Instituto Nacional de Pesquisas da Amazônia – INPA
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O papel de interações bióticas e abióticas na estruturação de comunidades de formigas na Amazônia Central

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Sinopse:

Este estudo se baseou em amostragens de campo em quatro sítios de coleta na Amazônia Central. Foi desenvolvido e testado um novo método de coleta para estimar a densidade de ninhos de formigas usando iscas e que pode ser usado em estudos sobre competição por recursos. O papel da competição entre espécies foi avaliado através de análises correlativas entre a abundância de espécies ecologicalmente dominantes e o número de espécies subordinadas. O efeito da escala amostral nas relações competitivas entre espécies foi avaliado através de uma rarefação espacialmente estruturada. A congruência entre padrões de diversidade de formigas e alguns de seus parasitas foram investigados em três sítios de coleta. A importância de restrições ambientais, como o nível do lençol freático, foi avaliada através do monitoramento quinzenal de piezômetros em um sítio de coleta. O efeito do nível do lençol freático sobre a assembléia de formigas foi estudado através da abordagem de grupos funcionais.

Palavras-chave: competição, co-ocorrência, densidade de espécies, florestas tropicais, Formicidae, lençol freático, *Ophiocordyceps*, parasitismo.

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You can't always get what you want
But if you try sometimes, you just might find
You get what you need

Mick Jagger and Keith Richards

Resumo

Um dos principais objetivos da ecologia é determinar quais fatores determinam a co-ocorrência de espécies em assembléias locais. Esta tese de doutorado documentou os padrões de diversidade de formigas em diferentes florestas e escalas espaciais na Amazônia Central, e explorou os possíveis mecanismos ecológicos que resultam nesses padrões. O papel das interações antagônicas entre espécies e restrições ambientais na organização de assembléias de formigas foi investigado através de estudos correlativos baseados em amostragem de campo em quatro locais. Os sítios estudados representam um gradiente latitudinal nas florestas amazônicas abrangendo ampla heterogeneidade ambiental, como áreas de savanas abertas e fechadas, florestas densas, e grande variação na disponibilidade de água do solo. A riqueza, abundância e composição de formigas também variou entre os sítios estudados. Modelos competitivos foram mais freqüentes em unidades amostrais menores ou nas assembléias de formigas amostradas com métodos interativos, como iscas artificiais. A distância percorrida entre as iscas e a entrada do ninho foi relativamente pequena, mesmo para as espécies ecologicamente dominantes. Ambos os resultados sugerem que a presença de espécies dominantes podem reduzir a riqueza de espécies de formigas em áreas pequenas, especialmente quando iscas artificiais são usadas, mas parece ser menos importante do que restrições ambientais na determinação da riqueza de espécies de formigas em escalas maiores. O papel de parasitas altamente especializados, que alteram o comportamento de seus hospedeiros para aumentar sua própria transmissão, na estruturação de comunidades de formigas também parece ser pequeno. Houve um desacoplamento entre os padrões de distribuição de espécies infectadas e não-infectadas, que sugere que o número de espécies hospedeiras adequadas para a manipulação comportamental é limitado. Esse resultado, associado ao pequeno número de indivíduos infectados ao redor das colônias, sugere que o efeito destes parasitas em escala regional também é limitado. A estrutura das assembléias de formigas estudadas foi mais fortemente relacionada com restrições ambientais do que interações antagônicas. Regionalmente, menos espécies de formigas foram encontradas em áreas com menor precipitação média em comparação com as áreas com maior disponibilidade de água. Localmente, a disponibilidade de água, estimada pela profundidade do lençol freático ao longo de um ano, também estiveram fortemente correlacionadas com alterações na estrutura das assembléias de formigas. Mais espécies de formigas foram encontradas em áreas com lençol freático relativamente raso. No entanto, as mudanças no número de espécies estão relacionadas com um aumento de espécies generalistas e a diminuição do número de predadores especialistas e espécies generalistas hipogéicas. Apesar da perturbação causada pelo lençol freático superficial aumentar a diversidade de formigas na escala do sítio, localmente ela reduz a diversidade funcional das assembléias de formigas.

The role of biotic and abiotic interactions in structuring ant communities in central Amazonia

Abstract

One of the main goals in ecology is to determine which factors govern species co-occurence in local assemblages. This doctoral thesis documented the patterns of ant diversity across different forests and scales in Central Amazonia, and explored the possible mechanisms leading to these patterns. The role of antagonistic species interactions and environmental constraints on ant co-occurrence patterns were investigated through correlative studies based on field sampling at four sites. 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 soil water availability. The ant abundance, richness and composition also showed a marked variation between sites. Interference–competition models tended to be more frequent in smaller sample units or in assemblages sampled with interactive methods, such as baits. The distance traveled between bait and nest entrance, including the dominant species, was relatively small. Both results suggests that competition from ecologically 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. The role of highly specialized parasites, which alter the behavior of their hosts to increase their own transmission, in structuring ant communities also appears to be small. There is a mismatch between infected and non-infected species distribution patterns suggesting that the number of host species suitable for behavioral manipulation is limited. These results, associated with small number of infected individuals around the colonies, probably limit the effect of these parasites regionally. The structures of ant assemblages studied were more strongly related to environmental restrictions than antagonistic interactions, such as inter-specific competition and parasitism. Regionally, fewer ant species were found in areas with lower average rainfall compared with areas with more water availability. Locally, the soil water availability, estimated by the water-table depth along one year, was also strong correlated with changes in ant assemblages structure. More ant species were found in areas with relative shallow water table. However, changes in number of species were mainly a result of an increase in generalist species associated with a decrease in the number of specialist predators and small hypogaeic generalist foragers. Although disturbance

by the water-table may increase ant diversity at site scale, it reduces the ant assemblage functional diversity locally.

Sumário

Introdução geral

A taxa crescente de extinção de espécies associada as tendências de aquecimento global demandam uma visão abrangente para prever a futura distribuição da biodiversidade (Cahill *et al.*, 2012; Stork, 2009). Em geral, a composição e diversidade das assembléias de espécies podem ser atribuídas ao somatório de restrições ambientais e evolutivas que ocorrem em larga escala temporal e espacial, como especiação e extinção de espécies, e a processos atuantes em escala local, como seleção de habitat e competição entre espécies (Chase & Leibold, 2003; Ricklefs, 2004). Consequentemente, determinar quais fatores permitem a co-ocorrência de espécies em diferentes escalas é um passo importante para compreender a dinâmica das assembléias e a manutenção da biodiversidade.

Localmente, a co-ocorrência de espécies é frequentemente atribuída a um balanço de diferentes tipos de interações entre organismos (Leibold & McPeek, 2006). As interações antagônicas ou competitivas entre organismos representam os principais mecanismos de teorias fundamentadas no conceito de nicho (Klopfer & MacArthur, 1961; MacArthur, 1972), e interações positivas ou mutualistas são os processos chaves de teorias co-evolutivas (Thompson, 2005). No entanto, apesar das relações ecológicas serem frequentemente classificadas em positivas ou negativas, o grau de associação entre espécies representa um gradiente entre mutualismo, parasitismo e predação que muitas vezes é influenciado por fatores ambientais onde as interações ocorrem. O ambiente pode favorecer interações competitivas, como observado em locais onde os recursos são mais escassos (Tilman, 1984), mas também pode favorecer relações mutualistas em locais com condições mais estáveis (Thompson & Laine, 2010).

Minha tese de doutorado integra estudos de comportamento e de associações de espécies para compreender os processos que criam e mantem a estrutura de assembléias de formigas e de seus parasitas em florestas tropicais. Formigas são ideais para examinar os fatores que moldam assembléias, porque são organismos interativos, abundantes, fáceis de serem amostrados e encontrados em praticamente todos os habitats terrestres (Hölldobler & Wilson, 1990).

Competição em assembléias de formigas

O uso de iscas artificiais é uma prática comum em estudos comportamentais envolvendo formigas (Bestelmeyer *et al.*, 2000; Gotelli *et al.*, 2011). As iscas são baratas, versáteis, facilitam a visualização das interações entre espécies, e são onipresentes em estudos sobre competição em comunidades de formigas (Parr & Gibb, 2010). Diversos trabalhos investigaram os efeitos do tipo (Davidson, 1997; Pearce-Duvet & Feener, 2010; Yanoviak & Kaspari, 2000) e densidade de iscas (Baccaro *et al.*, 2010; Baccaro *et al.*, 2011; Lester *et al.*, 2010), e de variações no micro-hábitat (Farji-Brener *et al.*, 2004; Kaspari & Weiser, 2000) e ambientais (Arnan *et al.*, 2012; Silva *et al.*, 2004; Feener Jr. *et al.*, 2008; Hahn & Wheeler, 2002; Pearce-Duvet *et al.*, 2011) na resposta comportamental das espécies de formigas. No entanto, amostragem com iscas não fornece uma boa estimativa da densidade de ninhos (Gotelli *et al.*, 2011), que é a unidade funcional básica de estudos competitivos. Logicamente, a presença de uma espécie de formiga em uma isca implica na presença de pelo menos um ninho ao redor, mas pouco se sabe sobre o tamanho da área de forrageio das espécies dominantes e consequentemente a área de influência de colônias dessas espécies. O capítulo 1 desta tese apresenta e testa um novo método para estimar a densidade de colônias de formigas usando iscas. Esse método é baseado na distância percorrida entre as iscas e os ninhos e pode ser usado para estimar com boa precisão a densidade de ninhos em um local.

