Resource distribution and soil moisture content can regulate bait control in an ant assemblage in Central Amazonian forest

FABRICIO BEGGIATO BACCARO,[1]* SUZANA MARIA KETELHUT[2] AND
JOSÉ WELLINGTON DE MORAIS[3]

[1]*Programa de Pós-Graduação em Entomologia, Coordenação de Pesquisas em Entomologia, Instituto Nacional de Pesquisas da Amazônia, CP 478, Manaus 69060-020 (Email: fabricera@gmail.com),* [2]*Tropical Ecology, Assessment, and Monitoring (TEAM) Initiative – Ant Monitoring Protocol, and* [3]*Coordenação de Pesquisas em Entomologia, Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil*

Abstract Resources influence population growth, interspecific interactions, territoriality and, in combination with moisture content, affect terrestrial arthropod distribution and abundance. Ants are usually described as interactive and compete in transitive hierarchies, where the dominants behaviourally exclude subordinate species from food resources. In this study, we evaluated the effects of (i) dominant ants, soil moisture and an artificial resource gradient on the number of ant species attracted to baits; and (ii) how soil moisture and an artificial resource gradient change the number of controlled baits in a Central Amazonian rain forest. We sampled 30 100-m-long transects, located at least 200 m apart. The transects were established with six different bait densities varying between six and 41 baits and the soil moisture content was measured at 10 points for each transect. Six ant species were considered dominant, and had negative correlations with the number of species at baits ($r^2 = 0.186$; $F_{1,28} = 6.419$; $P = 0.017$). However, almost half of the transects showed low abundance of dominant species (<30%), and relatively high number of species (mean of 20.1 ± 8.75). Resource availability and soil moisture had negative and positive correlations, with number of controlled baits. These results suggest that, even though the dominance is relatively poorly developed on the floor of this tropical forest, both resource availability and soil moisture affect resource control, and thus, the number of species that use baits.

Key words: ant community, competition, dominance, species richness, tropical forest.

INTRODUCTION

In a given community, one or several dominant species overshadow all others in their mass and biological activity, and may strongly affect environmental conditions for other species (Whittaker 1965). Understanding the effect of dominant species on diversity and species richness is fundamental for studies of resource availability (Tilman 1984), community dynamics (Connel & Lowman 1989) and habitat disturbance (Huston 1979), and has been a recurring theme in ant community ecology for several decades (Savolainen & Vepsäläinen 1988; Andersen 1992; Morrison 1996; Ribas & Schoereder 2002; Hoffmann & Andersen 2003; Gibb & Hochuli 2004; Parr *et al.* 2005; Parr 2008).

Dominant ant species can interfere with the foraging of other species (Savolainen & Vepsäläinen 1988) and often regulate community structure (Porter & Savignano 1990; Andersen 1992). In open forests and savannas in Australia, North America and South Africa, the number of ant species foraging at rich food sources is regulated by dominant species in a manner analogous to humped diversity models applicable to communities of plants and sessile marine invertebrates (Andersen 1992; Parr *et al.* 2005). The ascending part of the curve is thought to correspond to increasing habitat favourability for ants, showing low dominance and less species richness (Andersen 1995; Parr 2008). The descending portion of this relationship is attributed to an increase in the abundance of dominant ants, which reduce species richness via competitive exclusion (Andersen 1992; Morrison 1996; Parr 2008). However, in undisturbed areas, dominant species do not always regulate ant community structure (Floren & Linsenmair 2000; Gibb & Hochuli 2004) and the role of other important factors, such as soil moisture and food availability remain to be studied.

For arid and semi-arid environments, several studies have demonstrated that dominant species predominate

under conditions of low stress (e.g. low desiccation risks) and subdominant species exhibit a broad climatic tolerance (Cerdá *et al.* 1997, 1998; Bestelmeyer 2000). Humidity can influence composition and activity of terrestrial ant species even in tropical ecosystems, with an increase in ant activity in more humid seasons and habitats (Levings 1983; Kaspari 1996b; Kaspari & Weiser 2000; Hahn & Wheeler 2002). Terrestrial ants probably reduced their activity levels in response to a combination of resource limitation and increased desiccation risk because the activity of most litter arthropods is positively correlated with soil moisture (Levings & Windsor 1982, 1984).

The distribution of resources affect foraging behaviour, and ant colonies forage more intensely for closer and more abundant resources (Davidson 1977; Bernstein 1979; Sanders & Gordon 2002). Such responses to resource variation can result in many competitive outcomes (i.e. the ability to locate resources and the ability to monopolize resources once located) that affect the species dominance hierarchy (Fellers 1987; Savolainen & Vepsäläinen 1988; Hölldobler & Wilson 1990). Studies linking foraging strategies to resource distribution normally target the population level (Bernstein 1979; Deslippe & Savolainen 1994; Sanders & Gordon 2002) and little information is available about how control abilities respond to changes in resource distribution in ant communities (but see Sanders & Gordon 2003).

