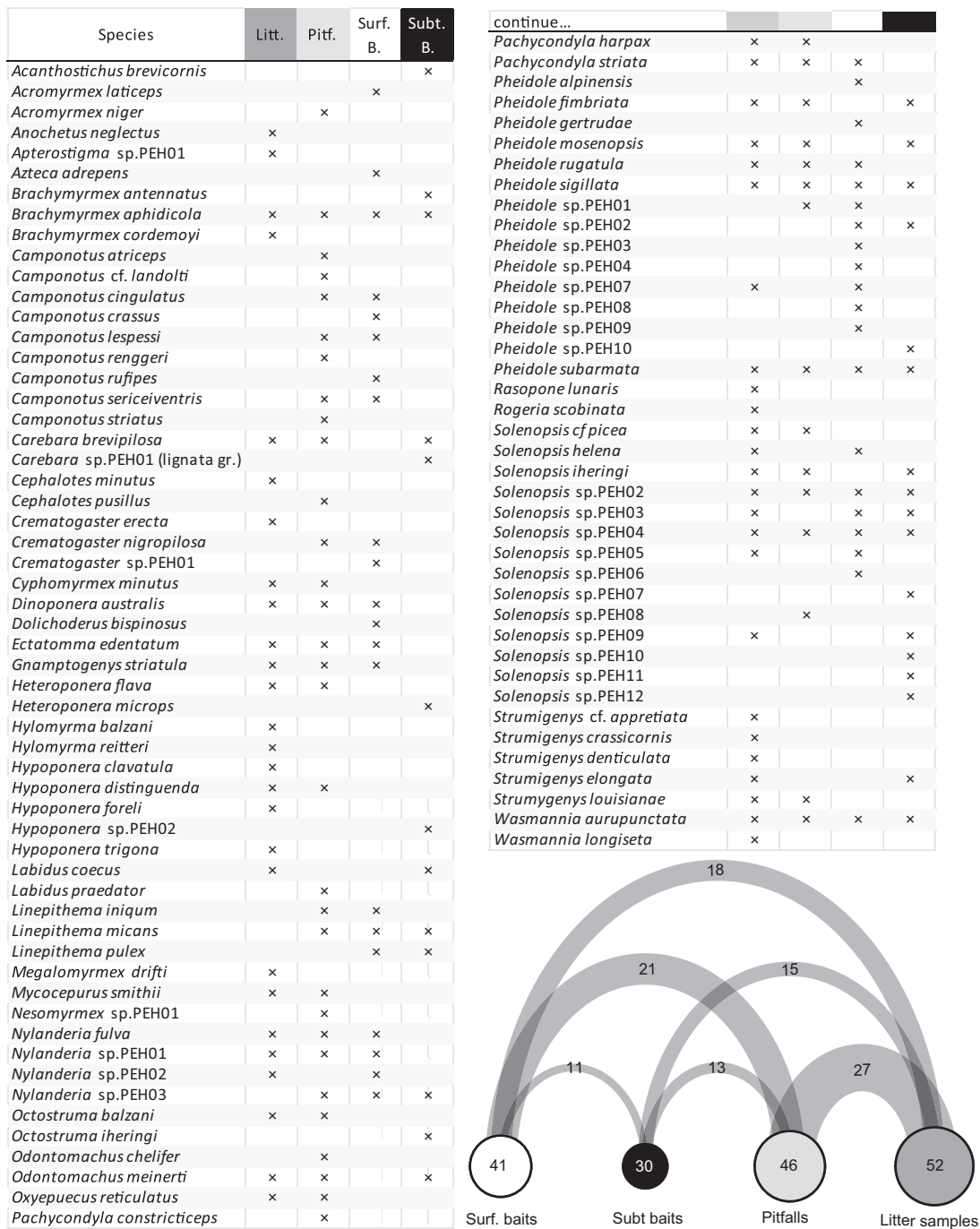
Species	Litt.	Pitf.	Surf. B.	Subt. B.
Acanthostichus brevicornis				×
Acromyrmex laticeps			×	
Acromyrmex niger		×		
Anochetus neglectus	×			
Apterostigma sp.PEH01	×			
Azteca adrepens			×	
Brachymyrmex antennatus				×
Brachymyrmex aphidicola	×	×	×	×
Brachymyrmex cordemoyi	×			
Camponotus atriceps		×		
Camponotus cf. *landolti*		×		
Camponotus cingulatus		×	×	
Camponotus crassus			×	
Camponotus lespessi		×	×	
Camponotus renggeri		×		
Camponotus rufipes			×	
Camponotus sericeiventris		×	×	
Camponotus striatus		×		
Carebara brevipilosa	×	×		×
Carebara sp.PEH01 (lignata gr.)				×
Cephalotes minutus	×			
Cephalotes pusillus		×		
Crematogaster erecta	×			
Crematogaster nigropilosa		×	×	
Crematogaster sp.PEH01		×		
Cyphomyrmex minutus	×	×		
Dinoponera australis	×	×	×	
Dolichoderus bispinosus			×	
Ectatomma edentatum	×	×	×	
Gnamptogenys striatula	×	×	×	
Heteroponera flava	×	×		
Heteroponera microps				×
Hylomyrma balzani	×			
Hylomyrma reitteri	×			
Hypoponera clavatula	×			
Hypoponera distinguenda	×	×		
Hypoponera foreli	×			
Hypoponera sp.PEH02				×
Hypoponera trigona	×			
Labidus coecus	×			×
Labidus praedator		×		
Linepithema iniqum		×	×	
Linepithema micans		×	×	×
Linepithema pulex			×	×
Megalomyrmex drifti	×			
Mycocepurus smithii	×	×		
Nesomyrmex sp.PEH01		×		
Nylanderia fulva	×	×	×	
Nylanderia sp.PEH01	×	×	×	
Nylanderia sp.PEH02	×		×	
Nylanderia sp.PEH03		×	×	×
Octostruma balzani	×	×		
Octostruma iheringi				×
Odontomachus chelifer		×		
Odontomachus meinerti	×	×		×
Oxyepuecus reticulatus	×	×		
Pachycondyla constricticeps		×		

continue...	Litt.	Pitf.	Surf. B.	Subt. B.
Pachycondyla harpax	×	×		
Pachycondyla striata	×	×	×	
Pheidole alpinensis			×	
Pheidole fimbriata	×	×		×
Pheidole gertrudae			×	
Pheidole mosenopsis	×	×		×
Pheidole rugatula	×	×	×	
Pheidole sigillata	×	×	×	×
Pheidole sp.PEH01		×	×	
Pheidole sp.PEH02			×	×
Pheidole sp.PEH03			×	
Pheidole sp.PEH04			×	
Pheidole sp.PEH07		×	×	
Pheidole sp.PEH08			×	
Pheidole sp.PEH09			×	
Pheidole sp.PEH10				×
Pheidole subarmata	×	×	×	×
Rasopone lunaris	×			
Rogeria scobinata	×			
Solenopsis cf picea	×	×		
Solenopsis helena	×		×	
Solenopsis iheringi	×	×		×
Solenopsis sp.PEH02	×	×	×	×
Solenopsis sp.PEH03	×		×	×
Solenopsis sp.PEH04	×	×	×	×
Solenopsis sp.PEH05	×		×	
Solenopsis sp.PEH06			×	
Solenopsis sp.PEH07				×
Solenopsis sp.PEH08		×		
Solenopsis sp.PEH09	×			×
Solenopsis sp.PEH10				×
Solenopsis sp.PEH11				×
Solenopsis sp.PEH12				×
Strumigenys cf. *appretiata*	×			
Strumigenys crassicornis	×			
Strumigenys denticulata	×			
Strumigenys elongata	×			×
Strumygenys louisianae	×	×		
Wasmannia aurupunctata	×	×	×	×
Wasmannia longiseta	×			

Fig. 1. Ant species found with each sampling method. Inset shows the richness of ant species sampled by each method and widths of the curved arches represent the number of shared ant species between methods.

