Limited effects of dominant ants on assemblage species richness in three Amazon forests

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Abstract. 1. Ants are highly interactive organisms and dominant species are considered to be able to control the species richness of other ants via competitive exclusion. However, depending on the scale studied, inter-specific competition may or may not structure biological assemblages. To date, ant dominance–richness relationships have only been studied in small sample units, where a few dominant colonies could plausibly control most of the sample unit.

2. We conducted a comprehensive survey of terrestrial ant assemblages using bait, pitfall, and litter-sorting methods in three sites in Brazilian Amazonia. Using a spatially structured rarefaction approach, based on sampling units with linear dimensions ranging from 25 to 250 m, the mesoscale patterns of ant dominance–richness relationships (sampling units covering hundreds of meters separated by kilometers) were investigated.

3. Interference–competition models (parabolic or negative linear relationships between species richness and the abundance of dominant ants) tended to be more frequent in smaller sample units or in assemblages sampled with interactive methods, such as baits. Using more inclusive sampling methods, the relationship was generally asymptotic rather than parabolic, with no reduction in species diversity because of the presence of dominants. Random co-occurrence patterns of species within sites support the interpretation of a limited role for present-day competition in structuring these assemblages.

4. Competition from dominant species may reduce species richness in small areas, especially when artificial baits are used, but appears to be less important than environmental constraints in determining ant species richness across scales of hectares and greater in these Amazon forests.

Key words. Behavioural dominance, competition, co-occurrence, numerical dominance, spatial scale, tropical forest.

Introduction

The contribution of small and large scale process in structuring diversity remains a contentious topic in ecology. In some cases,

the patterns emerge from small-scale deterministic interactions that generate assembly rules operating over small spatial and temporal scales (Brown *et al*., 2002; Chase & Leibold, 2003; Ernest *et al*., 2008). In other cases, the pattern is the result of constraints or regional processes that occur over larger areas and through evolutionary time (Huston, 1999; Rosenzweig & Ziv, 1999; Ricklefs, 2004; Harrison & Cornell, 2008). While both local and larger-scale processes may influence community

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dynamics, different processes, acting at scales from local to regional, may interact to influence patterns of species diversity (Kaspari *et al.*, 2003; Resetarits, 2005; Sanders *et al.*, 2007). For example, competitors can be positively associated at large spatial scales because a common resource is aggregated (Giller & Doube, 1994; Inouye, 2005; Schellhorn & Andow, 2005), but, at smaller scales, they may use behaviour or microhabitat selection to avoid direct competition (Byers, 1989; Albrecht & Gotelli, 2001). Therefore, depending on the scale studied, inter-specific competition may or may not appear to structure biological assemblages (Ellwood *et al.*, 2009).

Ants are considered to be highly interactive organisms, with the capacity to alter the communities in which they occur (Room, 1975; Hölldobler & Lumsden, 1980; Porter & Savignano, 1990; Holway *et al.*, 2002). This extends to interactions among ant species, and dominant species may control the species richness of other ants in the community (Andersen & Patel, 1994; Morrison, 1996; Parr, 2008). Dominant ants, defined as locally abundant and behaviorally dominant species that can monopolise concentrated food sources for short periods of time (Parr & Gibb, 2010), can reduce the density of species over small spatial scales within the colony's foraging area (Andersen, 1992, 1997; Parr *et al.*, 2005). The number of species sampled by bait trapping in small plots often initially increases as the abundance of dominant species increases, probably as a result of passive sampling or an environmental-stress effect (Andersen, 1992; Parr *et al.*, 2005). This relationship breaks down at medium densities of dominants, presumably because dominant species reduce species richness when they are at higher densities (Savolainen & Vepsäläinen, 1988; Andersen, 1992; Morrison, 1996; Punttila *et al.*, 1996; Parr *et al.*, 2005; Baccaro *et al.*, 2010). Although dominant species attracted to baits may only affect the number of other species while the bait is present at that point in space (Andersen & Patel, 1994; Gibb & Hochuli, 2004; King & Tschinkel, 2006), similar patterns have been found for pitfall samples, suggesting that interference competition may scale up to a higher assemblage level (Parr, 2008).

Observations of behavioural dominance indicate that interference competition is common among ant assemblages over distances of tens of metres (Fellers, 1987; Cerdá *et al.*, 1998; Bestelmeyer, 2000; Albrecht & Gotelli, 2001); however, it does not necessarily follow that interference competition is an important determinant of ant communities at larger scales. The prediction of dominance–diversity relationships among regions is complicated by the effects of environmental variability. For example, the number of species could be limited by productivity (Kaspari *et al.*, 2000), habitat complexity (Farji-Brener *et al.*, 2004; Armbrecht *et al.*, 2006), frequency of stressful conditions (Majer & Delabie, 1994), regional species richness (Kaspari *et al.*, 2003), and anthropogenic disturbance (Gibb & Hochuli, 2003; King & Tschinkel, 2008), as well as the interactions between ant species (Morrison, 1996). To date, ant dominance–richness relationships have only been studied at small (Savolainen & Vepsäläinen, 1988; Andersen, 1992; Perfecto & Vandermeer, 1996; Parr, 2008; Baccaro *et al.*, 2010) or regional scales (Morrison, 1996; Parr *et al.*, 2005), all

based on small sample units (70–100 m in largest dimension), where a few dominant colonies could plausibly control most of the sample unit. Although the effects of interference competition may be important in structuring local assemblages, most community ecologists and land managers are interested in local effects that cover larger areas (hectares to dozens or hundreds of km^2). Therefore, it is important to determine whether the relationships that have been reported for small plots can be extrapolated to larger areas.

In the present study, we investigated the mesoscale patterns of ant dominance-richness relationships (sampling units covering hundreds of metres separated by kilometres) in three areas of Amazonian tropical forest that vary in topography, soils, climate, and vegetation structure. Using a spatially structured rarefaction approach, based on sampling units with linear dimensions ranging from 25 to 225 m, we examined how the sampling-unit size and sample technique (baits, pitfalls, and Winkler) alters the interpretation of these relationships. Independent of the exact form of the relationship, we predicted that the evidence of interference competition (negative or unimodal relationship between abundance of dominants and subordinate species richness) will be less evident in larger sampling units and for methods (pitfalls and Winkler) that do not experimentally induce small scale-interactions.