Changes in the abundance of dominant ants, mediated by changes in food availability or moisture content may have important effects on terrestrial ant assemblages, because dominant ants interfere with the foraging of other species. In this paper, we evaluated the effects of dominant ants, soil moisture and an artificial resource gradient on the number of ant species using baits in a Central Amazonian rain forest, and how soil moisture and the resource gradient affect the number of controlled baits in this forest.

MATERIAL AND METHODS

Study site

The study was conducted in the Tropical Ecological Assessment Monitoring (TEAM) site, situated in forest reserve 3402 (Cabo Frio) of the Biological Dynamics of Forest Fragments Project (BDFFP) (59°54′59″W; 2°23′37″S), about 80 km northeast of Manaus. The site is in relatively undisturbed upland (terra-firme) forest on moderately rugged terrain (elevation 50–120 m a.s.l.), with small streams in the valleys. The flora is extremely diverse, with approximately 1000 species of trees. The canopy height is about 35 m, with some emergent trees reaching up to 50 m. The understorey is relatively open and characterized by an abundance of stemless palms. For more detailed description of the study site,

see Lovejoy and Bierregard (1991). Mean annual precipitation in Manaus is around 2200 mm, which is distributed seasonally. A rainy season occurs between November and May and a drier period between June and October (Ribeiro & Adis 1984). The mean annual temperature is 26°C (±3°C), and the greatest variation occurs diurnally (up to ±8°C) (Salati 1985).

Sampling design and baiting protocol

We sampled 30 100-m-long transects, located at least 200 m apart. The transects were placed with six different bait densities varying between 6 and 41 baits per 100-m-long transect (Table 1). We sampled one round (six transect treatments) in consecutive days in March, April, July, August and September of 2005 in order to sample a range of soil moisture conditions. Baiting was undertaken between 07:30 h and 16:00 h, and normally two transect treatments were sampled per day. Transect sampling sequence was organized to ensure transects of equal bait density were sampled at different times, minimizing possible confounding effects because of daily variation in ant activity.

Baits were composed of 500 g of canned sardine and 500 g of guava jelly mixed with 300 mL of warm water until homogeneous. At each bait station, approximately 5 g of bait was placed on a plastic card (10 cm by 7 cm). To minimize the effects of topographical variation on ant abundance and composition (Vasconcelos *et al.* 2003), all transects were established on level areas of the forest floor. After 60 min, only the ants species on the plastic card were recorded according to the 6-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. Samples of all species were collected and conserved in 70% alcohol for laboratory identification. Voucher specimens were deposited in the Entomological Collection of the Instituto Nacional de Pesquisas da Amazônia.

We followed Bestelmeyer (2000) and used a different measure of dominance, rather than bait monopolization only (e.g. Andersen 1992; Parr *et al.* 2005). A bait was considered controlled if there were >20 individuals (i.e. score of >4) of the same species using the resource without the presence of other ants (monopolization). In cases where there were >20 individuals of more than one species, the baits were considered controlled when one taxon was at least twice as

Table 1. Number of replicates, number of baits per transect, and distance between baits for transects at the Cabo Frio site Manaus, Brazil

Length (m)	No. of transects	No. of baits per transect	Bait density (10 m)	Distance between baits (m)
100	5	6	0.50	20.00
100	5	11	1.00	10.00
100	5	16	1.50	6.67
100	5	21	2.00	5.00
100	5	31	3.00	3.34
100	5	41	4.00	2.50

numerous as the second most numerous taxon. We adopted this procedure because species with slower movements, such as *Crematogaster* and *Wasmannia*, may permit the presence of a few workers of other species sharing the same resource, but they are still highly successful at bait control compared with other species. In order to compare transects that used different amounts of baits, we used the proportion of controlled baits (bait control ratio), ranging from 0 (no bait controlled) to 1 (all baits controlled).

Dominant species

We used a combination of numerical and behavioural dominance to define dominant ants. Dominant ant species were considered to be those that occurred at a large proportion of baits, numerically and behaviourally controlled many of the baits where they occurred, and had high mean abundance scores (Andersen 1992; Majer *et al.* 1994; Morrison 1996; Parr 2008). The dominant species were classified as those that were recorded in >5% of all baits (at least 32 baits), controlled >25% of baits where they occurred, and with a mean abundance score (calculated by dividing the sum of the abundance scores for the species at all baits by the number of baits at which the species was present) of >4. Mean abundance score of each species ranged from a possible minimum of 1 (always a single ant recorded whenever the species occurred) to a possible 6 (always >50 ants whenever the species occurred).

Environmental measurements

At every 10 m per transect about 200 g of soil (approximate 15 cm depth) was collected and packed in plastic bags. In the laboratory 10 g of soil was weighed on a semi-analytical balance, and re-weighed after 72 h in an oven at 120°C. The soil moisture was estimated by a mean of the difference between wet and dry masses of 10 soil samples per transect.