PEH01 (10–16% of baits), *Linepithema micans* (Forel) (8–18% of baits), *Crematogaster nigropilosa* Mayr (8–16% of baits) and *Camponotus sericeiventris* (Guérin-Méneville) (5–11% of baits) (Hymenoptera: Formicidae) (Fig. 4). In subterranean baits, the most common species were *P. subarmata* and *Solenopsis iheringi* Forel (Hymenoptera: Formicidae) (occurring in 43 and 38% of baits, respectively); these species had similar occurrence rates in litter samples (30 and 20%, respectively). In contrast, *L. micans* and *Labidus coecus* (Latreille) (Hymenoptera: Formicidae) occurred relatively frequently in subterranean baits (20 and 17%, respectively), but had low occurrence in litter samples (0 and 3%, respectively). Despite that litter samples had the most shared species with

subterranean baits (15 species in common; Fig. 1), the overall composition of ants sampled by these two methodologies were distinct (ANOSIM pairwise test, $R = 0.72$, $P < 0.001$; Fig. 3).

Activity at Surface Baits

Ants discovered between 43 and 61% of the baits during the first observation period (15 min after placement) across all three sample times of the day. By the last observation period (45 min after placement), between 91 and 96% of baits were discovered. There was a tendency for a higher number of species per bait during midday, but this difference was not significant (LMMs; $F = 2.49$, $P = 0.09$). The number of species co-occupying baits increased with observation
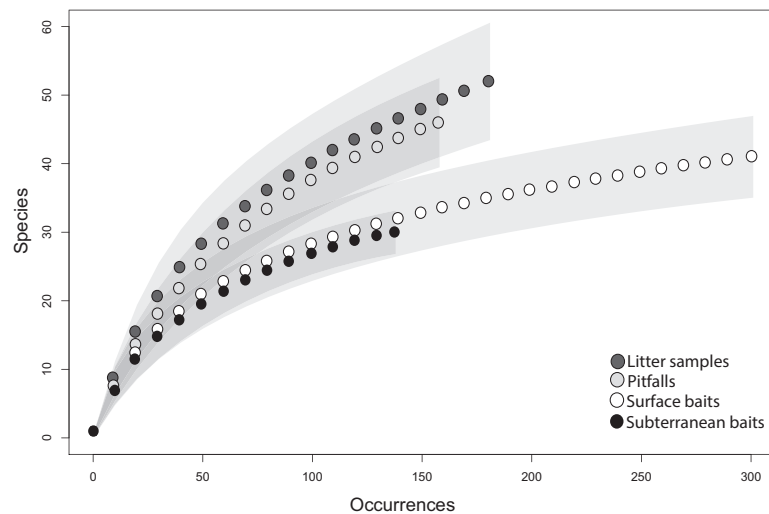
Fig. 2. Occurrence-based rarefaction of species richness with 95% confidence intervals collected by surface baits (white), pitfall traps (light gray), litter samples (dark gray) and subterranean baits (black).
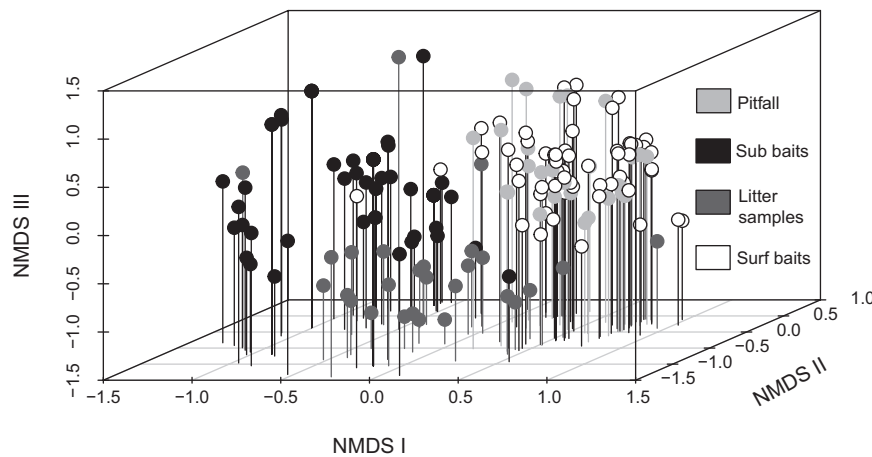
Fig. 3. Ordination of ant community collected by surface baits (white), pitfall traps (light gray), litter samples (dark gray), and subterranean baits (black). The ordination was performed by a NMDS analysis using the Jaccard similarity index (stress = 0.20).

period (from an average of 0.8 species per bait at 15 min to 1.7 species per bait at 45 min after placement) (LMMs; $F = 32.66$, $P < 0.001$).

Generally, species co-occurrence patterns suggested random co-occurrence of ant species at baits during all times of the day and monitoring events, as most of the observed C-scores did not differ from mean C-scores ($P > 0.05$). However, there were three exceptions. At the last monitoring event (45 min) of the morning and afternoon sample periods, observed co-occurrence indexes (C-score$_{obs}$) were higher than the mean calculated indexes (C-score$_{mean}$) (Morning: C-score$_{obs}$ = 9.63, C-score$_{mean}$ = 9.08, $P = 0.022$; Afternoon: C-score$_{obs}$ = 9.12, C-score$_{mean}$ = 8.53, $P = 0.006$). This pattern arose when bait occupancy (91 and 96% morning and afternoon, respectively) and co-occurrence at baits (53 and 50% morning and afternoon, respectively) were at their highest levels. This pattern was also observed, during the second observation period (30 min) at midday with 95% bait occupancy and 60% had species co-occurring (C-score$_{obs}$ = 14.85, C-score$_{mean}$ = 13.98, $P = 0.0068$).

Variation of temperature (LMMs; $F = 88.00$, $P < 0.0001$) (mean ± SD °C, morning: 25.82 ± 1.01, midday: 29.83 ± 1.54, afternoon: 28.61 ± 1.33) and humidity (LMMs; $F = 6.86$, $P = 0.0133$) (mean ± SD %, morning: 92.83 ± 1.72, midday: 76.67 ± 4.31, afternoon: 86.83 ± 2.55) among survey periods did not appear to influence patterns of co-occurrence as observed C-scores were never below

C-scores means. The results for all the observation periods are summarized in Supp. Table S1. Finally, according to the ordination analysis, the ant community composition did not differ across different times of day (NMDS, followed by ANOSIM; $R = -0.0006$, $P = 0.49$) (Supp. Fig. S4).