A competição entre espécies é frequentemente citada como um mecanismo importante para a estruturação das assembléias de formigas (Davidson, 1998; Hölldobler & Wilson, 1990). Evidência para o papel da competição inclui hierarquias comportamentais na utilização de recursos (Feener Jr. *et al.*, 2008; Fellers, 1987; Sanders & Gordon, 2003; Savolainen & Vepsäläinen, 1988; Vepsalainen & Pisarski, 1982), a forma unimodal da relação entre abundância das espécies dominantes e a riqueza de formigas (Andersen, 1992; Parr *et al.*, 2005) e a drástica modificação das comunidades de formigas nativas na presença de espécies dominantes introduzidas (Holway *et al.*, 2002; Sanders *et al.*, 2003; Vonshak *et al.*, 2009). No entanto, a maioria desses trabalhos investigou os efeitos da presença de espécies dominantes sobre a riqueza de espécies subordinadas em pequena escala e usando recursos alimentares artificiais (mas veja, Parr 2008 para uma abordagem com métodos de coleta menos seletivos). Consequentemente, pouco se sabe sobre o efeito da abundância de espécies dominantes na riqueza de formigas subordinadas em escalas maiores ou sobre o restante das espécies que não são atraídas por iscas. O capítulo 2 investigou o papel das espécies dominantes na estruturação de comunidades de formigas em diferentes escalas e usando métodos de coleta mais inclusivos.

Diversidade entre níveis tróficos: formigas e seus parasitas

As florestas tropicais são os ecossistemas terrestres com maior biodiversidade (Gaston, 2000). Embora parecendo relativamente homogêneas, grandes extensões de florestas tropicais apresentam alta heterogeneidade ambiental resultando em grande mudança na distribuição de espécies de plantas e na estrutura florestal (Emilio *et al.*, 2010). A composição de espécies de formigas também apresenta alta rotatividade de espécies especialmente em larga escala (Vasconcelos *et al.*, 2010), e por serem membros dominantes dos biomas terrestres são alvos recorrentes para infecção por parasitas.

Parasitas tendem a ser especialistas porque seus hospedeiros servem tanto como habitat e agentes de dispersão (Combes, 2001). Isto implica que as mudanças na abundância do hospedeiro muitas vezes levam a mudanças na abundância de seus parasitas (Dobson *et al.*, 2008). No entanto, alguns parasitas manipulam o comportamento de seu hospedeiro para aumentar sua transmissão (Poulin, 2011), podendo afetar o acoplamento de diversidade entre níveis tróficos. A interação entre formigas e os fungos ascomicetos *Ophiocordyceps* é um modelo útil para entender os papel da manipulação comportamental de hospedeiros nos padrões de diversidade dos parasitas. Formigas infectadas por espécies de *Ophiocordyceps* morrem fora do ninho em locais onde o microambiente é melhor para esporulação do fungo e dispersão para novas operárias (Andersen *et al.*, 2009; Pontoppidan *et al.*, 2009). O capítulo 4 desta tese, investigou a correlação entre os padrões de diversidade das formigas e de *Ophiocordyceps* e como essa relação é afetada por diferentes modos de manipulação comportamental que esses parasitas apresentam.

Diversidade de formigas ao longo de um gradiente ambiental

A disponibilidade de água é um importante preditor da dinâmica das comunidades de formigas (Levings & Windsor, 1984; Levings, 1983). No Panamá, Kaspari & Weiser (2000) encontraram um aumento de 25% nas visitas de formigas em iscas na estação chuvosa em relação à estação seca, e mais de 200% de aumento de atividade num gradiente topográfico, entre o platô (mais seco) e o baixio (relativamente mais úmido). A disponibilidade de água também influencia a distribuição de espécies e, na Amazônia Central, maior número de espécies foi coletado nos baixios do que nos platôs (Vasconcelos *et al.*, 2003). Viver próximo a corpos d'água pode diminuir os riscos de dessecação, mas a variação natural do nível da água no solo pode dificultar o estabelecimento ou manutenção de ninhos de formigas. Áreas com lençol freático superficial estão mais sujeitas a alagamentos temporários e apresentam menor volume de solo disponível para nidificação de formigas (Seal & Tschinkel, 2010; Tschinkel *et al.*, 2012). A persistência das espécies de formigas nessas áreas podem depender de adaptações comportamentais ao alagamento (LeBrun *et al.*, 2011; Majer & Delabie, 1994) que por sua vez determinam a capacidade de colonização e persistência das espécies (Ballinger *et al.*, 2007). O capítulo 3 investigou a relação entre o nível do lençol freático e a dinâmica de assembleias de formigas em uma área que não apresenta alagamento sazonal de longa duração. Áreas com lençol freático superficial representam uma porção significativa das florestas Amazônicas (Rennó *et al.*, 2008; Sombroek, 2000), e até o momento só foi estudada em maior detalhe em sistemas sub-tropicais (Tschinkel *et al.*, 2012).

Objetivo geral

Determinar o papel de interações bióticas e abióticas na estruturação de assembléias de formigas na Amazônia Central.

Objetivos específicos

1. Desenvolver um novo método de amostragem para estimar a densidade de ninhos de formigas de solo e folhiço usando iscas;
2. Determinar o papel da abundância de formigas dominantes no número de espécies de formigas subordinadas em diferentes escalas;
3. Descrever os padrões de diversidade de formigas e de alguns de seus parasitas ao longo de um gradiente ambiental em relação ao grau de manipulação comportamental dos parasitas.
4. Investigar como a profundidade do lençol freático afeta a estrutura de assembleias de formigas de solo e folhiço;

Capítulo 1

Baccaro, F.B. & Ferraz, G. Estimating density of ant nests using distance sampling. *Insectes Sociaux* (no prelo).

Estimating density of ant nests using distance sampling

F.B. Baccaro[1*] and G. Ferraz[2,3]

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Abstract

The quantification of ant nest densities is a useful but challenging task given the group's high abundance and diversity of nesting sites. We present a new application of a distance-sampling method which follows standard distance-analytical procedures but introduces a sampling innovation that is particularly useful for ants: instead of having an observer look for ants we let ants find a bait station and measure the distances covered between nest and station. We test this method by estimating the density of epigaeic ant nests in an Amazon tropical forest site near Manaus, Brazil. We distributed 220 baits of canned sardine mixed with cassava flour among 10, 210-m long transects in old-growth upland forest. Forty-five minutes after baiting, we followed the ants' trails and measured the linear distance between the bait and each nest's entrance. We then used the freely available program DISTANCE to estimate the number of nests per unit area while accounting for the effect of distance on the probability that a colony will find a bait. We found 38 species nesting in 287 different colonies, with an estimated 2.66 nests/m^2. This estimate fell within the 95% confidence bounds of nest density predicted for a similar number of species based on a literature survey of ant species richness and nest density. Our sampling solution, however, takes less than 30% of the time used by conventional sampling approaches for a similar area, with the advantage that it produces not only a point estimate but also a quantification of uncertainty about density.

Key words: distance sampling, species density, Formicidae, litter, tropical forest

Introduction

The quantification of population size is a fundamental component of ecological science and environmental management. There is a vast literature on the estimation of size and other population parameters (Williams *et al.*, 2002) with particular focus on species that are hard to detect (Thompson, 2004); yet, the estimation of ant population density (i.e. number of colonies per unit area) is still a challenging task due to the small size of the organisms, the large variety of nest sites, and their high local abundance. This task is particularly relevant in tropical forests where ants make up to 25% of total animal biomass (Fittkau and Klinge, 1975) and their density can reach up to 30 colonies per square meter (Soares and Schoereder, 2001).

Tropical forest ground and litter ant colonies (hereafter epigaeic ants) can be very small, often including merely a dozen individuals living in a small soil chamber, a dead twig, a dried fruit, between leaves, or in a combination of different sites for species with polydomous nests (Byrne, 1994; Carvalho and Vasconcelos, 2002; Debout *et al.*, 2007). The conventional approach for estimating nest density of epigaeic ants involves sifting thoroughly through the leaf litter of an entire sampling area, inspecting each piece of rotten wood, looking through twigs, and searching for nest entrances in the soil. This technique consumes from one half to more than two hours per person per square meter (Levings and Franks, 1982; McGlynn *et al.*, 2009; Mertl *et al.*, 2009; Shik and Kaspari, 2010) and offers limited area coverage.