Data analysis

The transects had different sampling efforts (number of baits), so in order to compare the number of ant species, we used a mean from 100 randomizations of six baits selected per transect. This procedure was used rather than a mean of number of species per bait, because it retains the observed niche breadth (Albrecht & Gotelli 2001) and probably the hierarchical organization of the species at baits. Then, we used multiple regression analysis to explore the factors accounting for the observed variability in the estimated number of species (here after, relative number of species). Predictor variables included in the model were: relative abundance score of dominant species, number of baits per transect and soil moisture. The abundance of dominant species was standardized, dividing the abundance of dominant species (sum of all dominant species' abundance scores), by the total ant abundance (sum of all species' abundance scores) per transect. The effect of abundance of domi-

nant species on relative number of species was investigated using quadratic and linear models.

We also used multiple regression analysis to investigate the observed variability in bait control ratio. Predictor variables included in the model were number of baits per transect and soil moisture. As the control ratio may not always reflect true domination/control interactions (i.e. the numerical dominance of one species may simply reflect the possibility that other ant species in the area have not located the bait), we investigated the effect of those predictor variables on the observed variability in bait control ratio calculated with the monopolized baits excluded. We used partial regression plots to graphically show the influence of each variable in the model. Partial regression plots show the expected effect of a variable when the other variables in the model are statistically held constant (Velleman & Welsch 1981). Those plots have easier interpretation than three dimensional graphics, in which the interpretation depends on the angle at which the graph is projected. Data on proportion of controlled baits were arcsine transformed prior to the analyses to homogenize variance. All analyses were performed using R software (R Development Core Team 2009), and were followed by residual analyses to check the error distribution and the suitability of the model.

RESULTS

The ant abundance was relative high with an overall mean abundance score of 3.16 per bait after 1 h of exposure. Almost half of baits offered (48%) were considered controlled and only 22 baits (less than 4%) were not visited during the bait session. However, approximately 53% of controlled baits had just one species after 1 h of exposure (Fig. 1).

Overall, 112 ant species were recorded, with a mean of 20.1 (±8.75) per transect and 1.97 species per bait (supplementary material). The maximum number of
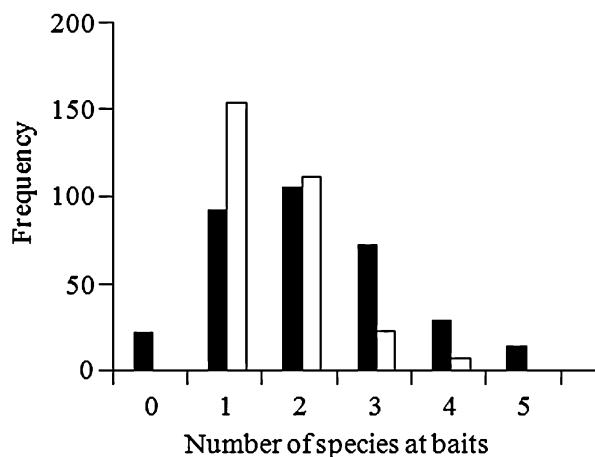

Fig. 1. Distribution of number of baits considered controlled (white bars) and not controlled (black bars) by the number of ant species found at baits, after one hour of exposure. Overall, 630 baits were offered.

Table 2. Summary of occurrence of dominant and subordinate ants species at baits at the Cabo Frio site, near Manaus, Brazil

	Baits recorded (%)	Baits controlled (%)	Mean abundance score
Dominant			
Crematogaster brasiliensis Mayr	12.66	28.57	4.03
Crematogaster limata Smith	5.10	41.94	4.23
Crematogaster tenuicula Forel	11.02	77.61	5.33
Ochetomyrmex semipolitus Mayr	5.92	55.56	4.47
Pheidole sp.13	6.09	91.89	5.54
Wasmannia auropunctata (Roger)	6.09	40.54	4.19
Subordinate			
Blepharidatta brasiliensis Wheeler	1.97	16.67	3.92
Camponotus femoratus (Fabricius)	1.64	10.00	2.80
Ectatomma lugens Emery	8.72	0	1.42
Megalomyrmex goeldii Forel	2.14	30.77	3.54
Odontomachus caelatus Brown	2.96	0	2.00
Odontomachus haematodus (Linnaeus)	0.33	0	2.00
Pachycondyla harpax (Fabricius)	2.96	0	1.33
Pachycondyla obscuricornis Emery	0.33	0	1.50
Pheidole scolioceps Wilson	2.30	35.71	4.07
Trachymyrmex cornetzi (Forel)	3.95	0	1.83

Table 3. Results of multiple regression models for the effects of abundance of dominant ants, bait density and soil moisture on number of ant species using baits based on a randomization procedure, and for the effects of bait density and soil moisture on the proportion of controlled baits