A total of thirty-nine species were detected at baits with another species present, and at the last sample period (45 min), between 50 and 58% of the discovered baits were visited by two or more ant species (range: 2 to 6 species). Most species were characterized as neutral—ants exhibited more neutral interactions at co-occupied baits than aggressive interactions (or no aggression at all) (Fig. 5). In contrast, a few species were often observed interacting antagonistically with other species, these species typically had high recruitment rates (*C. sericeiventris*, *Pheidole gertrudae* Forel, *Cr. nigropilosa*) and most frequently interacted aggressively with two ponerines that commonly visited most of the baits but at low numbers, *P. striata* and *D. australis*. Most of the aggressive interactions were between *C. sericeiventris*–*D. australis* and *D. australis*–*P. striata* (four observations for each species pair) followed by *P. gertrudae*–*D. australis*, *L. micans*–*D. australis*, and *P. striata*–*Cr. nigropilosa* (three observations for each species pair) (Fig. 6). Some interactions left injured individuals. For example, on one occasion *D. australis* killed a *C. sericeiventris* worker. Only a 10% of baits were considered monopolized after 45 mins, and these were occupied by
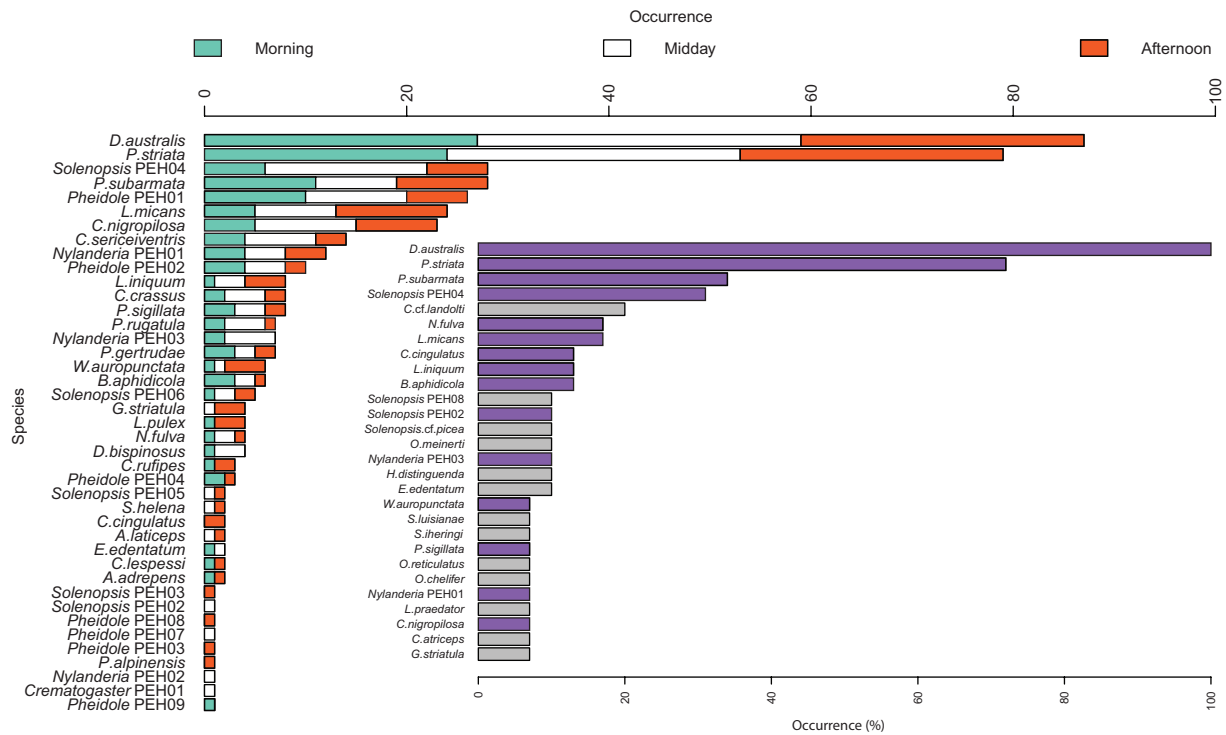
Fig. 4. Species occurrence of ants at 60 baits placed during the morning (green), midday (white) and afternoon (orange) at the 45 min observation period. The inset figure shows the occurrence (%) for species collected in two or more pitfall traps. Species with purple in the inset were also detected at surface baits.
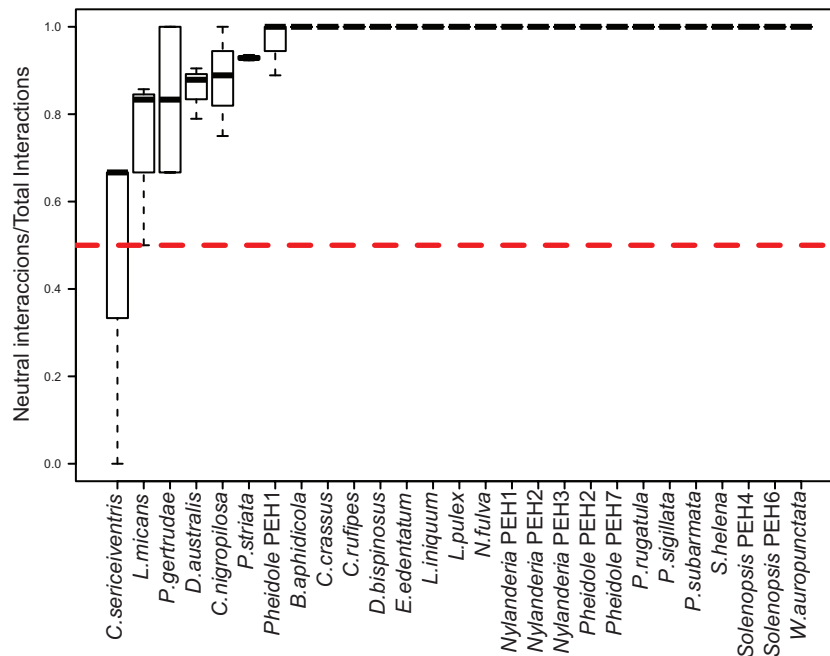

Fig. 5. Proportion of neutral interactions for species present at the 45 min bait observation period (across all three sample times). The Y axis is the proportion of neutral interactions defined as the number of neutral interactions/number of shared baits.

C. sericeiventris (five baits), *L. micans*, *Cr. nigropilosa*, and *P. gertrudae* (four baits), *P. striata* (one bait), and *Dolichoderus bispinosus* (Olivier) (Hymenoptera: Formicidae) (one bait).