We describe and test a time-efficient, easily applicable solution to estimating density of epigaeic ant nests based on an unconventional application of a distance-sampling method (Buckland *et al.*, 1993). Our solution reduces the cost of sampling per unit area, enabling coverage of larger areas than the conventional approach. Distance sampling always involves recording linear distances between an observer and a study organism (Buckland *et al.*,2001; Thomas *et al.*, 2010); the resulting density estimates, therefore, are based on a detection function that describes the probability of detecting an object given it is a certain distance from the observation point. Distance-sampling can be implemented on sets of sites, allowing for differences in detectability among sites and, if appropriate assumptions are met, provides unbiased estimates of density for each surveyed site (Buckland *et al.*, 1993; 2001). While we analyze our data in a standard distance-sampling approach, we introduce a sampling innovation that is especially appropriate for ants: instead of having an observer look for ants, we have the ants look for a bait station. Detectability still decreases with distance from an observation point (bait) but it reflects the ability of ants to detect food, instead of the human ability to detect their nests. To test our technique, we estimate the density of epigaeic ant nests in an upland tropical forest site. We also compare our results with published ant density estimates and illustrate the biological usefulness of our method by exploring the relation between ant nest detection probability and leaf litter depth.

Methods

Study site and ant nest sampling

Fieldwork took place at Reserva Ducke, 25 km north of downtown Manaus, Central Amazonia, Brazil (2°57'S, 59°56'W) from the 20-23 February, 2008. Reserva Ducke is a 10,000-ha rainforest reserve covered by old-growth upland forest on moderately rugged terrain (elevation 50-120 m a.s.l.) drained by small streams. The climate is tropical humid with mean annual temperature around 26ºC (± 3ºC) and mean annual precipitation of 2.2 m, which is distributed seasonally (Marques-Filho *et al.*, 1981).

We sampled ant nests on 10, 210-m-long transects, regularly distributed over 10 km^2 (Fig. 1). Ducke is covered by a trail grid with 1-km^2 cells and all transects started on the side of one cell, following terrain contour lines to minimize the effects of topographical variation on ant distribution within the transect (Oliveira *et al.*, 2009). Sampling always took place between 7:30 and 17:00 h with bait stations placed every 10 m along each transect, totaling 22 stations per transect. Bait consisted of canned sardine and manioc flour mixed in equal weight proportions until homogeneous. We used approximately 3 g of bait per station placed on a 10 x 10 cm piece of paper. After 45 min, we looked for ant trails starting at each bait station and followed them through the litter measuring the linear distance between the bait and a presumed nest entrance. The yellow crumbs of manioc flour facilitated the visualization of ants carrying food through the leaf litter. After locating an entrance, we carefully inspected inside, looking for brood in order to confirm that the entrance led to a real nest. We only used distance data corresponding to nests with brood or (occasionally) to nests where we found a queen. The Supplementary Online Material lists the types of nests found as accessory natural history information.

To ensure that we made the correct connection between trail start and nest entrance we sampled individuals from each trail, at the bait and inside the nest. Specimens were fixed in alcohol 70% and sorted to species or morphospecies in the laboratory, with voucher specimens deposited at INPA's Entomological Collection. As an ant colony may have more than one nest opening or occupy more than one chamber (Byrne, 1994; Debout *et al*., 2007), we always counted a species only once per bait. Thus, in the 13 instances where we found more than one nest of the same species at the same bait, we used the shortest linear distance between the bait and the nest entrance in the analysis.

Estimating nest density

Distance-based estimation of population density measures how the probability of detecting animals goes down with distance from the observer and employs this measure in estimating how many animals should have been counted if detection were perfect. We estimated the nest density of epigaeic ants using the ‘point transect survey’, one distance analytical option that has the observer stationed at a point, rather than moving along a transect line (Buckland *et al*., 2001). We let the colony find the observer and not the other way around, but the distance information is used in the standard way. Our sampling design led to estimates of nest density estimates at two spatial scales: the transect, and whole study area (comprising 10 transects).

Following exploratory analyses and standard distance-sampling procedure we truncated our data by discarding observations of nests that were further than 1 m away from the bait. Truncation improves precision without increasing bias of density estimates because the retained data can contain sufficient information for defining the shape of the detection function and because outlying points are generally least informative and most difficult to model (Buckland *et al*., 2001, 2004; Marques *et al*., 2007). Analyses were performed with the freely available software DISTANCE (Thomas *et al*., 2010), producing one estimate of nest density (D) for each transect and for the entire study area. We fitted our observations with two commonly used detection functions: half normal and hazard-rate (Thomas *et al*., 2010). For each function, we tried three types of fit-improving adjustment terms (cosine, simple polynomial or Hermite polynomial adjustments) adding up to six different types of detection functions. The quantification of uncertainty about density is based on estimates of the variance of D. For single transects we obtain the variance analytically, but for the whole study, because the data are stratified by transect, we use a nonparametric bootstrap procedure with 999 resamples, which takes transect as stratum (Buckland *et al*., 2001). This stratification recognizes the grouped structure of the data, i.e. not treating each baiting station as independent from all others.

In addition to distance, a variety of habitat structural factors may influence the ants' ability to detect baits. For example, litter presents barriers to the movement of ants through the forest floor and may limit a colony's ability to find a bait station (Farji-Brener *et al.*, 2004; Bernadou *et al.*, 2011). If two sites had the same nest density of a given species but site 1 had twice more litter than site 2 we should expect individuals of site 1 to explore a smaller area around the nest entrance in a given amount of time than individuals of site 2. Therefore, we found it reasonable to explore the possibility that litter depth may affect the scale but not the shape of the detection function by including litter depth as a covariate of detection in our analyses (Marques *et al.*, 2007).

We measured litter depth in the same day as nest sampling, at one randomly selected location within 20 cm of every bait station. Measurements consisted of forcing a stick of 0.5 cm in diameter into the litter until it reached the soil and noting the distance in cm between the top piece of litter and the soil. We added litter depth as a covariate to the detection functions described above, using the multiple-covariate distance-sampling engine (MCDS) available in DISTANCE (Thomas *et al.*, 2010). Litter depth entered the models as a nonfactor covariate in both scales, transect and site. As in the conventional analysis of the whole data setwe used nonparametric bootstrap (999 resamples) to estimate the variance of D in MCDS analyses (Marques *et al.*, 2007). Therefore, since we used six types of detection function, we fitted 12 models of nest density (D): six without litter depth and six with litter depth as a nonfactor covariate. These 12 models were fit both for each transect and for the entire study area, and ranked following Akaike's Information Criterion (AIC).

To place our estimates in the context of existing knowledge, we compared D from the highest-ranking whole-area model with published estimates of ant nest density. Since different studies focused on different types of ants we chose to establish a comparison through the species-nest density relationship (Kaspari *et al.*, 2000) placing our results within a relation between the study-site-level number of species per unit area and the study-site-level number of nests of all species per unit area. The computation of species density, however, requires dividing an estimate of species richness by an area. DISTANCE provides information about area in the form of an 'effective area surveyed' or v parameter, which is the area around the observer where the number of undetected objects equals the number of objects detected beyond that area (Buckland *et al.*, 1993). In our case, where the 'observer' is the bait, this area can be interpreted as the area over which an average ant colony can detect a bait station. The *v* parameter yields a more conservative estimate of the area sampled per bait station than alternative measures based on the mean or maximum distance traveled to the bait. We quantified the total area sampled in the whole study site by multiplying the effective area surveyed by the total number of baits offered (220 baits). To estimate richness we used Chao 1 (Chao, 1984) estimator, using transects as replicates and implementing the estimation with the R package *vegan* (Oksanen *et al*., 2011; R Development Core Team, 2011). To obtain species density we divided the Chao 1 estimate by the total area sampled. Finally, we constructed a regression model of the relation between species density and nest density based on published information, and checked whether our estimates fell within the 95% confidence intervals of the literature-based model. We based the regression analysis on log-transformed richness and nest density to improve normality of the data.

Results

We found 11 ant genera and 38 species in 287 different nests located in the soil, litter, twigs, hollow fruits, and litter accumulated on stem-less palms (Table A1 - Supplementary Online Material). The maximum number of nests detected per bait was 4 (mean = 1.45) and only 6 baits were not visited by ants (Table 1). The number of nests encountered on each transect ranged between 22 and 35. We were able to locate nests for all ant trails observed in four transects and failed to locate nests for 13 trails in the remaining six transects (Table 1). Chao (1984) estimate of epigaeic ant species richness for the whole sampling area was 56.07 ± 14.39 species (mean ± s.e.). The mean litter depth varied twofold among transects (min = 1.1 cm; max = 2.44 cm), but more than 1 order of magnitude within transects, showing a patchy distribution of litter at the transect scale.