Dependent variable	Predictor variable	Coefficient	T	b
Number of ants species	Abundance of dominant ants	−0.048	−2.441	−0.431*
	Number of baits	0.003	0.145	0.023
	Soil moisture	−0.060	−1.318	−0.234
Proportion of controlled baits	Number of baits	−0.006	−2.931	−0.435**
	Soil moisture	0.010	2.897	0.430**
Proportion of controlled baits (monopolized baits excluded)	Number of baits	−0.006	−1.875	−0.306
	Soil moisture	0.014	2.523	0.412*

Standardized partial regression coefficients (*b*) represent the relative degree of influence of a predictor variable in the model. The model results are described in the text. *$P < 0.05$, **$P < 0.01$.

species collected at one bait was 5. Although species richness was high, only nine species were always abundant and six of those species (*Crematogaster brasiliensis*, *C. limata*, *C. tenuicula*, *Ochetomyrmex semipolitus*, *Pheidole* sp.13 and *W. auropunctata*) were considered dominant. The workers of those species are omnivorous scavengers and predators and can rapidly recruit to food resource. The dominant species occurred at a large proportion of baits, controlled most of the baits at which they occurred and had high mean abundance scores at baits (Table 2). The abundance of dominant species ranged from zero to 78% of total ant abundance per transect. Despite the high abundance of dominant species in some areas, almost half the transects (47%), showed relatively low abundance of dominant species (<30% of total ant abundance).

Subordinate species were those with no mass recruitment behaviour, or species with monopolization abilities, but low occurrences. Some species, such as

P. scolioceps and *Megalomyrmex goeldii*, showed high monopolization ratios and high mean abundance scores, but were recorded at few baits (Table 2). Their potential behavioural displacement was restricted to small portions of the forest floor, where they occurred. The soil moisture varied from 7.24% to 32.34% per transect (mean = 18.13%).

The model using the relative abundance of dominant ants as a quadratic term was not significant and the linear model had a better fit, explaining about 33% of the variance in the species richness ($R^2 = 0.329$; $F_{3,26} = 4.131$; $P = 0.016$). The abundance of dominant ants was the only significant variable (Table 3) and had a negative effect on relative number of species (Fig. 2).

The proportion of controlled baits (Fig. 3) was significantly and positively related to soil moisture and negatively related to the number of baits per transect (Table 3), with the overall regression model accounting for 40% of the observed variance in bait control
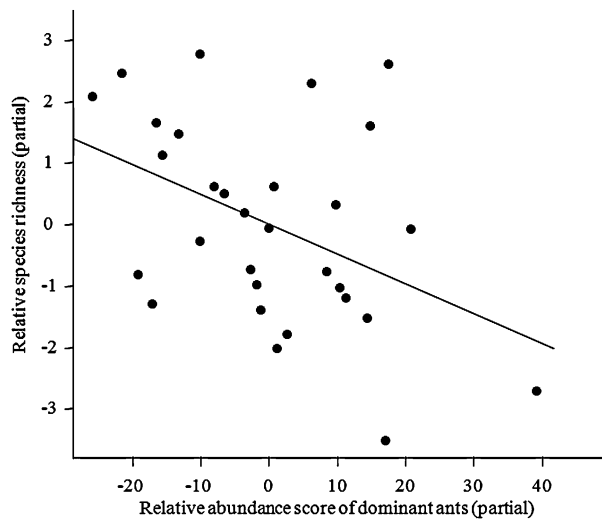
Fig. 2. Partial regression plot ($r^2 = 0.186$; $F_{1,28} = 6.419$; $P = 0.017$) for the statistically significant relationship between relative abundance score of dominant ants and ant species richness at the Cabo Frio site, Manaus, Brazil.

ratio ($R^2 = 0.409$; $F_{2,27} = 9.35$; $P < 0.001$). Using the baits considered controlled that had two or more species only, the regression model accounted for 28% of the observed variance in bait control ratio ($R^2 = 0.287$; $F_{2,27} = 5.422$; $P = 0.010$, Table 3). The proportion of controlled baits (excluding the monopolized baits) was still positively correlated with soil moisture but was not significantly related to the number of baits per transect (Fig. 3). Residual analyses supported the use of the multiple and simple regression models and confirmed normal error distribution.

DISCUSSION

Six taxa (*C. brasiliensis*, *C. limata*, *C. tenuicula*, *O. semipolitus*, *Pheidole* sp.13 and *W. auropunctata*) matched all the criteria established by Andersen (1992) to define a dominant species, with the exception of the fifth criterion (representation in baits relative to pitfall traps) for which data were not available. The dominance results were consistent with the known numerical and behavioural dominance of some species of *Cremato-gaster*, *Pheidole* and *Wasmannia* (Benson & Harada 1988; Vasconcelos *et al.* 2003) and reveal *O. semipolitus* as a dominant species.