Discussion

Obtaining results from different sampling methodologies not only increases diversity estimates, but also provides information on community structure including how species may partition habitats and resources (Longino and Colwell 1997, Agosti and Alonso 2000, Fisher 2005, Underwood and Fisher 2006, Ellison et al. 2007, Gotelli et al. 2010). The four methodologies we applied sampled 97 ant species, and a particular composition was revealed by each method (Figs. 1 and 3). Moreover, 52% of species were collected by only one of the methodologies, suggesting considerable microhabitat specialization (Fig. 1). As seen in other studies (e.g., Fisher 1999), litter
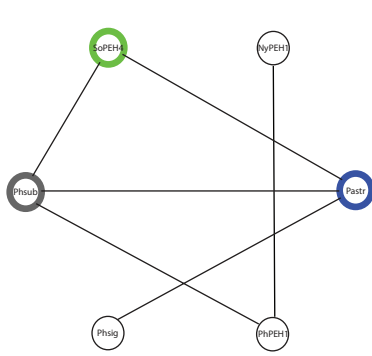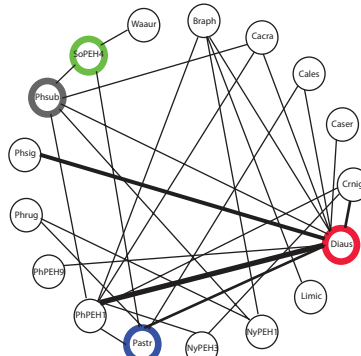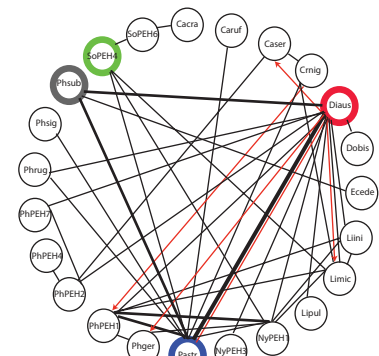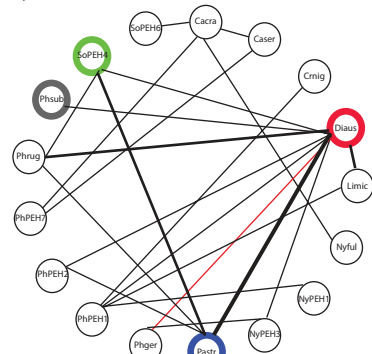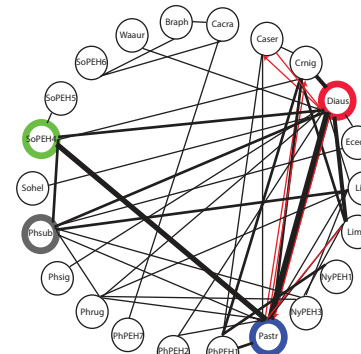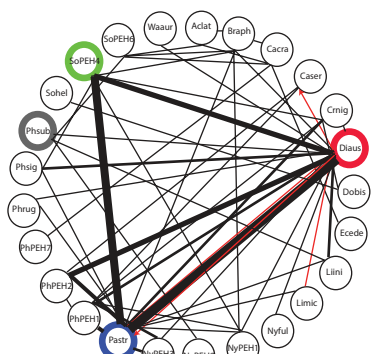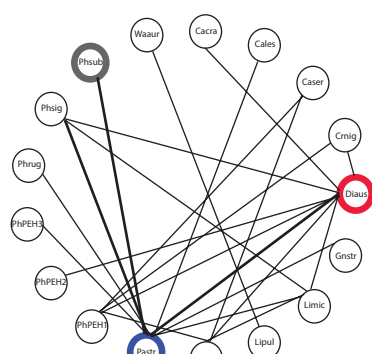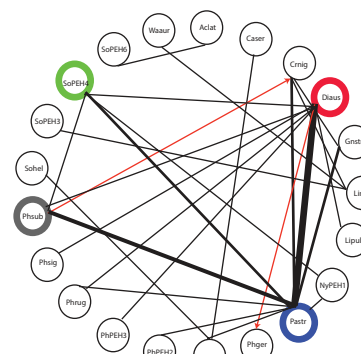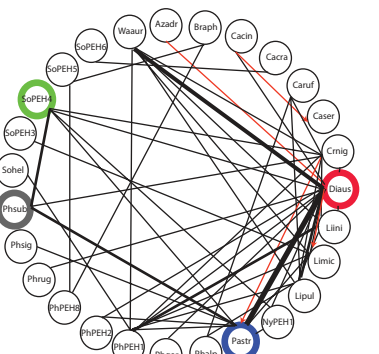
Fig. 6. Network of species-pair interactions at 15, 30 and 45 min observation periods across all three bait sample times. Neutral interactions are represented by black lines and antagonistic interactions are represented by red lines. If a species was clearly displaced during the interaction, an arrow indicates the "winner". Thicker lines indicate a higher number of interactions among the pair of species. Species name abbreviation shows the first two letters of the genus followed by the three letters of the species name. Complete names of ant species are shown in Fig 1. For clarification, the four most frequent species are highlight: *D. australis* (red circle), *P. striata* (blue circle), *Solenopsis* PEH04 (green circle) and *P. subarmata* (grey circle).

sampling collected the highest richness overall and the highest number of unique species. Ant composition was most similar between pitfall traps and surface baits followed by litter samples and subterranean baits (Fig. 3). While pitfall traps and litter samples were the best methods to maximize ant richness (Fig. 2), surface baits provided information about foraging biology and insight into species interactions. Meanwhile, subterranean baits were still effective at detecting uncommonly collected ants. For example, this method collected the termite-predator *Acanthostichus brevicornis* Emery (Hymenoptera: Formicidae) (AntWeb specimen number CASENT0246290), a species that is rarely collected and whose ecology is not well known (Mackay 2004). The fact that several individuals were captured both

in the tuna and honey baits may suggest for scavenging behavior and a more generalized diet.

Our observed species interactions at surface baits revealed a prevalence of neutral interactions and random species co-occurrence, patterns consistent with other research (e.g., Baccaro et al. 2012; Stuble et al., 2013, 2017). However, with increasing time of bait placement (30 min at midday and 45 min at morning and afternoon), patterns of co-occurrence were less frequent than expected by chance (Supp. Table S1). These were the times when the few agonistic interactions were most often observed (Fig. 6) and bait occupancy was highest (Supp. Table S1). Aggressive interactions were recorded for six of the 41 species that visit the baits (*C. sericeiventris, L. micans, Ph.*

gertrudae, D. australis, Cr. nigropilosa, and *P. striata*). With the exception of *D. australis* and *P. striata*, these species usually recruit a high number of individuals and behaved like 'extirpators' (Wilson 1971) by occasionally preventing other species from feeding on the bait. Additionally, *C. sericeiventris, L. micans,* and *P. gertrudae* had the fewest proportion of neutral interactions (Fig. 5). Notably, northern Argentina includes the native range of many introduced ant species that are considered to be highly competitive and ecologically dominant where they occur (LeBrun et al. 2007, Calcaterra et al. 2008, Foucaud et al. 2009). Four of these species are known to occur at INP: *Linepithema humile* (Mayr), *Solenopsis invicta* Buren, *Nylanderia fulva* (Mayr) (Hymenoptera: Formicidae), and *W. auropunctata* (Hanisch et al. 2015). However, only *W. auropunctata* was collected in this study, where it occurred at relatively low abundance in all the sampling methods, and it did not monopolize or dominate any of the baits. While competition might be an important factor in structuring some ant communities, other biological processes or stochastic events can explain positive or negative patterns of species co-occurrence (Ribas and Schoereder 2002, Cerdá et al. 2013, Ellwood et al. 2016). Additionally, competitive interactions can be diffuse (Davidson 1985) and the simple observation of agonistic behavior (or its absence) does not necessarily imply the presence or absence of interspecific competition (Ribas and Schoereder 2002).