Truncation at 1 m retained approximately 66% of the distance data. This exclusion of outlying points allowed us to fit simpler models (with fewer adjustment terms) without substantially decreasing the precision of density estimates. Preliminary analysis of truncated and non-truncated data revealed lower density estimates from the non-truncated data (1.36 nests/m^2, but using 4 adjustment terms to increase model fit); truncation to distances shorter than one meter, however, resulted in up to a two-fold increase in uncertainty (i.e. truncation at 0.5 m resulted in a 95% CI of 0.91-11.17 nests/m^2). We thus settle with the 1-m truncation for all the results reported below. At the scale of the whole study area models based on the half-normal detection function had clearly higher AIC than the top-ranking hazard-rate model without adjustment terms (Table 2). Nevertheless, estimates of nest density fall within a narrow range of 0.89 to 2.66 nests per m^2 for all models. Models using litter depth as a covariate generally had higher AIC than similar models without the covariate. Based on the top-ranking model in Table 2 we estimate that our sampling area has 2.66 ant nests/m^2, with a 95% CI of 0.87-6.52 nests/m^2. At the transect scale the top-ranking detection models differed between transects, with five hazard-rate models and five half-normal having the lowest AIC (Table 1). However, as with the whole-area models, transect models with the litter covariate had highest AIC than those without it. When compared with the whole-area analysis, nest density estimates for transects were more uncertain, with their point estimates of density ranging fivefold from 0.7 to 3.9 nests/m^2 (Table 1).

The distance between bait and nest entrance was highly variable both within and among ant species, ranging from a few centimeters to almost 6 meters (Fig. 2a). Overall, when pooled across species, bait-nest distances were highly right-skewed, with most (66 %) falling in the first meter (Fig. 2b). The effective area surveyed (v) was 0.37 m^2 around the nest at the whole-area scale, and ranged from 0.28 to 0.66 m^2 in the individual transect analyses (Table 1). Using the estimate of v for the whole area combined with the Chao estimate of species richness we expect to find 0.65 species of epigaeic ants attracted to baits per square meter in Reserva Ducke. To build our model of species density versus nest density we used information from 16 other sites published in 12 studies of ant density in tropical forests (Table A2 - Supplementary Online Material). Nest density accounted for 76% of the variation in species density across different tropical forests ($r^2 = 0.76$; $F_{1,14} = 44.02$; $P < 0.001$), and our nest density estimate for Reserva Ducke fell within the 95% confidence intervals of the model prediction (Fig. 3). Although our method in part also relies in the ability of the observer to follow ants through leaf-litter as in conventional sampling method, the sampling time per unit area using the distance approach was approximately 30% of the time for other studies reporting comparable measures of effort. On average, the time spent on a conventional litter-sifting survey was 1 ± 0.21 hours (mean ± s.d.) per square meter (Table A2 - Supplementary Online Material); with the point-transect method we were able to estimate ant-nest density for the same area in approximately 16 minutes of ant-trail searching.

Discussion

Size is a central metric of population state in both theoretical and applied ecology;

thus, in estimating number of individuals per unit area, distance-sampling techniques (Buckland *et al.*, 2001) offer a valuable contribution to population biology. Distance-sampling has been applied to estimating density of a large variety of animals, plants, and associated structures (Thomas *et al.*, 2010), including conspicuous mounds of invasive fire ants (Forbes *et al.*, 2000) and red wood ants (Borkin *et al.*, 2012). The foraging behavior of ants, however, allows a particularly unique albeit unconventional application of distance sampling, where the animal finds the observer rather than the other way around. In this study, we estimated epigaeic ant nest density based on a sampling area of 81.4 m^2 and tested a hypothesized relation between habitat structure and nest detection probability. For this we spent less than 30% of the time that would be necessary for the same purpose with a conventional ant-nest searching technique.

One key contribution of distance-sampling is the quantification of uncertainty about density estimates. We estimated 2.66 nests per square meter in our sampling area, with a 95% confidence interval between 0.87 and 6.52. The relatively low nest density in comparison with other tropical forest ant studies (McGlynn *et al.*, 2009; Mertl *et al.*, 2009; Shik and Kaspari, 2010) probably reflects our focus on the subset of ants that are attracted to sardine baits. Nevertheless, we feel reassured that this result makes biological sense because it fits the published relation between species density and nest density (Kaspari *et al.*, 2000). This relation can be used for predicting nest density of a broader scope of species, as long as one has an estimate of species density derived from a wider variety of sampling techniques (e.g. Winkler samples, pitfall traps, different types of bait). Furthermore, our distance sampling approach could be employed with a variety of baits as well, and it should work well across a variety of ant groups and sampling environments. In particular, as the nests of tropical forest epigaeic ants are especially hard to find (Byrne, 1994; Soares and Schoereder, 2000), we anticipate that our application of distance sampling to estimate ant nest density may be even more useful in environments where nests are more easily found.

The validity of our approach relies on three key assumptions of distance-sampling: i) the detection probability at the observation point is 1, in other words, all nests immediately under the bait are detected; ii) nests are detected at their initial position (particularly relevant for distance-sampling of moving objects); and iii) the distance to each detected nest is recorded accurately (Thomas *et al.*, 2010). All assumptions are easily met for ant surveys but it is remarkable how assumptions ii and iii, which are usually hard to meet in closed-forest surveys of moving animals (e.g. Simons *et al.*, 2009), do not present any particular difficulty in a sample of ant baits. Perhaps the most serious hurdle is that of achieving a sufficiently large sample size. Buckland *et al.* (1993) recommend about 60 observations as a practical minimum to adequately model the detection function. We notice that our transect-specific estimates were much more uncertain than the whole-area estimate. This suggests there is room for improvement using more baits per transect.

By changing the focus of the detection process from the observer to the observed, we should expect the detection function to reveal relevant information about ants and how they use their environment. For example, we initially hypothesized that litter depth (and associated amount of environmental interstices) would have a negative effect on the probability of detecting a nest located at a given distance from the bait. However, we found limited evidence to support such effect, as the models with the litter covariate in the detection function had higher AIC than those without. Some common species sampled with baits, such as *Crematogaster tenuicula, C. brasiliensis* and *Wasmannia auropunctata*, that pooled together visited more than half of the baits, are relatively small and live in polydomous nests (Le Breton *et al.*, 2005; Longino, 2003). Such nesting behavior can create large foraging areas and should increase the chance of being nearby when a food source appears. Perhaps this ability of some ant species to be in many places at once might partially suppress the negative effect of litter depth on detection, but we regard this as an open question that should motivate further exploration of the point-transect method with ants.

We are encouraged by our results but it is appropriate to point out a number of caveats in the application of distance sampling to ant assemblages. First, baits are a selective method that attracts mainly omnivorous ant species that recruit to food sources (Ribas and Schoereder 2002). Therefore, this sampling technique misses specialized predators, cryptic ants, and fungus-growing species, which may account for a considerable proportion of the ant fauna (King and Porter, 2005, Baccaro *et al.*, 2012). Second, it is clear that some species take less time to find resources than others (Feener *et al.*, 2008, Parr and Gibb, 2012), and it appears that colonies with more scouts find resources faster than colonies with few scouts (Pearce-Duvet *et al.*, 2011). Therefore, large colonies nesting near a bait station may find the bait first, monopolize its use and could bias our perception of ant abundance and community composition. Finally, while our estimate of υ suggests that the distance between bait stations was far longer than the typical foraging distance of an ant colony, one should not exclude the possibility that in some circumstances (i.e. for species with polydomous nests) the same colony can visit different baits, leading to an overestimation of colony density. These caveats, however, can be seen as opportunities for improvement. For example, if the distance between baits is a concern, one may conduct a pilot sampling with colony identification to determine the minimum distance that insures independence between baits. When selectivity or monopolization of the bait is a problem, one may experiment with different types of attracting substances and different periods of bait observation. Even the use of the standard sardine/tuna bait can be advantageous if one is interested in numerically and behaviorally dominant species. When this is the case, the standard bait will work for monitoring changes in population density of invasive species, with possible advantages in assessing long-term ecosystem changes, or exploring the effects of land management actions on dominant ant nest density. The broader potential of applying distance sampling to ants, however, is to free the researcher to address larger-scale questions through the efficient sampling of larger areas and a wider variety of environments. In one person*hour of field work we obtained sufficient data for estimating nest density over an area approximately four times as large as that covered in the same time on average by conventional sampling solutions. Thus, the time saved with distance sampling can be used for increasing sample size, increasing spatial coverage, incorporating environmental heterogeneity, or exploring the use of different baits targeted to different ant groups.

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Table 1. Nest survey results and density estimates for transect-level analyses according to the best ranking model for each transect. 'v' is the effective area sampled around the bait in m^2, and 'D' is an estimated number of nests per m^2 with 95% confidence intervals based on a analytical estimate of variance.