Material and methods

Study sites

The study was conducted in three Brazilian Biodiversity Research Program (PPBio) sites. Two of them (Maracá Ecological Station, 3°22′N, 61°27′W and Viruá National Park, 1°27′N, 61°01′W) are situated in forest reserves in Roraima State (extreme north of Brazil). The third (Reserva Ducke, 2°57′S, 59°56′W) is situated 25 km north of Manaus, central Amazonia (Fig. 1). The PPBio site at Viruá is located on low-lying plains subject to flooding, with some residual hills with moderate altitudes (elevation 48–130 m a.s.l.). The soil is predominantly sandy, poorly drained, and the flood regime is similar to that of the Rio Branco River (RADAMBRASIL, 1978), although most flooding is caused by local rainfall rather than the river. The Maracá site is located on an island in the Uraricoera River in Roraima State, which is at the confluence of savannas and the Amazon rainforest. The terrain is flat (elevation 55–83 m a.s.l.), with small intermittent streams. The site at Reserva Ducke is covered by relatively undisturbed upland ('terra-firme') forest on moderately rugged terrain (elevation 50–120 m a.s.l.), with small perennial streams in valleys. The sites cover a latitudinal gradient in Amazonian forests and encompass wide environmental heterogeneity, including areas of open and closed savannas, dense forests, and areas subject to different degrees of seasonal flooding (Table S1).

Sampling design

Each site contains a grid of six regularly spaced north-south and six east-west trails. Each trail is 5 km long, forming a
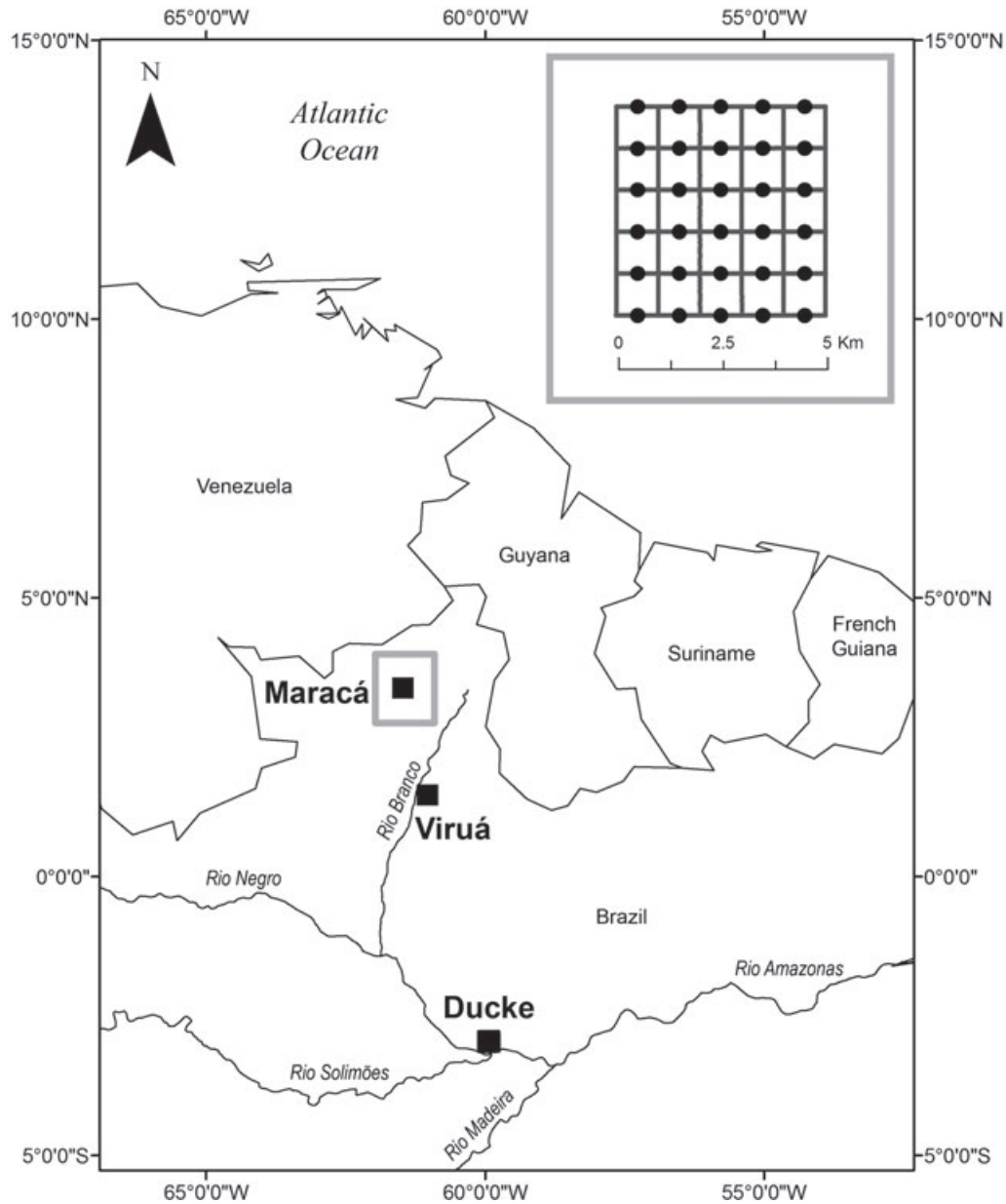
Fig. 1. Map of the study region. Squares represent the three sites sampled. In the detailed figure, the black circles represent the 250-m transects spatially arranged in a 5 × 5 km square grid.

5 × 5 km grid. The east–west trails have five 250-m-long plots that follow terrain contours (RAPELD method; Magnusson *et al.*, 2005). To minimise researcher disturbance along the centre lines, the vegetation is not cut, the contour line is marked with coloured plastic tape, and an upright PVC tube is placed on the ground at each 10-m interval to facilitate the collecting. As plot centre lines follow the contours lines, any variation in altitude within the plot is negligible, minimising the effects of topographical variation on ant community structure. In the present study, we used the plot centre lines as transects along which we sampled ants. A total of 30 equidistant (1 km) transects were sampled per site (Fig. 1).