While our sampling regime allowed us to infer the role of biotic interactions through co-occurrence patterns, we did not examine how variation in local abiotic factors may influence ant assemblages except at surface baits. Thermal tolerance can influence ant foraging biology and measures of dominance and competition including the discovery and monopolization of resources (Cerdá et al. 1997, Farji-Brener et al. 2004, Godoy and de Camargos 2013). The ability to forage at extreme temperatures may allow species to break trade-offs between resource discovery and dominance by providing foraging periods where dominant species are absent (Cerdá et al. 1997). The relatively narrow range of temperatures (25–30°C) across our three baiting periods at INP may not have included thermal conditions that prevented many ants from foraging. Only *Solenopsis* PEH04 appeared to benefit from higher temperatures. Nocturnal baiting would likely show greater variation in community structure and species interactions related to temperature as nighttime summer temperatures can decrease to 18°C. In addition, there is an entire guild of common crepuscular and nocturnal foraging species at INP including *Camponotus sericeiventris* (Yamamoto and Del-Claro 2008) and *Odontomachus chelifer* (Latreille) (Hymenoptera: Formicidae) (Raimundo et al. 2009). It would be worth documenting if these species show similar patterns of bait occupancy and species interaction as our most common diurnal foragers *D. australis* and *P. striata*. The lack of influence of temperature on community structure in this study is similar to the results of Dáttilo and Izzo (2012) who sampled contrasting environments (tree fall gaps vs. dense forest) within the Amazonian rain forest at five different hours of the day. However, more work is needed to examine how local abiotic conditions shape variation in habitat use and community assembly among microhabitats (Groc et al. 2013, Jacquemin et al. 2016).

Four of the species commonly collected in pitfall traps (occurring in more than 25% of the traps) were also common visitors at the surface baits (*D. australis, P. striata, P. subarmata,* and *Solenopsis* PEH04), indicating that their prevalence at baits may explained by their relative abundance. The two ponerines (*D. australis, P. striata*), with an occurrence between 72 and 100% (Fig. 4) clearly stand out from the rest of the ant community. Unlike other 'dominant' ants, which usually live in large colonies, these species have relatively small colony sizes. However, they exist at relatively high colony

densities at the study site. In INP, *D. australis* have an average of 44 workers per nest (range 18–86), with a density of ~ 180 nests/ ha (Tillberg et al. 2014). *Pachycondyla striata* nests have an average of 36.7 workers (range 7–80) (Rodrigues et al. 2010), but unfortunately there is no record of nest density for INP. Both of these species exhibit solitary foraging with little to no recruitment; *P. striata* will occasionally recruit a few nest mates using tandem running (Giannotti and Machado 1992) and *D. australis* appears to use tandem running only in the context of colony fission (Fowler 1985). This foraging behavior typically corresponds with the collection of small, fairly common resources that are distributed unpredictably in space and that are not depleted by colony foraging effort (Lanan 2014). The large size of these species allows them to quickly grab resources and run away, avoiding confrontations with other species. However, they have also been seen stealing prey or resources from smaller ants (PEH per sobs, Raimundo et al. 2009). In contrast, their large size may prevent them from exploiting smaller resources or foraging effectively within the leaf-litter (Agosti and Alonso 2000, Farji-Brener et al. 2004), reducing competition among species (Brown and Davidson 1977).

An uncontrolled source of variation in our study is that sampling was conducted across different years. While seasonal variation can influence capture rates in ant inventories (e.g., Longino and Colwell 1997, Jacquemin et al. 2016), our results suggest that sampling during the same season in different years does not greatly influence which species are detected. Therefore, we are confident that differences in species composition are due to the stratification of ant assemblages by the microhabitats where they nest and forage. For example, despite sampling over 3 yr, species sampled with pitfall traps and surface baits showed a similar composition suggesting that these two methods target the same ant assemblage. In contrast, the two methods applied simultaneously (pitfalls and litter samples), exhibited a distinct composition. Lastly, our species lists from different sampling methods were taxonomically and functionally similar to those reported in other studies in tropical forests (e.g., Delabie et al. 2000, Silva and Brandão 2010, Wilkie et al. 2010, Groc et al. 2013). These patterns include, e.g., small species with reduced eyes in the soil (e.g., *Heteroponera* Mayr and *Carebara* Westwood (Hymenoptera: Formicidae)), small predators and specialized hunters in the leaf litter (e.g., *Strumigenys* Smith and *Hypoponera* Santschi (Hymenoptera: Formicidae)), and medium- to large-sized generalists on the surface (e.g., *Camponotus* Mayr and *Pheidole* Westwood).

Sampling methodologies employed in this study underestimated the presence of two important groups of ants, leaf-cutting ants (genera *Atta* Fabricius and *Acromyrmex* Mayr) and army ants (genera *Cheliomyrmex* Mayr, *Eciton* Latreille, *Labidus* Jurine, *Neivamyrmex* Borgmeier, *Nomamyrmex* Borgmeier). This omission may be a consequence of the foraging strategies of these groups (trunk trails from a central nest in leaf-cutting ants; column or swarm raids from bivouac in army ants) which make them hard to detect with pitfall traps, litter samples or baits. These taxa are key components of neotropical rainforest ecosystems acting as dominant herbivores and insect predators (Fowler et al. 1986, Kaspari and O'Donnell 2003). Subsequently, they may strongly influence ant community structure. For example, leaf-cutting ants can modify habitat structure and microclimate by influencing seedling emergence, creating gaps, and changing soil texture and composition (Farji-Brener and Illes 2000, Wirth et al. 2007). While some army ants are insect generalists, many specialize on raiding other ants including large, behaviorally dominant species (Franks and Bossert 1983). These raids can consist of thousands to millions of individuals and estimates among 20 tropical localities suggest that every square meter of forest is raided

approximately once every 17 d (Kaspari and O'Donnell 2003). Surface-foraging army ants are usually sampled by visual searching (O'Donnell et al. 2010), meanwhile, for subterranean-foraging army ants, soil samples and litter shifting are used (Sanabria-Blandón and Achury 2011). In our study, we only sampled *L. coecus* and *Labidus praedator* (Smith) by subterranean baits, litter samples (*L. coecus*) and pitfalls (*L. praedator*). Our inadequate sampling of these ecologically relevant taxa may distort our perception of ant community structure and dominance at our site.

The Atlantic Forest is a highly heterogeneous region, divided into several ecoregions along its distribution. Given the unique nature of the Atlantic Forest, and the extent to which it has been deforested, it has become a priority for diversity and conservation research. A comprehensive survey of the ants of INP produced 203 ant species including unidentified morphospecies (Hanisch et al. 2015). Moreover, a recent COI barcoding study of 312 INP specimens, suggests that ant diversity could be between 6 and 10% higher than currently recognized (Hanisch et al. 2017). Our efforts here, while only detecting less than 50% of INP fauna, provided information about microhabitat use and foraging biology for ants in this important forest. Additional surveys covering a larger area, nocturnal baiting periods and canopy sampling, are necessary to obtain information on a greater diversity of species. We also advocate using a wider variety of bait types and more frequent bait monitoring to evaluate the role of competition in resource use and community structure.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

Acknowledgments

References Cited

Adler, F. R., E. G. LeBrun, and D. H. Feener Jr. 2007. Maintaining diversity in an ant community: modeling, extending, and testing the dominance-discovery trade-off. Am. Nat. 169: 323–333.