Transect	Number of nests	Number of nests missed	Baits not visited	υ	D [95% CI]
L3-2500	28	2	-	0.45	1.27 [0.28 - 5.70]
L3-3500	22	2	2	0.54	0.87 [0.52 - 1.47]
L3-4500	35	3	-	0.59	0.77 [0.45 - 1.34]
L4-1500	31	1	-	0.61	0.82 [0.60 - 1.15]
L4-2500	28	1	-	0.31	3.94 [0.89 - 17.58]
L4-3500	32	-	1	0.46	1.13 [0.41 - 3.17]
L4-4500	26	-	1	0.66	0.72 [0.44 - 1.20]
L5-2500	27	-	2	0.44	1.03 [0.55 - 1.95]
L5-3500	32	-	-	0.44	0.95 [0.29 - 3.12]
L5-4500	26	4	-	0.28	3.60 [0.58 - 22.28]

Table 2. AIC-based model-ranking results for the analysis at the whole-area scale. Models were fitted with program Distance using conventional distance sampling or, when litter-depth was included, the multiple-covariates distance sampling (MCDS) engine. ΔAIC shows the difference between each candidate model and the model with the lowest AIC value. 'D' is the estimate of nest density with 95% of confidence intervals based on bootstrap variance estimation. Note there are only 8 (and not 12) models in this table because some adjustment terms were not selected by the Distance adjustment algorithm; we ended up excluding hermit polynomial adjustments for the half-normal functions and all adjustments terms for the hazard-rate models.

Detection function	Adjustment terms	covariate	Δ AIC	Number of parameters	D [95% C.I.]
Hazard-rate	-	-	0	2	2. 66 [0.87 – 6.52]
Half-normal	cosine	-	3.994	2	1.41 [0.99 – 1.79]
Half-normal	simple polynomial	-	4.050	3	1.26 [0.97 – 1.81]
Half-normal	cosine	litter depth	5.236	3	1.45 [0.92 – 2.07]
Half-normal	simple polynomial	litter depth	5.321	4	1.20 [0.86 – 1.62]
Hazard-rate	-	litter depth	7.016	3	1.43 [0.78 – 3.34]
Half-normal	-	-	14.893	1	0.89 [0.73 – 1.07]
Half-normal	-	litter depth	15.885	2	0.92 [0.71 – 1.19]

Figure legends

Fig 1. Map of the Reserva Ducke. Black diamonds represent the 210-m long sampled transects regularly distributed at every 1 km. The dotted lines represent the grid of trails.

Fig 2. Distance between bait and nest entrance for the 15 most frequently detected species/morphospecies (A) and for all the colonies detected in this study (B). Panel A shows median (thick vertical line), 25 and 75% quantiles (boxes), and minimum-maximum values (horizontal lines) of distance per species. The number after each horizontal bars represent the number of nests encountered for each species. In panel B, the line shows the detection probability as a function of distance overlaid with the histogram of observed bait-nest distances. The histogram was scaled by dividing the number of colonies detected in each distance class by the distance midpoint of that class, in order to adjust for increasing area surveyed at increasing distances from the survey point.

Fig 3. Species to nest density relationship showing the results from this study (empty circle) in the context of a linear regression model based on 12 published epigaeic ant surveys in tropical forests (filled circles; see Table A2 - Supplementary Online Material for details). Dotted lines represent 95% confidence intervals for the regression model. Error bars on the white point represent the 95% CI for nest density. Please note, that the species density was estimated at site level.

Fig 1

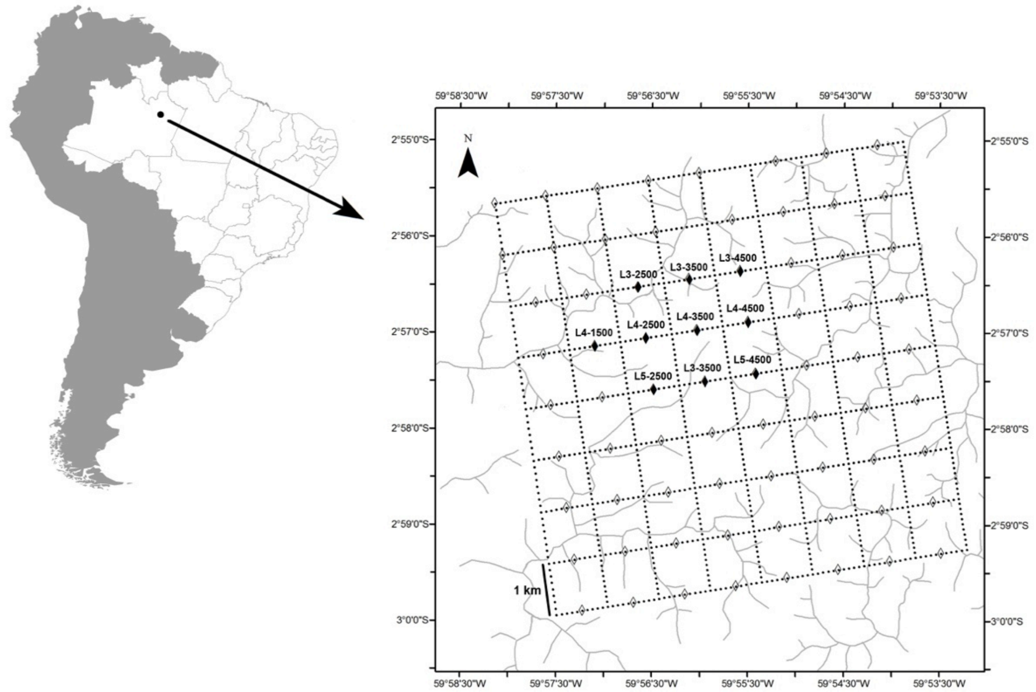

59°58'30"W
59°57'30"W
59°56'30"W
59°55'30"W
59°54'30"W
59°53'30"W
2°55'0"S
2°56'0"S
2°57'0"S
2°58'0"S
2°59'0"S
3°0'0"S
N
L3-2500
L3-3500
L3-4500
L4-1500
L4-2500
L4-3500
L4-4500
L5-2500
L3-3500
L5-4500
1 km

Fig 2

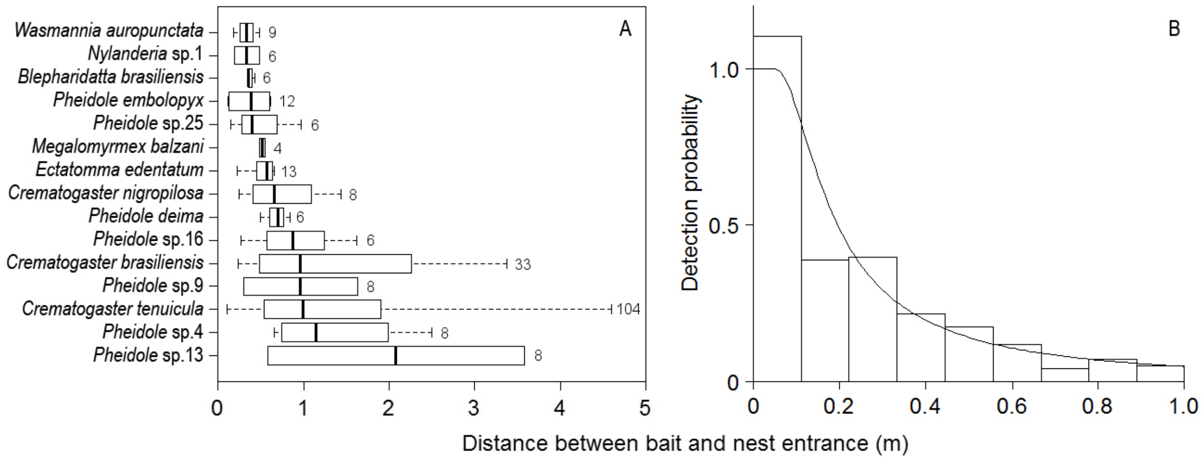
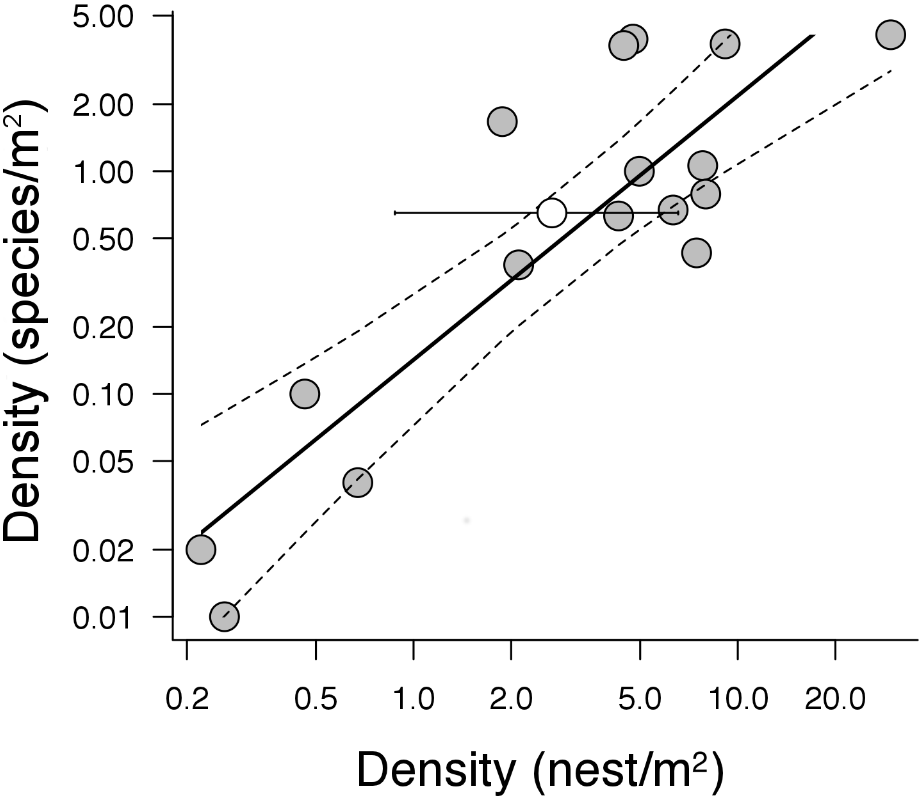