Abundance of dominant ants was the only significant variable that was correlated with relative number of species using baits. However, the relationship between dominance and species richness did not reveal the unimodal relationship detected in previous studies (Andersen 1992; Parr *et al.* 2005; Parr 2008). The ascendant part of the relationship, between abundance of dominant ants and species richness, was not

detected. Normally that part of the pattern is attributed to environmental stress (Andersen 1992) or to species frequency distributions (Parr *et al.* 2005). Our study site is relatively undisturbed, and despite being heterogeneous, does not show the level of environmental stress expected to control species richness. Others causes of patchiness mediated by stress, disturbance, such as predation by swarm-raiding ants (Franks & Bossert 1983; Kaspari 1996a), or topography (Vasconcelos *et al.* 2003) can reduce ant abundance or diversity, but were not enough to produce low richness and consequently low dominance at the scale of our study.

We detected the descending part of the relationship between abundance of dominant ants and species richness. That part of the relationship is normally attributed to an increase in the abundance of dominant ants, which reduces the number of species via competitive exclusion (Andersen 1992; Morrison 1996; Parr 2008). Interspecific competitive exclusion was supported by observations of displacement of other ants by dominant species, principally by *C. tenuicula* and *Pheidole* sp.13. Some dominant species in this study, such as *C. tenuicula*, can build polidomic nests, and a single colony can occupy more than one nest (Longino 2003). Some species in these genera are also polygynous and it is hard to define colony boundaries. Such nesting behaviour can create large areas with less intra-specific competition that should favour bait control (Cerdá *et al.* 2002). For example, in 10 transects, *C. tenuicula* controlled neighbouring baits, creating patches more than 30 m in extent with few subordinate species sharing baits. However, the observation of displacement of subordinate by dominant species at baits does not imply that these species compete and exclude each other under natural conditions. Baits are widely used to investigate the activity of terrestrial ants in response to microclimate changes, but this is a selective method which samples mainly omnivorous species that recruit to rich food sources. The results discussed here are applicable to modelling resource control or ant activity, but the importance of dominance in a broader sense and its implications in patterns of diversity in tropical forests require further investigation.

Despite the fact that dominant ants may control the presence of other species at ephemeral rich food sources, almost half the transects showed relatively low abundance of dominant species (<30% of total abundance). This result is in keeping with other studies suggesting that behavioural dominance is relatively poorly developed on the floor of tropical rainforests, in comparison with the canopy or open environments (Andersen 2000; Kaspari 2000). Moreover taxonomically and functionally, the dominant ants found at the Cabo Frio site differ from Andersen's (1997) classification scheme. At a global scale, the dominant species in this study are known as Generalized Myrmicinae, which also recruit quickly and
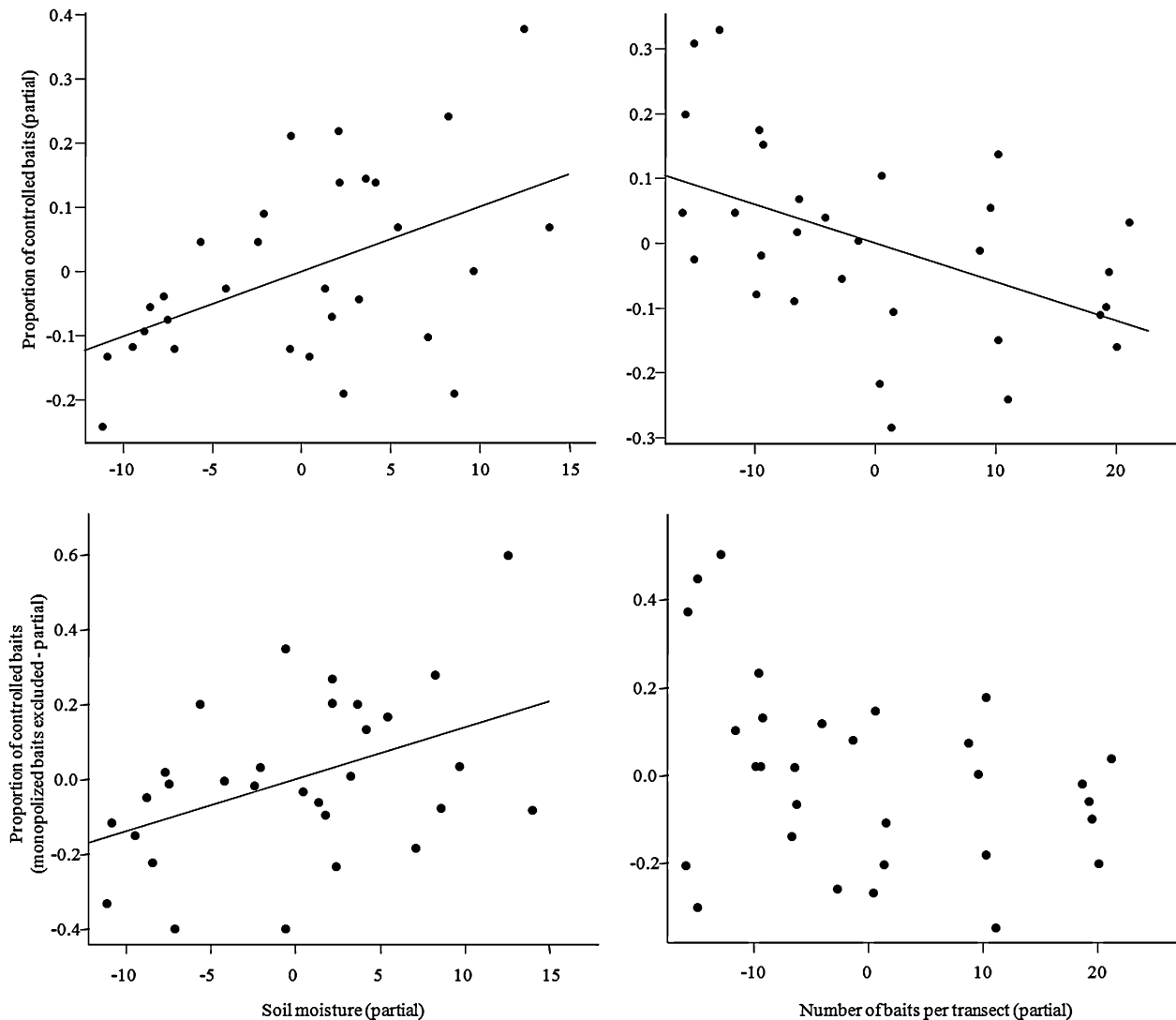
Fig. 3. Partial regressions plots for statistically significant effects of soil moisture ($r^2 = 0.237$; $F_{1,28} = 8.702$; $P = 0.006$) and number of baits ($r^2 = 0.241$; $F_{1,28} = 8.910$; $P = 0.005$) on proportion of controlled baits; and partial regressions plots for a statistically significant effect of soil moisture ($r^2 = 0.191$; $F_{1,28} = 6.602$; $P = 0.016$) and a tendency with number of baits ($r^2 = 0.115$; $F_{1,28} = 3.647$; $P = 0.066$), on proportion of controlled baits with monopolized baits excluded, at Cabo Frio site, Manaus, Brazil.