Agosti, D., and L. Alonso. 2000. The ALL protocol, pp. 204–206. *In* D. Agosti, J. D. Majer, L. E. Alonso, and T. Schultz (eds.), Ants - Standard Methods for Measuring and Monitoring Biodiversity. Smithsonian Institution Press, Washington, DC.

Andersen, A. N. 1983. Species diversity and temporal distribution of ants in the semi-arid mallee region of northwestern Victoria. Austral. Ecol. 8: 127–137.

Andersen, A. N. 1992. Regulation of "Momentary" diversity by dominant species in exceptionally rich ant communities of the Australian Seasonal Tropics. Am. Nat. 140: 401–420.

Baccaro, F. B., J. L. P. De Souza, E. Franklin, V. L. Landeiro, and W. E. Magnusson. 2012. Limited effects of dominant ants on assemblage species richness in three Amazon forests. Ecol. Entomol. 37: 1–12.

Baudier, K. M., A. E. Mudd, S. C. Erickson, and S. O'Donnell. 2015. Microhabitat and body size effects on heat tolerance: implications for responses to climate change (army ants: Formicidae, Ecitoninae). J. Anim. Ecol. 84: 1322–1330.

Bestelmeyer, B. T., L. E. Alonso, C. R. F. Brandão, W. L. Brown Jr., J. H. C. Delabie, and R. Silvestre 2000. Field techniques for the study of Ground-Dwelling ants, pp. 122–144. *In* D. Agosti, J. D. Majer, L. E. Alonso, and T. Schultz (eds.), Ants - Standard Methods for Measuring and Monitoring Biodiversity. Smithsonian Institution Press, Washington, DC.

Boudinot, B. E., T. P. Sumnicht, and R. M. Adams. 2013. Central American ants of the genus *Megalomyrmex* Forel (Hymenoptera: Formicidae): six new species and keys to workers and males. Zootaxa 3732: 1–82.

Brown, W. L. 1976. Contributions toward a reclassification of the Formicidae. Part VI. Ponerinae, Tribe Ponerini, subtribe Odontomachiti. Section B. Genus *Anochetus* and bibliography. Stud. Entomol. 19: 549–638.

Brown, J. H., and D. W. Davidson. 1977. Competition between seed-eating rodens and ants in desert ecosystems. Science 196: 880–882.

Brühl, C. A., G. Gunsalam, and K. E. Linsenmair. 1998. Stratification of ants (Hymenoptera, Formicidae) in a primary rain forest in Sabah, Borneo. J. Trop. Ecol. 14: 285–297.

Calcaterra, L. A., J. P. Livore, A. Delgado, and J. A. Briano. 2008. Ecological dominance of the red imported fire ant, *Solenopsis invicta*, in its native range. Oecologia 156: 411–421.

Cerdá, X., J. Retana, and S. Cros. 1997. Thermal disruption of transitive hierarchies in Mediterranean ant communities. J. Anim. Ecol. 66: 363–374.

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

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Austral. Ecol. 18: 117–143.

Colwell, R. K. 2013. EstimateS: statistical estimation of species richness and shared species from samples. https://purl.oclc.org/estimates.

Dash, S. T. 2011. A taxonomic revision of the new world *Hypoponera* Santschi, 1938 (Hymenoptera: Formicidae). ETD Collection for University of Texas, El Paso, TX.

Dáttilo, W., and T. J. Izzo. 2012. Temperature influence on species Co-Occurrence patterns in treefall gap and dense forest ant communities in a Terra- Firme Forest of Central Amazon, Brazil. Sociobiology 59: 351–367.

Davidson, D. W. 1985. An experimental study of diffuse competition in harvester ants. Am. Nat. 125: 500–506.

Delabie, J. H., D. Agosti, and I. C. Nascimento. 2000. Litter ant communities of the Brazilian Atlantic rain forest region, pp. 1–17. *In* D. Agosti, J. Majer, L. E. Alonso, and T. R. Schultz (eds.), Sampling ground-dwelling ants: case studies from the world's rain forests. Curtin University of Technology, School of Environmental Biology Bulletin 18, Perth, Australia.

Del Toro, I., R. R. Ribbons, and S. L. Pelini. 2012. The little things that run the world revisited. Myrmecological News 14: 133–146.

Devoto, F., and M. Rothkugel. 1936. Informe sobre los bosques del Parque Nacional Iguazú. Boletín del Ministerio de Agricultura de la Nación, Ciudad Autónoma de Buenos Aires.

Di Rienzo, J. A., F. Casanoves, M. G. Balzarini, M. Tablada, and C. W. Robledo. 2017. InfoStat. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina.

Ellison, A. M., S. Record, A. Arguello, and N. J. Gotelli. 2007. Rapid inventory of the ant assemblage in a temperate hardwood forest: species composition and assessment of sampling methods. Environ. Entomol. 36: 766–775.

Ellwood, M. F., N. Blüthgen, T. M. Fayle, W. A. Foster, and F. Menzel. 2016. Competition can lead to unexpected patterns in tropical ant communities. Acta Oecol. 75: 24–34.

Farji-Brenner, A., and A. E. Illes. 2000. Do leaf cutting ant nest make "bottom-up" gaps in neotropical rain forest?: a critical review of evidence. Ecol. Lett. 3: 219–227.

Farji-Brener, A. G., G. Barrantes, and A. Ruggiero. 2004. Environmental rugosity, body size and access to food: a test of the size-grain hypothesis in tropical litter ants. Oikos 104: 165–171.

Fernandes, I. O., M. L. De Oliveira, and H. C. Delabie. 2014. Description of two new species in the Neotropical *Pachycondyla foetida* complex (Hymenoptera: Formicidae: Ponerinae) and taxonomic notes on the genus. Myrmecological News 19: 133–163.

Fisher, B. L. 1999. Improving inventory efficiency: a case study of leaf-litter ant diversity in Madagascar. Ecol. Appl. 9: 714–731.

Fisher, B. L. 2005. A model for a global inventory of ants: a case study in Madagascar. Proceedings-California Acad. Sci. 56: 86–97.

Folgarait, P. J. 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. Biodivers. Conserv. 7: 1221–1244.

Foucaud, J., J. Orivel, D. Fournier, J. H. C. Delabie, A. Loiseau, J. Le Breton, P. Cerdan, and A. Estoup. 2009. Reproductive system, social organization, human disturbance and ecological dominance in native populations of the little fire ant, *Wasmannia auropunctata*. Mol. Ecol. 18: 5059–5073.

Fowler, H. G. 1985. Populations, foraging and territoriality in *Dinoponera australis* (Hymenoptera, Formicidae). Rev. Bras. Entomol. 29: 443–447.