Ant sampling

We sampled ants along the 30 transects per site. In each transect, 10 sampling stations were established at 25-m intervals. Each sampling station consisted of one pitfall trap, a 1-m² litter sample (Winkler sacks), and one sardine bait. In total, 300 subsamples for each sampling technique (Winkler, pitfall, and baits) were taken in each study site. These sampling methods are normally combined to describe diverse ant assemblages (Olson, 1991; Bestelmeyer *et al.*, 2000), and the sample sequence was organised to minimise disturbances by one technique on the others.

At each sampling station, 1 m² of sifted litter was collected through a 1-cm² mesh, placed in Winkler sacks, and hung in a room at an ambient temperature (about 28 °C) for 2 days to extract the ants. A 9.5-cm, internal-diameter pitfall trap, partially filled with 70% alcohol and a drop of detergent, was established adjacent (distant ∼2 m) to each litter sampling point and left for 48 h. After removing the pitfall traps, approximately 5 g of canned sardine was placed on a plastic card (10 cm by 7 cm) on the litter surface and after 45 min, all ants on the plastic card were collected and preserved in 70% alcohol. In order to minimise differences as a result of colony size and distance to the bait, and to facilitate comparisons with other studies, ants at baits were quantified on the six-point abundance scale proposed by Andersen (1997): 1 = 1 ant; 2 = 2–5 ants; 3 = 6–10 ants; 4 = 11–20 ants; 5 = 21–50 ants; 6 > 50 ants. The baiting and litter-sampling procedures were undertaken between 08.00 and 17.00 hours. The Ducke site was sampled in September 2006 and the Viruá and Maracá sites in February 2007, during the respective dry seasons.

The ants from the Winkler sacks, pitfall traps, and bait samples were identified to species or morphospecies, using specialised papers and the reference collection in the Entomological Collection of the Instituto Nacional de Pesquisas da Amazônia (INPA, Manaus, Brazil). A full reference collection for this material is deposited in the INPA Entomological Collection. The raw data are available in the PPBio website http://ppbio.inpa.gov.br.

Defining dominant species

We used a combination of numerical dominance (abundance at baits and species occurrence per site) and behavioural dominance (proportion of monopolised baits) to define the dominant species (Andersen, 1992; Parr *et al.*, 2005; Parr, 2008). A bait was considered monopolised if there were >20 individuals of the same species using the resource without the presence of other ants. Dominant ant species were considered to be those that monopolised >25% of the baits at which they occurred, and those with a mean abundance score (calculated by dividing the sum of the abundance score for the species at all baits per site by the number of baits at which the species was present) of >3. The mean abundance score of each species ranged from a possible minimum of one (always a single ant recorded whenever the species occurred) to a possible six (always >50 ants whenever the species occurred). These values were based on thresholds from previous studies, and our own field data (Andersen, 1997; Parr *et al.*, 2005; Parr, 2008; Baccaro *et al.*, 2010).

Data analysis

The number of subordinate species (defined as all non-dominant species) sampled by baiting, pitfalls, and litter sorting per transect were individually regressed against the sum of the abundance score of dominant species at baits, the abundance of dominant ant species in pitfall traps, and the abundance of dominant species in litter samples in linear and non-linear (logarithmic and quadratic) models. We used the number of subordinate species rather than the total number of species sampled, because the number of dominant species was correlated with the abundance of dominant species in all sampling techniques (baits: Pearson's $r = 0.478$, $P < 0.001$, pitfall: Pearson's $r = 0.485$, $P < 0.001$, and Winkler: Pearson's $r = 0.500$, $P < 0.001$). If more than one of the models revealed a significant relationship, they were compared using model fit, Fisher's statistic, and residual analyses to check the error distribution and the suitability of the model. To investigate whether responses varied between sites, we tested which models (linear, quadratic, and logarithmic) had a better fit within each site, and added site as a categorical variable in the best fit model for each sampling technique.

Litter samples from five transects at Ducke were damaged during transport. Therefore analyses for this site were based on the results for 30 transects sampled with sardine baits and pitfall traps, and for 25 transects sampled with the Winkler technique.

As the species found together in pitfall traps or in leaf-litter samples may have weak to no competitive interactions with dominant ants, we also used a subset of the subordinate species to investigate the effects of dominant species on a more interactive ant assemblage. The subset of subordinate species included all species sampled with baits that were obviously interacting with the dominant species, and the species sampled with the other methods that belong to the 'Large-sized epigaeic generalist predators', 'Medium-sized epigaeic generalist predators' and the 'Generalists: generalised dolichoderines, formicines, and myrmicines' according to the guild classification suggested by Silva and Brandão (2010). The subset of subordinate species that are more prone to interact with the dominant species was regressed against the sum of abundance of dominant ant species per transect in linear and non-linear (logarithmic and quadratic) models. As we were interested in the effects of interference competition at the assemblage level, we used the combination of Winkler and pitfall data for this analysis. The subset of subordinate species is listed in the Table S2.

To provide further understanding of the role of sampling scale on the relationship between abundance of dominant ants and the number of subordinate species, we tested the linear, parabolic, and asymptotic models after reducing the sample area (number of subsamples) for each transect using a spatially structured rarefaction approach. Each transect was initially composed of 10 subsamples with 25-m spacing, and in our rarefaction procedure we took randomly selected subsamples ranging from 1 to 9 continuous sampling stations. For example, when selecting three subsamples we randomly sampled one of the subsamples and selected the two adjacent subsamples (one to the left and one to the right side, or both on one side of the subsample randomly sampled). In this example, at the end of the first round of permutations, we had a matrix composed of three continuous sampling stations for each transect. We tested the three models (linear, quadratic or logarithmic) between the number of species and the abundance of dominant ants per transect. It is important to note that this procedure

keeps the original identity of the transect, so the number of subordinate species was only regressed against the abundance of dominant ants in the same transect. We ran this procedure 1000 times for each subsample size (ranging from one to nine sampling units) and for each sampling technique separately. We compared the three models for each subsample size using Akaike's Information Criterion (AIC). This technique was used to evaluate which of the three models had a better fit for a given subsample size. We plotted the percentage of better-fit linear, asymptotic, and quadratic models from the spatially structured randomisations against the number of subsamples per transect. All analyses were undertaken using R software (R Development Core Team, 2009).