A
Wasmannia auropunctata 9
Nylanderia sp.1 6
Blepharidatta brasiliensis 6
Pheidole embolopyx 12
Pheidole sp.25 6
Megalomyrmex balzani 4
Ectatomma edentatum 13
Crematogaster nigropilosa 8
Pheidole deima 6
Pheidole sp.16 6
Crematogaster brasiliensis 33
Pheidole sp.9 8
Crematogaster tenuicula 104
Pheidole sp.4 8
Pheidole sp.13 8
0
1
2
3
4
5
B
Detection probability
1.0
0.5
0
0
0.2
0.4
0.6
0.8
1.0
Distance between bait and nest entrance (m)

Fig.3


Density (species/m^2)
5.00
2.00
1.00
0.50
0.20
0.10
0.05
0.02
0.01
0.2
0.5
1.0
2.0
5.0
10.0
20.0
Density (nest/m^2)

Online Resource – Insectes Sociaux

Estimating density of ant nests using distance sampling

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Table A1 - Frequency of nesting sites of the species sampled with sardine baits at Reserva Ducke forest, Amazon, Brazil.

Species	between leaves	hollow nut	stem-less palm litter	rotten wood (> 5 cm diameter)	twig (< 5 cm diameter)	Soil
Blepharidatta brasiliensis Wheeler						100
Camponotus rapax (Fabricius)				100		
Crematogaster brasiliensis Mayr	28.6		28.6	42.9		
Crematogaster nigropilosa Mayr	25.0			75.0		
Crematogaster tenuicula Forel	40.8		28.6	30.6		
Ectatomma edentatum Roger						100
Ectatomma lugens Emery						100
Megalomyrmex balzani Emery				50.0		50.0

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Table A1 - Frequency of nesting sites of the species sampled with sardine baits at Reserva Ducke forest, Amazon, Brazil. (continued)

Species	between leaves	hollow nut	stem-less palm litter	rotten wood (> 5 cm diameter)	twig (< 5 cm diameter)	Soil
Nylanderia sp.1	100					
Nylanderia sp.2	100					
Odontomachus caelatus Brown						100
Odontomachus scalptus Brown						100
Pachycondyla crassinoda (Latreille)						100
Pheidole deima Wilson						100
Pheidole embolopyx Brown						100
Pheidole fracticeps Wilson						100
Pheidole meinerti Forel				100		
Pheidole sp.1	25.0					75.0
Pheidole sp.10						100
Pheidole sp.12				100		
Pheidole sp.13				100		
Pheidole sp.16		33.3		33.3		33.3
Pheidole sp.2						100
Pheidole sp.23						100
Pheidole sp.24						100
Pheidole sp.25						100
Pheidole sp.25g				25.0		75.0

Continued on next page

Table A1 - Frequency of nesting sites of the species sampled with sardine baits at Reserva Ducke forest, Amazon, Brazil. (continued)

Species	between leaves	hollow nut	stem-less palm litter	rotten wood (> 5 cm diameter)	twig (< 5 cm diameter)	Soil
Pheidole sp.25p						100
Pheidole sp.3						100
Pheidole sp.4	25.0			25.0	25.0	25.0
Pheidole sp.5						100
Pheidole sp.6						100
Pheidole sp.7					100	
Pheidole sp.8	100					
Pheidole sp.9					100	
Solenopsis sp.1						100
Wasmannia auropunctata (Roger)			33.3			66.7

Table A2 - Study details, nest density and species density estimates for this study and 12 published tropical forest epigaeic ant surveys. Nest and species density estimates from this study are shown with their standard error (se); se for species density equals the Chao estimate se divided by the sampling area. Please note, that the species density was estimated at site level.

Location	Habitat surveyed	Level	Area sampled (m^2)	Time spent in hours (m^2/person)	Nest/m^2	Species/m^2	Reference
Barro Colorado, Panama[a]	Litter	assemblage	50	NA	8.14	1.08	Kaspari (1996)
Barro Colorado, Panama[a]	Litter	assemblage	54	NA	6.39	0.67	Kaspari (1996)
Barro Colorado, Panama	Soil / dead wood	population	380	0.6-1.18	0.67	0.04	Levings and Franks (1982)
Barro Colorado, Panama	Litter	assemblage	40	1	5.18	1.57	Shik and Kaspari (2010)
Barro Colorado, Panama[b]	Soil / litter	assemblage	30	NA	4.73	3.92	Kaspari et al. (2000)
BDFFP, Brazil	Twigs	assemblage	2880	NA	0.22	0.02	Carvalho and Vasconcelos (2002)
Ft Sherman, Panama[b]	Soil / litter	assemblage	30	NA	4.43	3.67	Kaspari et al. (2000)
La Selva, Costa Rica[c]	Litter	population	450	NA	0.26	0.01	Black II (1987)
La Selva, Costa Rica	Litter	assemblage	75	NA	7.43	0.43	Byrne (1994)
La Selva, Costa Rica[a]	Litter	assemblage	70	NA	4.47	0.63	Kaspari (1996)

Continued on next page.

Table A2 - Study details, nest density and species density estimates for this study and 12 published tropical forest epigaeic ant surveys. (continued)

Location	Habitat surveyed	Level	Area sampled (m^2)	Time spent in hours (m^2/person)	Nest/m^2	Species/m^2	Reference
La Selva, Costa Rica[a]	Litter	assemblage	28	NA	5.00	1.00	Kaspari (1996)
La Selva, Costa Rica	Litter	assemblage	180	0.83	2.10	0.38	McGlynn et al. (2009)
Monteverde, Costa Rica[b]	Soil / litter	assemblage	30	NA	1.87	1.67	Kaspari et al. (2000)
Tiputini, Ecuador	Litter	assemblage	756	0.9-2.25	0.46	0.10	Mertl et al. (2009)
Viçosa, Brazil	Soil / litter	assemblage	10	NA	29.50	4.10	Soares and Schoereder (2001)
Yasuni, Ecuador	Soil / litter	assemblage	30	NA	9.10	5.67	Kaspari et al. (2000)
Reserva Ducke, Brazil	Soil / litter	assemblage	81.4	0.27	2.66 ±0.54	0.65 ±0.13	this study

[a] nest density data of each site retrived via package "digitize" in R (Poisot 2011).

[b] site-specific data kindly provided by M. Kaspari.

[c] mean of 3x100 m^2 permanent transects plus 6 x 25 m^2 temporary transects.

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Capítulo 2

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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, interspecific 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, we investigate the mesoscale patterns of ant dominance-richness relationships (sampling units covering hundreds of meters separated by kilometers).

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 dynamics, different processes, acting at scales from local to regional, may interact to influence patterns of species diversity (Kaspari *et al.* 2003; Resetarits Jr 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 behavior or microhabitat selection to avoid direct competition (Byers 1989; Albrecht & Gotelli 2001). Therefore, depending on the scale studied, interspecific 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 monopolize 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; Andersen 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 due to 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 meters (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. 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), 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 meters in largest dimension), where a few dominant colonies could plausibly control most of the sample unit. Although 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 this study, we investigate the mesoscale patterns of ant dominance-richness relationships (sampling units covering hundreds of meters separated by kilometers) 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 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), though 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 5 x 5 km grid. The east-west trails have five 250m-long plots that follow terrain contours (RAPELD method - Magnusson *et al*. 2005). To minimize researcher disturbance along the center lines, the vegetation is not cut, the contour line is marked with colored plastic tape, and an upright PVC tube is placed on the ground at each 10 m interval to facilitate the collecting. As plot center lines follow the contours lines, variation in altitude within the plot is negligible, minimizing the effects of topographical variation on ant community structure. In this study, we used the plot center 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 1 pitfall trap, a 1m^2

litter sample (Winkler sacks) and 1 sardine bait. In total, 300 subsamples for each sampling technique (Winkler, pitfall, 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 organized to minimize disturbances by one technique on the others.