Fowler, H. G., L. C. Forti, V. Pereira-da-Silva, and N. B. Saes. 1986. Economics of grass-cutting ants, pp. 18–35. *In* C. S. Lofgren, and R. K. Vander Meer (eds.), Fire ants and leaf-cutting ants: biology and management. Westview Press, Boulder, CO.

Franks, N. R., and W. H. Bossert. 1983. The influence of swarm raiding army ants on the patchiness and diversity of a tropical leaf litter ant community, pp. 151–163. *In* S. L. Sutton, T. C. Whitmore, and A. C. Chadwick (eds.), Tropical rain forest: ecology and management. Blackwell Scientific Publications, Oxford.

Giannotti, E., and V. L. L. Machado. 1992. Notes on the foraging of two species of Ponerinae ants: food resources and daily hunting activities (Hymenoptera, Formicidae). Bioikos 6: 7–17.

Godoy, B. S., and L. M. de Camargos. 2013. Does body size of neotropical ant species influence their recruitment speed? Biota Neotrop. 13: 91–96.

Gotelli, N. J. 2000. Null model analysis of species co-occurrence patterns. Ecology 81: 2606–2621.

Gotelli, N. J., and G. L. Entsminger. 2004. EcoSim: null models software for ecology. Version 7. Acquired Intelligence Inc. & Kesey-Bear. Jericho, VT 05465. http://garyentsminger.com/ecosim/index.htm.

Gotelli, N. J., A. M. Ellison, R. R. Dunn, and N. J. Sanders. 2010. Counting ants (Hymenoptera: Formicidae): biodiversity sampling and statistical analysis for myrmecologists. Myrmecological News 15: 13–19.

Graham, C. H., A. C. Carnaval, C. D. Cadena, K. R. Zamudio, T. E. Roberts, J. L. Parra, C. M. Mccain, R. C. K. Bowie, C. Moritz, S. B. Baines, et al. 2014. The origin and maintenance of montane diversity: integrating evolutionary and ecological processes. Ecography 37: 711–719.

Greenslade, P. J. M. 1973. Sampling ants with pitfall traps: digging-in effects. Insectes Soc. 20: 343–353.

Groc, S., J. H., Delabie, F. Fernandez, M. Leponce, J., Orivel, R. Silvestre, H. L. Vasconcelos, and A. Dejean. 2013. Leaf-litter ant communities (Hymenoptera: Formicidae) in a pristine Guianese rainforest: stable functional structure versus high species turnover. Myrmecological News 19: 43–51.

Hammer, Q., D. Harper, and P. Ryan. 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontol. Electron. 1: 9.

Hanisch, P. E., L. A. Calcaterra, M. Leponce, R. Achury, A. V. Suarez, R. R. R. Silva, and C. Paris. 2015. Check list of ground-dwelling ant diversity (Hymenoptera: Formicidae) of the Iguazú National Park with a comparison at a regional scale. Sociobiology 62: 213–227.

Hanisch, P. E., P. D. Lavinia, A. V. Suarez, D. A. Lijtmaer, M. Leponce, C. I. Paris, and P. L. Tubaro. 2017. Mind the gap! Integrating taxonomic approaches to assess ant diversity at the southern extreme of the Atlantic Forest. Ecol. Evol. 7: 10451–10466.

Harrison, S., and H. Cornell. 2008. Toward a better understanding of the regional causes of local community richness. Ecol. Lett. 11: 969–979.

Hölldobler, B., and E. O. Wilson. 1990. The ants. Harvard University Press, Cambridge, MA.

Jacquemin, J., Y. Roisin, and M. Leponce. 2016. Spatio-temporal variation in ant (Hymenoptera: Formicidae) communities in leaf-litter and soil layers in a premontane tropical forest. Myrmecological News 22: 129–139.

Jiménez, E., F. Fernández, T. M. Arias, and F. H. Lozano-Zambrano. 2008. Sistemática, biogeografía y conservación de las hormigas cazadoras de Colombia. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia.

Kaspari, M., and S. O'Donnell. 2003. High rates of army ant raids in the neotropics and implications for ant colony and community structure. Evol. Ecol. Res. 5: 933–939.

Kempf, W. W. 1962. Retoques à classificação das formigas neotropicais do gênero *Heteroponera* Mayr (Hym., Formicidae). Pap. Avulsos Zool. (São Paulo). 15: 29–47.

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). Stud. Entomol. 8: 161–200.

Kozak, K. H., and J. J. Wiens. 2012. Phylogeny, ecology, and the origins of climate-richness relationships. Ecology 93: 167–181.

Kugler, C., and W. L. J. Brown. 1982. Revisionary and other studies on the ant genus *Ectatomma*, including the descriptions of two new species. Search Agric. New York State Agric. Exp. Station. Ithaca. 24: 8.

Lach, L., C. L. Parr, and K. L. Abott. 2010. Ant ecology. Oxford University Press, Oxford.

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

Lattke, J. E., F. Fernández, and E. E. Palacio. 2007. Identification of the species of *Gnamptogenys* Roger in the Americas, pp. 254–270. *In* R. R. Snelling, B. L. Fisher, and P. S. Ward (eds.), Advances in ant systematics (Hymenoptera: Formicidae): Homage to E.O. Wilson – 50 Years of contributions. Memoirs of the American Entomological Institute, Gainesville, FL.

LeBrun, E. G. 2005. Who is the top dog in ant communities? Resources, parasitoids, and multiple competitive hierarchies. Oecologia 142: 643–652.

LeBrun, E. G., C. V. Tillberg, A. V. Suarez, P. J. Folgarait, C. R. Smith, and D. A. Holway. 2007. An Experimental study of competition between Fire ants and Argentine ants in their native range. Ecology 88: 63–75.

Lenhart, P., S. T. Dash, and W. P. Mackay. 2013. A revision of the giant Amazonian ants of the genus *Dinoponera* (Hymenoptera, Formicidae). J. Hymenopt. Res. 31: 119–164.

Longino, J. T., and R. K. Colwell. 1997. Biodiversity assessment using structured inventory: capturing the ant fauna of tropical rain forest. Ecol. Appl. 7: 1263–1277.

Longino, J. T., and F. Fernández. 2007. A taxonomic review of the genus *Wasmannia*, pp. 271–289. *In* R. R. Snelling, B. L. Fisher, and P. S. Ward (eds.), Advances in ant systematics (Hymenoptera: Formicidae): Homage to E.O. Wilson – 50 Years of contributions. American Entomological Institute, Gainesville, FL.

MacKay, W. P. 1996. A revision of the ant genus *Acanthostichus*. Sociobiology 27: 129–179.

Mackay, W. R. 2004. A new species of the ant genus *Acanthostichus* Mayr (Hymenoptera: Formicidae) from Paraguay, and a description of the gyne of *A. brevicornis* Emery. Proc. Entomol. Soc. Washingt. 106: 97–101.

MacKay, W. P., and E. Mackay. 2010. Systematics and biology of the New World ants of the genus *Pachycondyla* (Hymenoptera: Formicidae). Edwin Mellen Press, Lewiston, NY.

McCune, B., and M. J. Mefford. 1999. PC-ORD: multivariate analysis of ecological data. Version 5.0. MjM Softward, Gleneden Beach, Oregon.