We tested for non-random patterns of species co-occurrence to evaluate if deterministic assembly rules, such as those resulting from competition, may be occurring at the site scale (Gotelli, 2000). The subset of the species pool included the subordinate species selected for the dominance-richness models and the dominant species. A presence–absence matrix was produced where each row was a different species, and each column was a different transect within that study site, for each sampling technique and for the subset of species pool. As the Viruá site had a mixture of closed and open vegetation types that may be a strong structuring factor for ant assemblages (see Table S1), the patterns of species co-occurrence within the vegetation types (forest, open, and closed savannas) were also investigated. The C-score, which measures the tendency for species to segregate in space, was used to quantify co-occurrence (Stone & Roberts, 1990). A larger C-score than that of a randomly assembled community is expected if a community is structured by competition. For each presence–absence matrix, 5000 random matrices were produced by permutation using a fixed algorithm that retains the row and column sums of the original matrix (Gotelli, 2000). All null-model analyses were conducted with Ecosim Version 6.0 (Gotelli & Entsminger, 2001), which calculated the C-score values for each randomly permuted matrix, and then determined the probability of encountering the observed matrix by comparing it with the simulated values. In contrast to the regression analyses, co-occurrence analysis does not account for differences in abundances in transects (Gotelli, 2000). Therefore, this analysis avoids the possibly circular argument of including species relative densities as a part of the definition of dominance and as a measure of co-occurrence. In this regard, co-occurrence analysis is an alternative strategy to investigate the role of competition in structuring those assemblages that does not focus only on interference competition.

Results

A total of 123 ant species was recorded at baits with 58, 59, and 68 species sampled at the Viruá, Maracá and Ducke sites, respectively. Eight species, belonging to four genera (*Cremato-gaster*, *Pheidole*, *Solenopsis*, and *Wasmannia*), were identified as dominant species because they were responsible for most bait monopolisation (66%), had mean abundance scores >3, and were recorded in more than 5% of baits within the sites (Table 1). As we used a classification within sites, some dominant species did not reach all dominance threshold levels in one or two sites (i.e. percentage of monopolised baits of *Crematogaster brasiliensis* Mayr at Ducke, or percentage of baits with *C. limata* Smith at Maracá). However, in spite of the geographical coverage of the present study, the dominant species classifications for the more forested areas of Ducke and Maracá were similar. The relative environmental similarity between the Ducke and Maracá sites was also reflected in other dominance metrics. Around half of the baits offered were monopolised at Ducke and Maracá (56% and 43%, respectively), whereas only 20% of baits were monopolised at Viruá. Only 9% and 10% of baits were not visited after 45 min of exposure at Ducke and Maracá, respectively, but approximately 29% of baits were not visited during the bait session at Viruá. In general, dominant species represented 67% of the individuals sampled with baits,

Table 1. The occurrence of dominant and a summary of the occurrence of some subordinate ants species at baits in three Amazonian forests: Viruá, Maracá, and Ducke.

Species	Percentage of bait recorded			Mean abundance score			Percentage of baits monopolized		
	Viruá	Maracá	Ducke	Viruá	Maracá	Ducke	Viruá	Maracá	Ducke
Dominant									
Crematogaster brasiliensis	5.16	4.43	18.91	2.18	3.25	3.46	0.00	41.67	36.54
Crematogaster limata	4.23	1.48	9.09	2.33	2.50	3.24	11.11	75.00	24.00
Crematogaster tenuicula	8.45	8.49	52.00	1.89	3.00	3.71	11.11	30.43	45.45
Pheidole sp. 13	4.23	9.23	8.00	4.22	4.28	4.23	55.56	64.00	54.55
Pheidole sp. A	13.62	–	–	3.21	–	–	31.03	–	–
Pheidole sp. Ptrm	–	8.12	–	–	4.05	–	–	45.45	–
Solenopsis geminata	1.88	18.08	–	3.00	4.22	–	25.00	71.43	–
Wasmannia auropunctata	3.76	5.54	5.09	2.38	3.53	3.86	12.50	60.00	50.00
Subordinate									
Ectatomma lugens	5.82	8.36	0.73	1.25	1.35	1.00	0.00	0.00	0.00
Ochetomyrmex semipolitus	2.55	3.64	–	2.71	4.20	–	14.29	50.00	–
Pachycondyla constricta	1.09	1.09	0.73	1.33	1.33	1.50	0.00	33.33	0.00
Pheidole sp. 25	–	7.01	1.09	–	5.00	3.00	–	66.67	21.05

Abundance scale: 1 = 1 ant; 2 = 2–5 ants; 3 = 6–10 ants; 4 = 11–20 ants; 5 = 21–50 ants; 6 > 50 ants.

Table 2. A summary of inter-specific encounters between dominant and subordinate species at baits in three sites at Central Amazonia.

Dominant species	Number of baits (%)		Total encounters	Number of species interacting
	Subordinate > double of dominant	Dominant > double of subordinate		
Crematogaster brasiliensis	13 (25.49)	26 (50.98)	51	30
Crematogaster limata	3 (21.43)	8 (57.14)	14	12
Crematogaster tenuicula	31 (25.00)	52 (41.94)	124	50
Pheidole sp. 13	2 (8.70)	6 (26.09)	23	14
Pheidole sp. A	4 (19.05)	11 (52.38)	21	11
Pheidole sp. Ptrm	4 (23.53)	13 (76.47)	17	10
Solenopsis geminata	20 (41.67)	28 (58.33)	48	28
Wasmannia auropunctata	8 (30.77)	18 (69.23)	26	16

but only 25% and 46% of individuals sampled with pitfall and Winkler sacks, respectively.