defend clumped food resources (Andersen 1997). In the absence of competitively Dominant Dolichoderinae, those species seems to act as dominants and regulate the access of other species to baits.

Variations in soil moisture and resource density were approximately fivefold and sevenfold, respectively, but were not directly correlated with ant species richness in this study. Normally, variation in soil moisture and resource distribution affects the number of ant species at different temporal (i.e. between seasons) and spatial (i.e. forests compartments – valleys and plateaus) scales (Levings 1983; Kaspari & Weiser 2000; Vasconcelos et al. 2003). However, those variables seemed to affect ant species richness indirectly, via regulation of dominant-species abundance.

Our data showed that soil moisture was positively related with bait control ratios at this location. This relationship agrees with the activity patterns of the terrestrial assemblages in other tropical forests. Field data and watering experiments suggest that increases in humidity are associated with increased ant activity (Levings 1983; Kaspari & Weiser 2000; Hahn & Wheeler 2002). Levings and Windsor (1982) proposed that terrestrial ants probably reduced their activity levels in response to a combination of resource limitation and increased desiccation risk because the activity of most litter arthropods is positively correlated with soil moisture. Our manipulative experiment (variation in bait number) permitted an investigation of the independent effects of those normally correlated variables,

and showed that the bait control ratio may respond to soil moisture independent of resource availability. As previous studies suggest (Levings 1983; Kaspari & Weiser 2000), ant activity, measured here as bait control ratio, may be modulated by desiccation risk only.

Ant colonies forage more intensely for closer and more abundant resources (Davidson 1977; Bernstein 1979; Sanders & Gordon 2002), and consequently the resource density seems to affect resource monopolization. Our results on bait control ratio agree with predictions of feeding territoriality theory. The theory predictions deal with the costs of territorial defence and the energetic income that maintains territories. The territory is kept if defence activity gains more energy that it costs (Carpenter & MacMillen 1976; Hölldobler & Lumsden 1980). The terrestrial ants of tropical forests normally do not show territoriality in its stricter sense (Hölldobler & Wilson 1990; Byrne 1994), but it is reasonable to think of control of bait as an estimation of energy cost to maintain a food resource. In transects with less baits, bait control was favoured to keep the rich food source. Conversely, in transects with many baits, control confers less energetic advantage than spreading effort among closer baits. In many cases, we saw the same colony divide their trails between two or more baits, principally on transects with higher bait density (transects with 31 and 41 baits).