At each sampling station, 1 m^2 of sifted litter was collected through a 1 cm^2 mesh, placed in Winkler sacks and hung in a room at 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 minutes, all ants on the plastic card were collected and preserved in 70% alcohol. In order to minimize differences due to 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 (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 8:00 am and 17:00 pm. Ducke site was sampled in September 2006 and 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 specialized 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 web site 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 monopolized baits) to define the dominant species (Andersen 1992; Parr *et al.* 2005; Parr 2008). A bait was considered monopolized 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 monopolized >25% of 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 1 (always a single ant recorded whenever the species occurred) to a possible 6 (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 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 nonlinear (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 $r = 0.478$, $p < 0.001$, pitfall: Pearson $r = 0.485$, $p < 0.001$ and Winkler: Pearson $r = 0.500$, $p < 0.001$). If more than one of the models revealed a significant relationship, they were compared using model fit, Fisher 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: generalized dolichoderines, formicines, and myrmicines” following the guild classification suggested by Silva & 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 nonlinear (logarithmic and quadratic) models. As we were interested in 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 by 10 subsamples with 25-m spacing, and in our rarefaction procedure we took randomly selected subsamples ranging from one to nine continuous sampling stations. For example, when selecting 3 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 3 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 1,000 times for each subsample size (ranging from 1 to 9 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 randomizations against the number of subsamples per transect. All analyses were undertaken using R software (R Development Core Team 2008).

We tested for nonrandom 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 Viruá, Maracá and Ducke sites, respectively. Eight species, belonging to four genera (*Crematogaster*, *Pheidole*, *Solenopsis* and *Wasmannia*), were identified as dominant species because they were responsible for most bait monopolization (66 %), had mean abundance scores > 3, and were recorded in more than 5% of baits within 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 monopolized baits of *Crematogaster brasiliensis* Mayr at Ducke, or percentage of baits with *C. limata* Smith at Maracá). However, despite the geographical coverage of this study, the dominant species classifications for the more forested areas of Ducke and Maracá were similar. The relative environmental similarity between Ducke and Maracá sites was also reflected in other dominance metrics. Around half of the baits offered were monopolized at Ducke and Maracá (56% and 43%, respectively), while only 20% of baits were monopolized at Viruá. Only 9% and 10% of baits were not visited after 45 minutes 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, 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 subordinate species at baits which were not monopolized (Table 2). The dominant species interacted with 75 subordinate species, which represented approximately 60% of all species sampled with baits. Furthermore, we observed aggressive behaviors 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 behavior was normally directed towards other species that tried to get access to the bait. The workers of *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 behaviors. They usually ran around the bait keeping their gaster close to the ground, probably depositing pheromone. The smaller dominant species, *Wasmannia auropunctata* (Roger), normally monopolized 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 behavior (*e.g. Ectatomma lugens* Emery and *Pachycondyla constricta* (Mayr)), or species with monopolization 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 monopolization 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 to 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 5,333 individuals and 130 species (22, 35, 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 [$y = 18.622 + 3.368*\log(x + 1)$, $y = 0.866 + 3.600*\log(x + 1)$ and $y = 7.069 + 3.716*\log(x + 1)$, 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 $r^2 = 0.239$; $F_{1,27} = 4.258$, $P = 0.024$, 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 abundance of dominant species and number of subordinate species sampled with baits had a better fit in models that used 6 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 meters, the linear relationship between number of subordinate species and abundance of dominant species was negative in 8,985 of 9,000 randomizations (99.8%). For bait data, the asymptotic model always provided the poorest fit for any size of sampling unit.

The relationships between number of subordinate species and abundance of the dominant species for pitfall and 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 fit 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 linear relationship between number of species in the subset of subordinates and abundance of dominant species was positive in 8,768 of 9,000 randomizations (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 number of subordinate species differed between baits and other sampling techniques. As in other studies, bait data showed a unimodal relationship, where highest species richness occurs at intermediate dominance levels, and as the abundance of dominant 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, suggesting that the processes found at baits may sometimes extend to 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 abundance of dominant ants and 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 interspecific 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 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 abundance of dominant species and the number of subordinate species sampled at baits. Larger sampling units are expected to be more heterogeneous, favoring 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 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 meters 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 probably are influenced by the colony sizes of dominant species. Nests of *Crematogaster tenuicula* or *Wasmannia auropunctata*, both classified as dominant species in this 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 abundance of dominant ants and 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 due 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 Generalized Myrmicinae, which recruit quickly and defend clumped food resources, but usually present submissive behavior 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 Generalized Myrmicinae species that were responsible for most bait monopolization, were more abundant than subordinate species at baits, and the observed aggressive behaviors 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 abundance of dominant species increased. The same positive correlation between 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 favorable 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. Despite 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, our 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 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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Figure legends

Fig 1 Map of the study region. Squares represent the three sites sampled. In the detail figure, the black circles represent the 250m transects spatially arranged in a 5 x 5km square grid.

Fig 2 Relationship between the abundance of dominant ants and number of subordinate species across three sites at Central Amazonia, using baits, pitfalls, Winkler data and 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. Gray circles represent Viruá transects, black circles Maracá transects, and open circles Ducke transects.

Fig 3 Percentage of better-fit linear, asymptotic and quadratic models applied to data from 1,000 spatially-structured randomizations 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.

Table 1. Occurrence of dominant and a summary of occurrence of some subordinate ants species at baits in three Amazonian forests: Viruá, Maracá and Ducke. Abundance scale: 1 = 1 ant; 2 = 2-5 ants; 3 = 6-10 ants; 4 = 11-20 ants; 5 = 21-50 ants; 6 > 50 ants.

	Percentage of bait recorded			Mean Abundance Score			Percentage of baits monopolized		
Species	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

Table 2. Summary of interspecific encounters between dominant and subordinate species at baits in three sites at Central Amazonia.

	Number of baits (%)			
Dominant species	Subordinate > double of dominant	Dominant > double of subordinate	Total encounters	Number of species interacting
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

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

	Linear		Quadratic		Logarithmic	
Methods	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

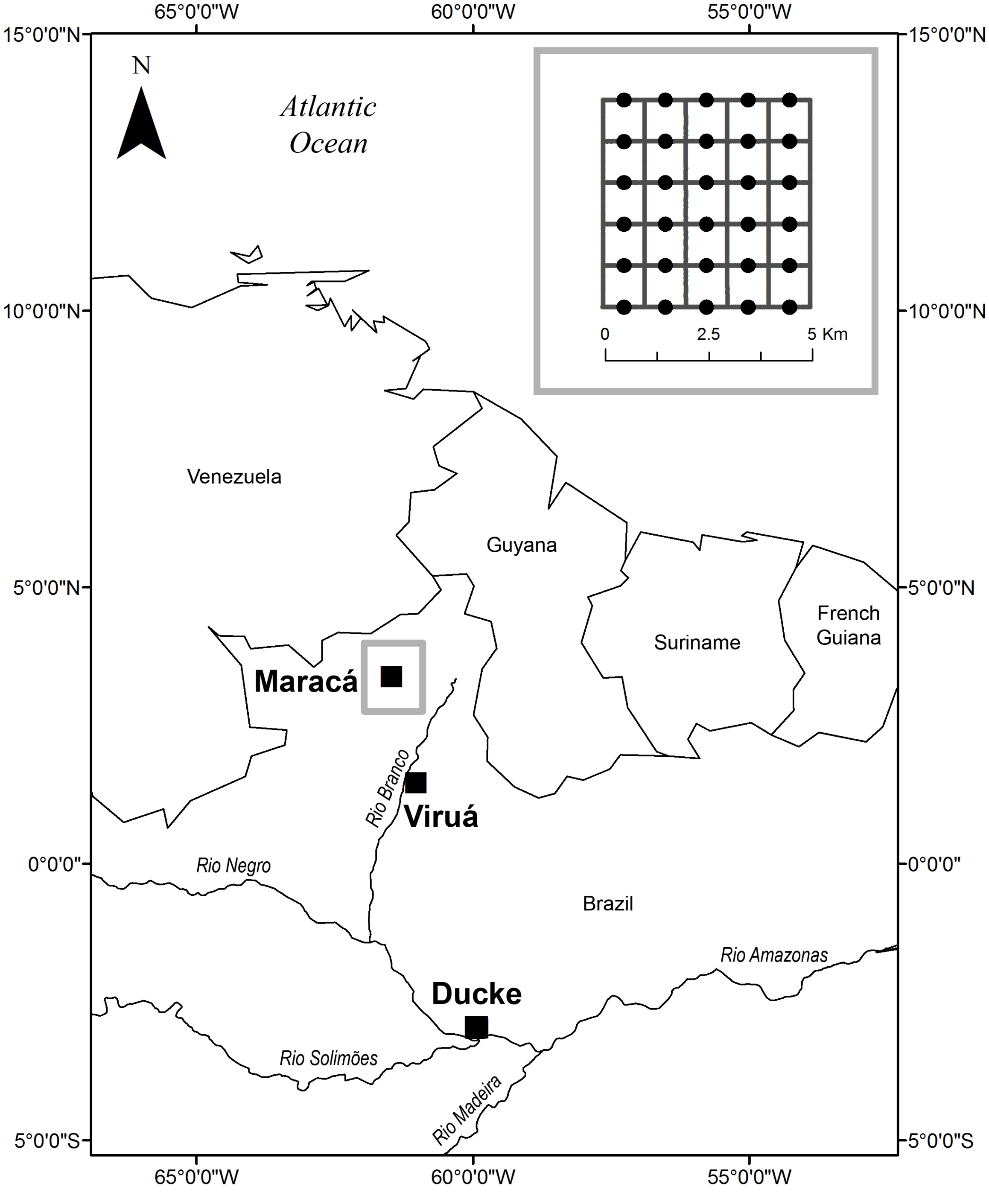
*** P< 0.001; * P<0.05

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.