Although behavioural dominance between all possible pairs of species was not tested directly, the dominant species were consistently more abundant than the subordinate species at baits which were not monopolised (Table 2). The dominant species interacted with 75 subordinate species, which represented approximately 60% of all species sampled with baits. Furthermore, we observed aggressive behaviours documented in previous studies for all dominant species (Clark *et al.*, 1982; Risch & Carroll, 1982; Longino, 2003; Le Breton *et al.*, 2005). The workers of *Crematogaster limata*, *C. tenuicula* Forel, and *C. brasiliensis* usually aggregate around the bait, raise, and shake their gasters in the air and exude a droplet of venom. This behaviour was normally directed towards other species that tried to get access to the bait. The workers of the *Pheidole* species defended the bait by running around and over the bait, and biting workers of other species that tried to reach it. The workers of *Solenopsis geminata* Fabricius used a mixture of those behaviours. They usually ran around the bait keeping their gaster close to the ground, probably depositing pheromone. The smaller dominant species, *Wasmannia auropunctata* Roger, normally monopolised the bait by massive recruitment and defending the position by crouching close to the ground with the antennae and legs close to the body.

Subordinate species were those with no mass recruitment behaviour (e.g. *Ectatomma lugens* Emery and *Pachycondyla constricta* Mayr), or species with monopolisation abilities, but low occurrences (e.g. *Ochetomyrmex semipolitus* Mayr and *Pheidole* sp. 25). As we used a combination of numerical and behavioural dominance, species with recruitment and monopolisation abilities but low occurrences were classified as subordinate. The potential behavioural displacement of those species was restricted to small portions of the forest floor and they probably interact with fewer species compared with those we classified as dominants.

A total of 301 species, and 39 166 individuals were collected in pitfall traps (129, 195, and 209 species recorded in the Viruá,

Maracá, and Ducke reserves, respectively). The number of species that occurred in more than one site was relatively high, varying from 40% between Viruá and Ducke to 58% between Viruá and Maracá in pairwise comparisons. Litter sorting (Winkler samples) collected 5333 individuals and 130 species (22, 35, and 108 species recorded in the Viruá, Maracá, and Ducke sites, respectively). The assemblage sampled by litter sorting had less overlap between sites than pitfall traps, varying between 13% between Viruá and Ducke to 34% between Viruá and Maracá in pairwise comparisons.

Dominance–richness relationships

The relationship between the abundance of dominant ants and the number of subordinate species at baits across the three sites (Fig. 2) was better described by a unimodal curve ($y = -0.002x^2 + 0.108x + 6.275$) than linear or asymptotic relationships (Table 3). However, at the assemblage level, data from pitfall traps, litter sorting, and the subset of the subordinate species (Fig. 2) indicated that the relationship between the abundance of dominant ants and species richness across all sites was better described by an asymptotic relationship [$y = 18.622 + 3.368 \times \log(x + 1)$, $y = 0.866 + 3.600 \times \log(x + 1)$ and $y = 7.069 + 3.716 \times \log(x + 1)$, respectively] than linear or quadratic fits (Table 3).

Site and abundance of dominant ants had significant effects on subordinate species richness for all sampling techniques, but no interaction between the explanatory variables was detected (Table S3). Within sites, the relationship between dominant and subordinate species sampled with pitfall traps at Maracá was better described as asymptotic ($r^2 = 0.257$; $F_{1,28} = 9.683$, $P = 0.004$) than linear or unimodal ($r^2 = 0.125$; $F_{1,28} = 3.999$, $P = 0.055$ and $r^2 = 0.239$; $F_{1,27} = 4.258$, $P = 0.0244$, respectively). Similarly, the relationship between dominant species and the subset of subordinate species that are more prone to interact with the dominant ants in Viruá was also better described as asymptotic ($r^2 = 0.168$; $F_{1,28} = 5.683$, $P = 0.024$) than linear or unimodal ($r^2 = 0.135$; $F_{1,28} = 4.377$, $P = 0.045$ and $r^2 = 0.2$; $F_{1,27} = 3.378$, $P = 0.049$, respectively). Ducke was the only site that did not show significant relationships (linear, quadratic or logarithmic) between subordinate and dominant species sampled for any method.

The quadratic relationship between the abundance of dominant species and the number of subordinate species sampled with baits had a better fit in models that used six or more continuous subsamples within a transect (>125 m). As the sampling unit was reduced, the linear model tended to have a better fit (Fig. 3). In cases where the size of the sample unit ranged from 25 to 100 m, the linear relationship between the number of subordinate species and the abundance of dominant species was negative in 8985 out of 9000 randomisations (99.8%). For bait data, the asymptotic model always provided the poorest fit for any size of sampling unit.