Bait control depends on discovery and behavioural abilities to maintain or take a food resource (Davidson 1998), and some controlled baits in this study may have resulted from discovery by a single species with mass recruitment behaviour rather than competitive exclusion. However, we do not expect that bait discovery and control by a single species generated an additional bias in our results. The results of the two models (with and without monopolized baits) were congruent. The proportion of controlled baits that resulted from known interactions between two or more species showed the same patterns with bait density and soil misture. Moreover, in this forest, we found almost 2.5 ant nests, or parts of polidomic nests, per square meter (F. B. Baccaro & G. Ferraz 2008, unpubl. data), many of them from species that nest in soil. Considering that transects with the highest bait density was of four baits per 10 m (0.4 baits per square meter) we suggest that variation in bait control ratio was more because of a result of recruitment ability modulated by resource distribution and soil moisture than from discovering.

Spatial variation of moisture content and resource distribution are important factors structuring ant communities, and affecting the activity of ant species. Our data suggest that, in this tropical forest, both mechanisms may be operating, given that changes in resource availability and soil moisture affected resource control and this, ultimately, may alter the number of species that feed on available resources. Those findings contribute to the understanding of the variation observed around the relationship between dominance and number of species in ant assemblages (Andersen 1992; Parr *et al.* 2005; Parr 2008).

ACKNOWLEDGEMENTS

REFERENCES

Albrecht M. & Gotelli N. K. (2001) Spatial and temporal niche partitioning in grassland ants. *Oecologia* **126,** 134–41.

Andersen A. N. (1992) Regulation of 'momentary' diversity by dominant species in exceptionally rich ant communities of the australian seasonal tropics. *Am. Nat.* **140,** 401–20.

Andersen A. N. (1995) A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. *J. Biogeogr.* **22,** 15–29.

Andersen A. N. (1997) Functional groups and patterns of organization in North American ant communities: a comparison with Australia. *J. Biogeogr.* **24,** 433–60.

Andersen A. N. (2000) Global ecology of rainforest ants. In: *Ants: Standard Methods for Measuring and Monitoring Biodiversity* (eds D. Agosti, J. D. Majer, L. E. Alonso & T. R. Schultz) pp. 25–34. Smithsonian Institution Press, Washington, DC.

Benson W. & Harada A. Y. (1988) Local diversity of tropical and temperature ant faunas (Hymenoptera: Formicidae). *Acta Amazônica* **18,** 275–89.

Bernstein R. A. (1979) Schedules of foraging activity in species of ants. *J. Anim. Ecol.* **48,** 921–30.

Bestelmeyer B. T. (2000) The trade-off between thermal tolerance and behavioural dominance in a subtropical South American ant community. *J. Anim. Ecol.* **69,** 998–1009.

Byrne M. M. (1994) Ecology of twig-dwelling ants in a wet low land tropical forest. *Biotropica* **26,** 61–72.

Carpenter F. L. & MacMillen R. E. (1976) Threshold model of feeding territoriality and test with a hawaiian honeycreeper. *Science* **194,** 639–42.

Cerdá X., Retana J. & Cros S. (1997) Thermal disruption of transitive hierarchies in Mediterranean ant communities. *J. Anim. Ecol.* **66,** 363–74.

Cerdá X., Retana J. & Manzaneda A. (1998) The role of competition by dominants and temperature in the foraging of subordinate species in Mediterranean ant communities. *Oecologia* **117,** 404–12.

Cerdá X., Dahbi A. & Retana J. (2002) Spatial patterns, temporal variability, and the role of multi-nest colonies in a monogynous Spanish desert ant. *Ecol. Entomol.* **27,** 7–15.

Connel J. H. & Lowman M. D. (1989) Low-diversity tropical rain forests some possible mechanisms for their existence. *Am. Nat.* **134,** 88–119.

Davidson D. W. (1977) Foraging ecology and community organization in desert seed-eating ants. *Ecology* **58,** 725–37.

Davidson D. W. (1998) Resource discovery versus resource domination in ants: a functional mechanism for breaking the trade-off. *Ecol. Entomol.* **23,** 484–90.

Deslippe R. J. & Savolainen R. (1994) Role of food supply in structuring a population of *Formica* ants. *J. Anim. Ecol.* **63,** 756–64.

Fellers J. H. (1987) Interference and exploitation in a guild of woodland ants. *Ecology* **68,** 1466–78.

Floren A. & Linsenmair K. E. (2000) Do ant mosaics exist in pristine lowland rain forests? *Oecologia* **123,** 129–37.

Franks N. R. & Bossert W. H. (1983) The influence of swarm raiding army ants on the patchiness and diversity of a tropical leaf litter ant community. In: *Tropical Rain Forest: Ecology and Management* (eds E. L. Sutton, T. C. Whitmore & A. C. Chadwick) pp. 151–63. Blackwell, Oxford.

Gibb H. & Hochuli D. F. (2004) Removal experiment reveals limited effects of a behaviorally dominant species on ant assemblages. *Ecology* **85,** 648–57.

Hahn D. A. & Wheeler D. E. (2002) Seasonal foraging activity and bait preferences of ants on Barro Colorado Island, Panama. *Biotropica* **34,** 348–56.