Mittelbach, G. G., D. W. Schemske, H. V. Cornell, A. P. Allen, J. M. Brown, M. B. Bush, S. P. Harrison, A. H. Hurlbert, N. Knowlton, H. A. Lessios, et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecol. Lett. 10: 315–331.

O'Donnell, S., A. Kumar, and C. Logan. 2010. Army ant raid attendance and bivouac-checking behavior by Neotropical montane forest birds. Wilson J. Ornithol. 122: 503–512.

Ortíz Sepúlveda, C. M. 2012. Revisión taxonómica de las hormigas del género *Brachymyrmex* Mayr (Hymenoptera: Formicidae: Formicinae). Universidad Nacional de Colombia, Bogota, Colombia.

Pacheco, R., and H. L. Vasconcelos. 2012. Subterranean pitfall traps: is it worth including them in your ant sampling protocol? Psyche. 2012: 1–9.

Pinheiro, J., D. Bates, S. DebRoy, and D. Sarkar. 2014. R Core Team (2014) nlme: linear and nonlinear mixed effects models. R package version 3.1–117. Available at https://cran.r-project.org/web/packages/nlme/index.html.

Raimundo, R. L. G., A. V. L. Freitas, and P. S. Oliveira. 2009. Seasonal patterns in activity rhythm and foraging ecology in the neotropical forest-dwelling

ant, *Odontomachus chelifer* (Formicidae: Ponerinae). Ann. Entomol. Soc. Am. 102: 1151–1157.

R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ribas, C. R., and J. H. Schoereder. 2002. Are all ant mosaics caused by competition? Oecologia 131: 606–611.

Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. Ecol. Lett. 7: 1–15.

Rico-Gray, V., and P. S. Oliveira. 2007. The ecology and evolution of ant-plant interactions. University of Chicago Press, Chicago.

Rodrigues, M., E. Vilela, D. Azevedo, and R. Hora. 2010. Multiple queens in founding colonies of the neotropical ant *Pachycondyla striata* Smith (Formicidae: Ponerinae). Neotrop. Entomol. 40: 293–299.

Ronque, M. U. V., M. Azevedo-Silva, G. M. Mori, A. P. Souza, and P. S. Oliveira. 2015. Three ways to distinguish species: using behavioural, ecological, and molecular data to tell apart two closely related ants, *Camponotus renggeri* and *Camponotus rufipes* (Hymenoptera: Formicidae). Zool. J. Linn. Soc. 176: 170–181.

Sanabria-Blandón, C., and R. Achury. 2011. Army ants (Formicidae: Ecitoninae) in productive systems of Caquetá (Colombia). Acta Biológica Colomb. 16: 219–224.

Schmidt, F. A., and R. R. C. Solar. 2010. Hypogaeic pitfall traps: methodological advances and remarks to improve the sampling of a hidden ant fauna. Insectes Soc. 57: 261–266.

Silva, R. R. and C. R. F. Brandão. 2010. Morphological patterns and community organization in leaf-litter ant assemblages. Ecol. Monogr. 80: 107–124.

Spicer, M. E., A. Y. Stark, B. J. Adams, R. Kneale, M. Kaspari, and S. P. Yanoviak. 2017. Thermal constraints on foraging of tropical canopy ants. Oecologia 183: 1007–1017.

Srur, M., F. Gatti, V. Benesovsky, J. Herrera, R. Melzew, and M. Camposano. 2007. Identificación, caracterización y mapeo de los ambientes del Parque Nacional Iguazú. Centro de Investigaciones Ecológicas Subtropicales, Iguazú, Argentina.

Stein, A., K. Gerstner, and H. Kreft. 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecol. Lett. 17: 866–880.

Stone, L., and A. Roberts. 1990. The checkerboard score and species distributions. Oecologia 85: 74–79.

Stuble, K. L., M. A. Rodriguez-Cabal, G. L. McCormick, I. Jurić, R. R. Dunn, and N. J. Sanders. 2013. Tradeoffs, competition, and coexistence in eastern deciduous forest ant communities. Oecologia 171: 981–992.

Stuble, K. L., I. Juric, X. Cerda, and N. J. Sanders. 2017. Dominance hierarchies are a dominant paradigm in ant ecology (Hymenoptera: Formicidae), but should they be? And what is a dominance hierarchy anyways? Myrmecological News 24: 71–81.

Tillberg, C. V., B. Edmonds, A. Freauff, P. E. Hanisch, C. Paris, C. R. Smith, N. D. Tsutsui, B. D. Wills, S. E. Wittman, and A. V. Suarez. 2014. Foraging ecology of the tropical giant hunting ant *Dinoponera australis* (Hymenoptera: Formicidae)-evaluating mechanisms for high abundance. Biotropica 46: 229–237.

Underwood, E. C., and B. L. Fisher. 2006. The role of ants in conservation monitoring: if, when, and how. Biol. Conserv. 132: 166–182.

Weiser, M. D., N. J. Sanders, D. Agosti, A. N. Andersen, A. M. Ellison, B. L. Fisher, H. Gibb, N. J. Gotelli, A. D. Gove, K. Gross, et al. 2010. Canopy and litter ant assemblages share similar climate-species density relationships. Biol. Lett. 6: 769–772.

Wild, A. L. 2005. Taxonomic revision of the *Pachycondyla apicalis* species complex (Hymenoptera: Formicidae). Zootaxa 834: 1.

Wild, A. L. 2007. Revision of the ant genus *Linepithema* (Hymenoptera : Formicidae). pp. 126: 1–151. University of California Press, Berkeley, CA.

Wilkie, K. T. R., A. L. Mertl, and J. F. A. Traniello. 2007. Biodiversity below ground: Probing the subterranean ant fauna of Amazonia. Naturwissenschaften 94: 725–731.

Wilkie, K. T. R., A. L. Mertl, and J. F. A. Traniello. 2010. Species diversity and distribution patterns of the ants of Amazonian Ecuador. PLoS One 5: 1–12.

Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: patterns, scale, and synthesis. Annu. Rev. Ecol. Evol. Syst. 34: 273–309.

Wills, B.D., S. Powell, M.D. Rivera, and A.V. Suarez. 2018. Correlates and consequences of worker polymorphism in ants. Ann. Rev. Ent. 63: 575–598.

Wilson, E. O. 1971. The insects societies. Harvard University Press, Cambridge, MA.

Wirth, R., S. T. Meyer, W. R. Almeida, M. V. Araújo, V. S. Barbosa, and I. R. Leal. 2007. Increasing densities of leaf-cutting ants (*Atta* spp.) with proximity to the edge in a Brazilian Atlantic forest. J. Trop. Ecol. 23: 501.

Wong, M. K. L., and B. Guénard. 2017. Subterranean ants: summary and perspectives on field sampling methods, with notes on diversity and ecology (Hymenoptera: Formicidae). Myrmecological News. 25: 1–16.

Yamamoto, M., and K. Del-Claro. 2008. Natural history and foraging behavior of the carpenter ant *Camponotus sericeiventris* Guérin, 1838 (Formicinae, Campotonini) in the Brazilian tropical savanna. Acta Ethol. 11: 55–65.

Yanoviak, S. P., and M. Kaspari. 2000. Community estruture and the habitat templet: ants in the tropical forest canopy and litter. Oikos 89: 259–266.