The relationships between the number of subordinate species and the abundance of the dominant species for pitfall and
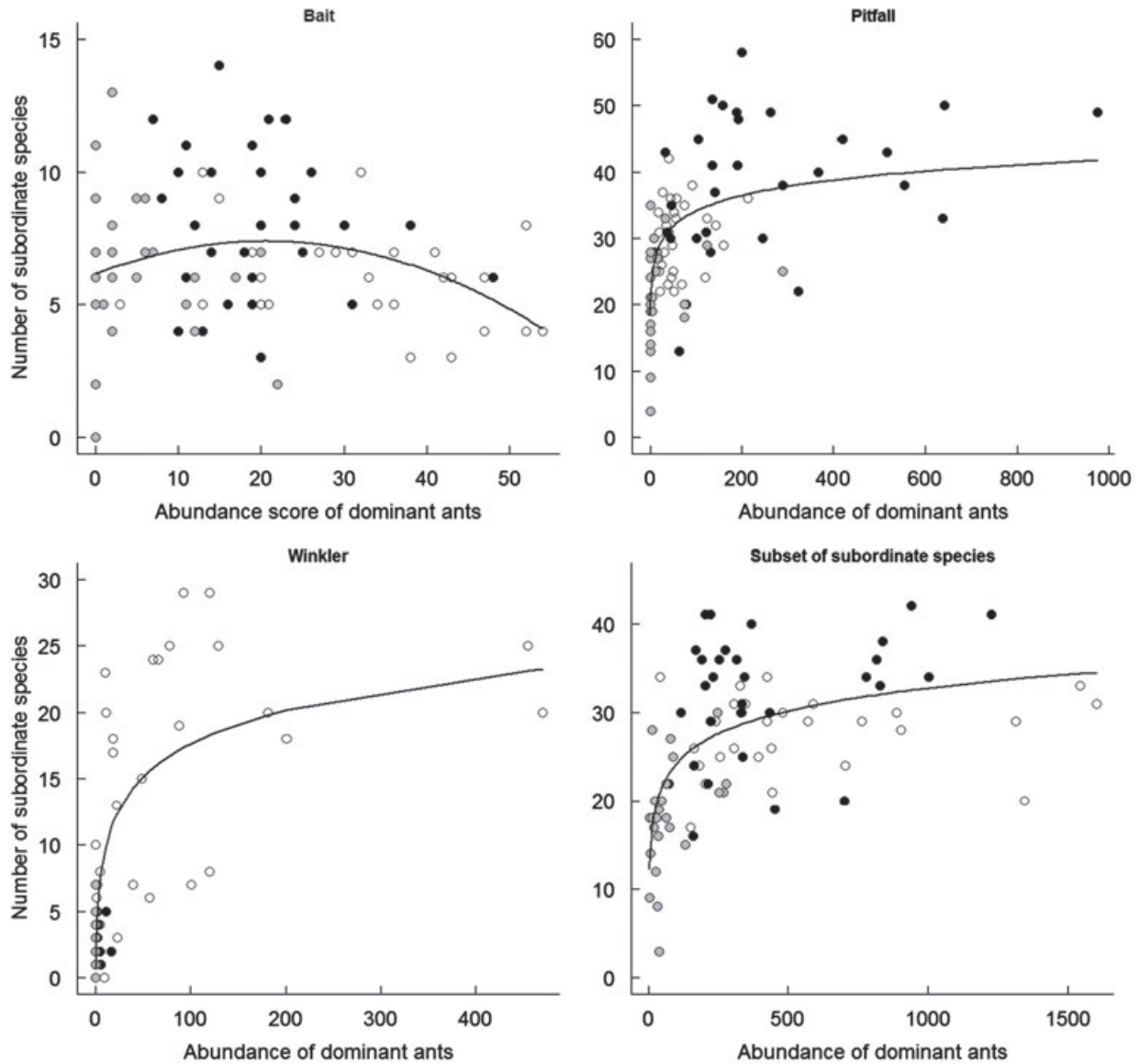
Fig. 2. The relationship between the abundance of dominant ants and the number of subordinate species across three sites at Central Amazonia, using baits, pitfalls, Winkler data, and a subset of subordinate species that are more prone to interact with dominant ants. The subset of subordinate species used data from pitfall and Winkler sampling techniques combined. Grey circles represent Viruá transects, black circles Maracá transects, and open circles Ducke transects.

Table 3. Models for the effects of abundance of dominant species on the number of subordinate ant species across three sites (Viruá, Maracá, and Ducke) at Central Amazonia.

Methods	Linear		Quadratic		Logarithmic	
	r^2	F	r^2	F	r^2	F
Bait	0.00	0.81	0.07[*]	3.36	0.00	0.32
Pitfall	0.28[***]	33.96	0.34[***]	22.38	0.42[***]	65.52
Winkler	0.37[***]	49.68	0.60[***]	61.01	0.65[***]	157.2
Subset of species pool	0.17[***]	17.41	0.30[***]	17.72	0.36[***]	46.98

[*]$P < 0.05$; [***]$P < 0.001$.

Winkler data varied similarly at the same subsample sizes. In both methods, the asymptotic model always fitted best (Fig. 3). However, small samples had a high proportion of simulations in which the quadratic model fitted better. The linear model had the poorest fit for pitfall and Winkler data for all subsample sizes.

The asymptotic models always showed the best fit for the relationship between the subset of subordinate species and abundance of the dominant species. However, in this case, the quadratic model had the poorest fit, and, as the sampling unit was reduced, the frequency in which the linear model had a better fit increased (Fig. 3). In contrast to bait data, the
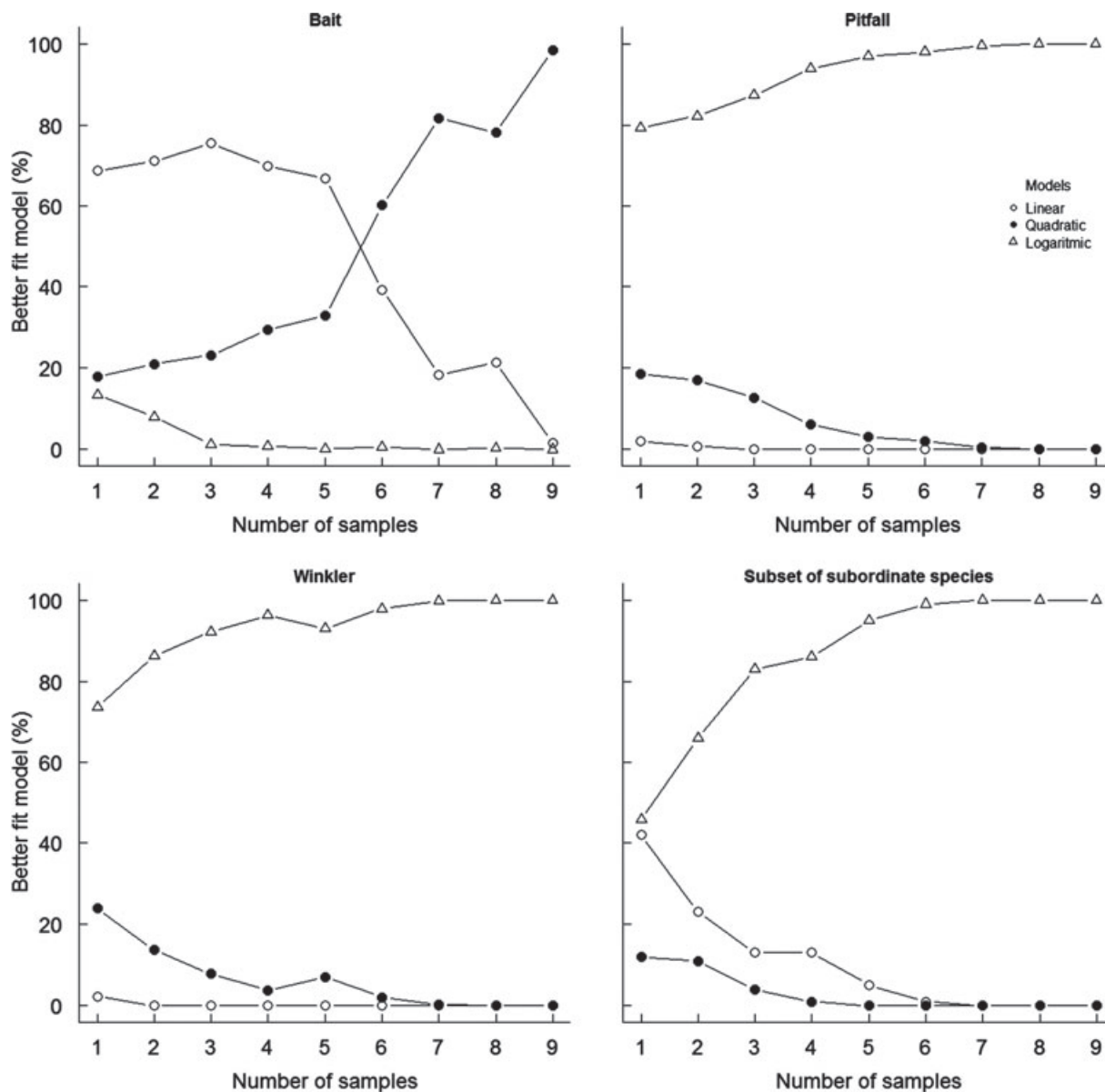
Fig. 3. The percentage of better-fit linear, asymptotic, and quadratic models applied to data from 1000 spatially-structured randomisations for each subsample, using baiting, pitfall trap, Winkler data, and for a subset of subordinate species that are more prone to interact with dominant ants. The subset of subordinate species used data from pitfall and Winkler sampling techniques combined. The subsamples were distributed along 225 m and spaced 25 m apart.