Hoffmann B. D. & Andersen A. N. (2003) Responses of ants to disturbance in Australia, with particular reference to functional groups. *Austral Ecol.* **28,** 444–64.

Hölldobler B. & Lumsden C. J. (1980) Territorial strategies in ants. *Science* **210,** 732–9.

Hölldobler B. & Wilson E. O. (1990) *The Ants.* Harvard University Press, Cambridge, MA.

Huston M. (1979) A general hypothesis of species diversity. *Am. Nat.* **113,** 81–101.

Kaspari M. (1996a) Litter ant patchiness at the 1-m^2 scale disturbance dynamics in three Neotropical forests. *Oecologia* **107,** 265–73.

Kaspari M. (1996b) Testing resource-based models of patchiness in four Neotropical litter ant assemblages. *Oikos* **76,** 443–54.

Kaspari M. (2000) A primer on ant ecology. In: *Ants: Standard Methods for Measuring and Monitoring Biodiversity* (eds D. Agosti, J. D. Majer, L. E. Alonso & T. R. Schultz) pp. 9–24. Smithsonian Institution Press, Washington, DC.

Kaspari M. & Weiser M. D. (2000) Ant activity along moisture gradients in a neotropical forest. *Biotropica* **32,** 703–11.

Levings S. C. (1983) Seasonal, annual and among-site variation in the ground ant community of a deciduous tropical forest: some causes of patchy species distributions. *Ecol. Monogr.* **53,** 435–55.

Levings S. C. & Windsor D. M. (1982) Seasonal and annual variation in litter arthropod populations. In: *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Change* (eds E. G. Leigh Jr, A. S. Rand & D. M. Windsor) pp. 355–88. Smithsonian Institution Press, Washington, DC.

Levings S. C. & Windsor D. M. (1984) Litter moisture content as a determinant of litter arthropod distribution and abundance during the dry season on Barro Colorado Island, Panama. *Biotropica* **16,** 125–31.

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

Lovejoy T. E. & Bierregard R. O. (1991) Central Amazonian forests and the minimal critical size of ecosystem project. In: *Four Neotropical Rainforests* (ed. A. H. Gentry) pp. 60–71. Yale University Press, New Haven.

Majer J. D., Delabie J. H. C. & Smith M. R. B. (1994) Arboreal ant community patterns in Brazilian cocoa farms. *Biotropica* **26,** 73–83.

Morrison L. W. (1996) Community organization in a recently assembled fauna: the case of Polynesian ants. *Oecologia* **107,** 243–56.

Parr C. L. (2008) Dominant ants can control assemblage species richness in a South African savanna. *J. Anim. Ecol.* **77,** 1191–8.

Parr C. L., Sinclair B. J., Andersen A. N., Gaston K. J. & Chown S. L. (2005) Constraint and competition in assemblages: a cross-continental and modeling approach for ants. *Am. Nat.* **165,** 481–94.

Porter S. D. & Savignano D. A. (1990) Invasion of polygyne fire ants decimates native ants disrupts arthropod community. *Ecology* **71,** 2095–106.

R Development Core Team (2009) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Ribas C. R. & Schoereder J. H. (2002) Are all ant mosaics caused by competition? *Oecologia* **131,** 606–11.

Ribeiro M. N. G. & Adis J. (1984) Local rainfall variability – a potential bias for bioecological studies in the Central Amazon. *Acta Amazônica* **14,** 159–74.

Salati E. (1985) The climatology and hydrology of Amazonia. In: *Amazônia: Key Environments* (eds G. T. Prance & T. E. Lovejoy) pp. 18–48. Pergamon Press, Oxford.

Sanders N. J. & Gordon D. M. (2002) Resources and the flexible allocation of work in the desert ant, *Aphaenogaster cockerelli*. *Insectes Sociaux* **49,** 371–79.

Sanders N. J. & Gordon D. M. (2003) Resource-dependent interactions and the organization of desert ant communities. *Ecology* **84,** 1024–31.

Savolainen R. & Vepsäläinen K. (1988) A competition hierarchy among boreal ants: impact on resource partitioning and community structure. *Oikos* **51,** 135–55.

Tilman G. D. (1984) Plant dominance along an experimental nutrient gradient. *Ecology* **65,** 1445–53.

Vasconcelos H. L., Macedo A. C. C. & Vilhena J. M. S. (2003) Influence of topography on the distribution of ground-dwelling ants in an Amazonian forest. *Stud. Neotrop. Fauna E.* **38,** 115–24.

Velleman P. & Welsch R. (1981) Efficient computing of regression diagnostiocs. *Am. Stat.* **35,** 234–42.

Whittaker R. H. (1965) Dominance and diversity in land plant communities. *Science* **147,** 250–60.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

APPENDIX I. Occurrence of dominant and subordinate ants at baits at Cabo Frio site, near Manaus, Brazil. The species were classified using all bait data.