linear relationship between number of species in the subset of subordinates and abundance of dominant species was positive in 8768 out of 9000 randomisations (97.4%), showing a similar trend to the asymptotic model.

Co-occurrence analyses within sites indicated random co-occurrence patterns (Table 4). Only the Viruá assemblage sampled with pitfalls and the subset of the species pool had significantly less co-occurrence than expected by chance. However, within the three vegetation types at Viruá (forest, open savanna, and closed savanna), co-occurrence patterns were not significantly different from random (Table 4).

Discussion

The relationships between dominance and the number of subordinate species differed between baits and other sampling techniques. As in other studies, bait data showed a uni-modal relationship, where highest species richness occurs at intermediate dominance levels, and as the abundance of domi-nant ants increases, species richness declines (Andersen, 1992; Parr *et al.*, 2005). Recently, Parr (2008) found the full unimodal dominance–richness relationship with pitfall-trap data, suggest-ing that the processes found at baits may sometimes extend to

Table 4. Patterns of species co-occurrence for ant assemblages in three Amazonian Reserves, and by vegetation type in the PPBio grid at Viruá National Park using bait, pitfall, litter sorting (Winkler) data, and a subset of the total species pool that are known or assumed to interact with the dominant species.

Sites	Bait		Pitfall		Winkler		Subset of species pool	
	C-score obs.	C-score exp.	C-score obs.	C-score exp.	C-score obs.	C-score exp.	C-score obs.	C-score exp.
Viruá	7.099	7.150	10.217[*]	10.116	2.341	2.366	11.996[***]	11.865
Forest	4.226	4.263	5.86	5.821	1.467	1.531	6.290	6.273
Closed savanna	1.061	1.060	0.844	0.854	0.200	0.200	0.927	0.939
Open savanna	0.769	0.818	0.984	0.962	—[†]	—[†]	0.894	0.856
Maracá	11.159	11.199	9.872	9.907	5.398	5.415	13.134	13.107
Ducke	7.414	7.401	10.022	10.001	6.204	6.246	11.088	11.071

[*]$P < 0.05$; [***]$P < 0.001$.
[†]All open savanna transects shared the same species.

the larger pool of species with which the dominant species are likely to interact. However, using pitfall, litter-sorting data, and a subset of the species pool that are more prone to interact with dominant species, we found an asymptotic relationship between the abundance of dominant ants and the number of subordinate species. These models did not show the descending portion of the dominance–richness relationship normally attributed to competitive exclusion of subordinate by dominant species (Savolainen & Vepsäläinen, 1988; Morrison, 1996; Parr, 2008), suggesting that interference competition does not have a strong effect in these Amazonian forests.

Different sampling techniques may lead to contradictory conclusions regarding the role of inter-specific competition in these Amazon forests. Our data for more inclusive sampling techniques suggest that the abundance of dominant ants has little effect on the number of species in ant assemblages. In contrast, using data collected with baits, which induce interactions between colonies, interference-competition models between the abundance of dominant ants and species richness fitted better than alternative models for all scales studied. Bait data may have limited relevance to conclusions about competition among ant species at the population level (Ribas & Schoereder, 2002). Baits mainly attract omnivorous species (Bestelmeyer *et al.*, 2000) that normally forage more intensely for closer (Davidson, 1998) and better-quality resources (Kay, 2004). The bait density also may change the strength of interference competition, facilitating the co-occurrence of species in areas where resources are more dispersed (Lester *et al.*, 2010). Furthermore, as baits represent only momentary interactions, differences in foraging time or microhabitat selection that avoid direct competition may be underestimated (Cerdá *et al.*, 1997; Albrecht & Gotelli, 2001). Consequently, as many mechanisms facilitating co-occurrence may be operating at the same time, the observation of displacement of subordinate by dominant species at artificial baits does not necessary imply that these species compete strongly at the population level (Andersen & Patel, 1994; Ribas & Schoereder, 2002).

The area sampled may explain part of the variation and the poor fit of the correlation between the abundance of dominant species and the number of subordinate species sampled at baits. Larger sampling units are expected to be more heterogeneous,

favouring patchy distributions of dominant species. Therefore, high or low numbers of subordinate species at baits may occur, especially in transects with low abundance of dominants, and the variation in the number of subordinate species seems to be constrained in transects with a high abundance of dominants probably as a result of stronger interference competition. In bait samples, as the number of subsamples becomes smaller, the behavioural effect of the dominant species becomes larger. In models using samples covering less than 100 m in the largest dimension, linear relationships (99.7% negative) are more common than the unimodal models, suggesting a stronger effect of interference competition between dominant and subordinate species. These results are probably influenced by the colony sizes of dominant species. Nests of *Crematogaster tenuicula* or *Wasmannia auropunctata*, both classified as dominant species in the present study, may cover distances of 30 m or more. These species increase their foraging area by building polydomous nests, in which the colonies have several nesting sites (Clark *et al.*, 1982; Longino, 2003). Therefore, competitive exclusion is expected to be high within foraging areas of these colonies.

However, the effect of the competitive exclusion within foraging areas of dominant species was not detected in more inclusive sampling techniques, even for smaller sampling units. The probability of detecting a quadratic relationship between the abundance of dominant ants and the number of subordinate species was greater in smaller sampling units, but non-competitive models always had the best fit for pitfall, Winkler data, and for the subset of subordinate species. In contrast to bait data, most of the linear relationships between the subset of subordinate species and the abundance of dominant ants were positive (97.4%). Although, dominant species may decrease the fitness and the abundance of subordinate species at the colony level (Savolainen, 1990, 1991), relatively short-term manipulative experiments (2–12 months) suggested a limited role of competition between dominant and other ant species at the population level (Andersen & Patel, 1994; Gibb & Hochuli, 2004). The exclusion of a dominant species did not change the abundance of other species (King & Tschinkel, 2006) or led to changes only in the abundance of behaviourally and ecologically similar species (Gibb & Hochuli, 2004; Gibb, 2005; but see King & Tschinkel, 2008).

Co-occurrence analyses that did not account for differences in abundances indicated random co-occurrence patterns in all sites for all sampling techniques. The structured co-occurrence matrix for Viruá pitfall data, and for the subset of the ant assemblage with potentially frequent interactions with dominants, probably reflects the high environmental variability within this site. High heterogeneity may constrain co-occurrence of some species owing to environmental requirements, and result in a structured matrix (Simberloff & Martin, 1991; Wright *et al.*, 1998). Some species may be associated with different environmental features of the sampling units, which lead to less co-occurrence than expected by chance. When the Viruá transects were grouped by vegetation type, the co-occurrence matrix did not differ from randomly generated matrices, suggesting that, for this highly stressful site, environmental constraints may be more important than present-day interference competition among dominant and subordinate ant species. We can think of two plausible alternatives to explain why we find evidence of limited effects of dominant ants on assemblage species richness in these forests: (i) the dominant species are not truly dominant; and (ii) the environmental gradient is not long enough to show the full unimodal relationship.

At a global scale, the dominant species in this study can be classified as Generalised Myrmicinae, which recruit quickly and defend clumped food resources, but usually present submissive behaviour when confronted by 'Dominant Dolichoderinae' species (Andersen, 1997). In the Neotropics, species of the Dominant Dolichoderinae are generally restricted to the canopy or open environments rather than the floor of tropical forests (Andersen, 2000). However, the eight Generalised Myrmicinae species that were responsible for most bait monopolisation, were more abundant than subordinate species at baits, and the observed aggressive behaviours suggest that those species are behaviourally dominant rather than better resource discoverers. The negative relationships between dominance levels and the number of subordinate species in smaller sampling units using bait data, also suggests competitive exclusion of subordinate by dominant species. Although the level of behavioural dominance may be relatively lower, the species classified as dominant in these Amazon forests, appear to play a similar role to Dominant Dolichoderinae in other regions.

The full relationship between dominant ants and species richness is better detected across a wide range of environments that covers different stressful conditions and productivity for ants (Andersen, 1992; Parr, 2008). Partial sampling may only produce part of the relationship, such as the descending portion of the curve (Baccaro *et al.*, 2010), or the ascendant part of the relationship, normally attributed to a combination of species-frequency distributions and environmental stress (Parr *et al.*, 2005). As predicted, the full relationship was apparent for pitfall data at Maracá and for the subset of subordinate species at Viruá, probably because those sites combine areas with low to high levels of stressful conditions for ants. However, in Maracá, the number of subordinate species did not decrease as the abundance of the dominant ants increased. Instead, the number of subordinate species increased slowly as the abundance of dominant species increased.

The same positive correlation between the abundance of dominants and subordinate species was found at the Viruá site, but the amplitude of both variables was smaller. The high environmental stress experienced by ants at Viruá, such as flooding during the wet season and high desiccation risk during the dry season, may be responsible for the reduced abundance of ants, including dominant species sampled by non-interactive methods. In more favourable environments (i.e. less seasonal flooding and relatively short dry season), such as the Ducke site, the abundance of dominant species with pitfall and Winkler data was more than 2 and 10 times higher than in Viruá, respectively. In spite of the fact that the three sites had a wide range of natural variation in tree density, rainfall regimes and dry-season length, there was little evidence for interference competition structuring assemblage richness within and between sites.

Overall, the present results are consistent with a limited role of competition between dominant and subordinate ant species in these Amazon forests. Although some support for competition was found for bait data, most of our results suggest that both dominant and subordinate species were probably responding similarly to changes in abiotic conditions (more evident at the Viruá site). The positive correlation between the abundance of dominant species and subordinate species richness reported here has been detected previously in a meta-analysis across an environmental gradient of stressful conditions for ants in Australia (Andersen, 1995). However, a novel feature of our results is that environmental constraints may be more important than interference competition from small to large sampling units, across scales of tens to hundreds of hectares in these Amazon forests. Further studies are needed to identify which environmental factors decrease diversity and abundance of ants in these forests, and to investigate how they operate across different spatial scales.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/j.1365-2311.2011.01326.x

Table S1. Type of vegetation, vegetation density, soil characteristics, rainfall, stream seasonality and flooded area (mean ± SE) in the three sites (Viruá, Maracá, and Ducke) in the Brazilian Amazon.

Table S2. Subordinate species occurrence per sampling technique (+) included in the subset of subordinate species.

The subset of subordinate species included all species sampled with baits, and the species that belong to the 'Large-sized epigaeic generalist predators', 'Medium-sized epigaeic generalist predators', and the 'Generalists: generalised dolichoderines, formicines, and myrmicines' according to the guild classification suggested by Silva and Brandão (2010).

Table S3. Summary statistics for the effects of abundance of dominant ants and site on the subordinate species richness and a more interactive subset of subordinate species in three Amazon forests. The results were given per sampling technique and the subset of subordinate species used pitfall and Winkler data combined. Significant values are in bold.

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