	Bait		Pitfall		Winkler		Subset of species pool	
Sites	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	---[a]	---[a]	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

[a] All open savanna transects shared the same species.


65°0'0"W
60°0'0"W
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15°0'0"N
10°0'0"N
5°0'0"N
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N
Atlantic Ocean
0
2.5
5 Km
Venezuela
Guyana
Suriname
French Guiana
Maracá
Viruá
Ducke
Brazil
Rio Branco
Rio Negro
Rio Amazonas
Rio Solimões
Rio Madeira

Figure1

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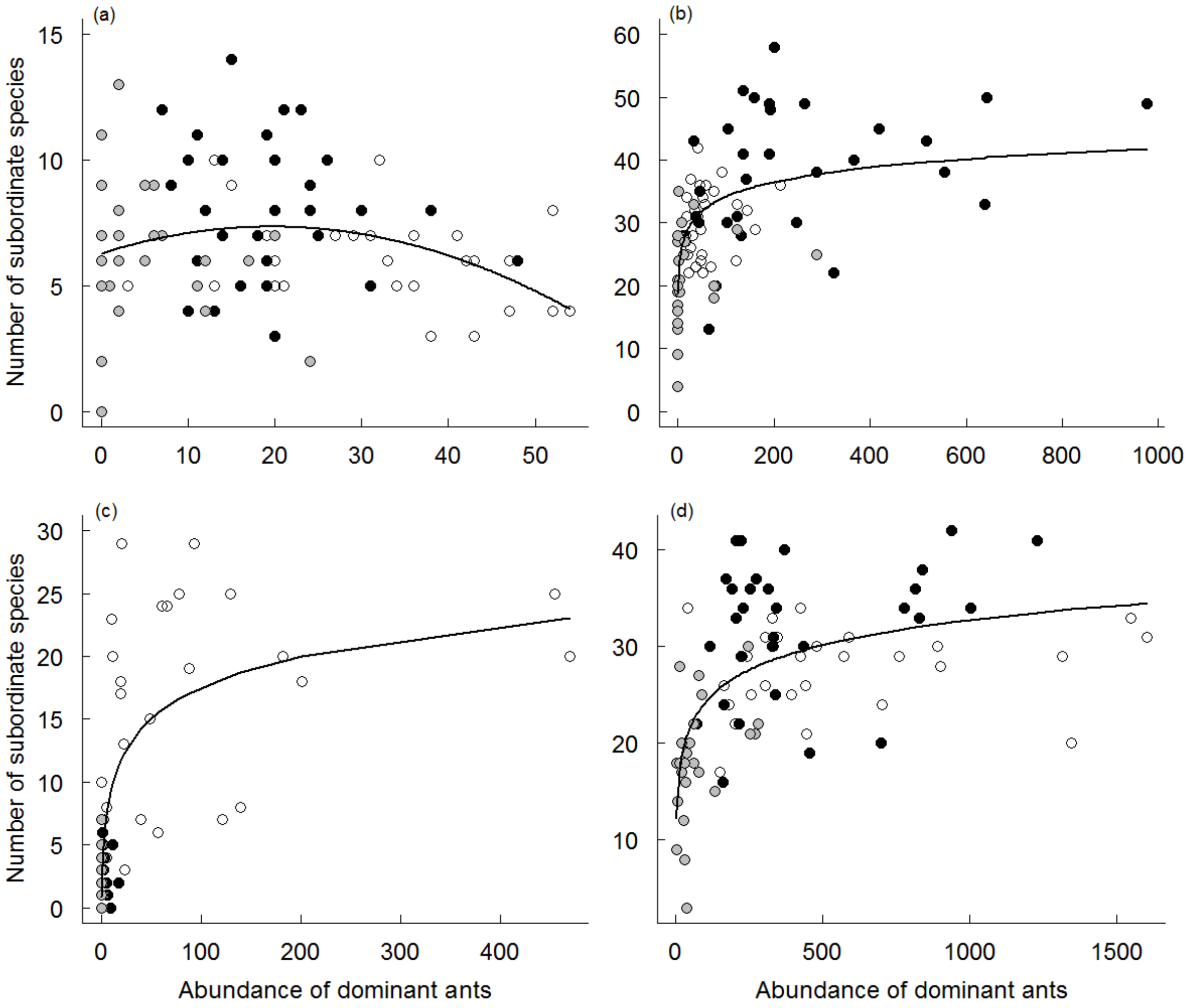

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701 **Figure 2**

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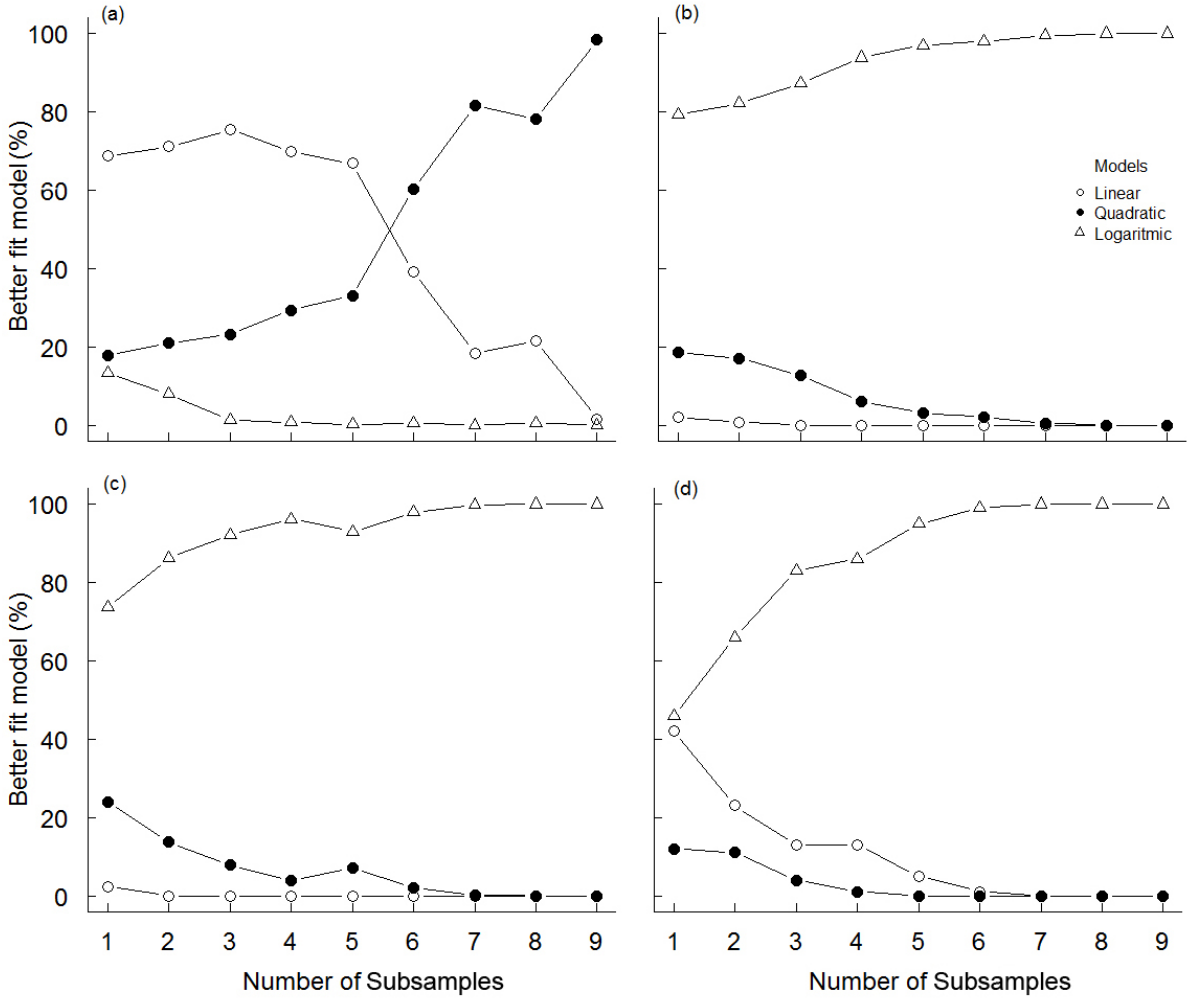
(a)
(b)
(c)
(d)
Better fit model (%)
0
20
40
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80
100
1
2
3
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5
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7
8
9
Number of Subsamples
Models
Linear
Quadratic
Logaritmic

Figure 3

SUPPLEMENTARY MATERIAL

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.

	Viruá	Maracá	Ducke
Vegetation types	open and closed savannas, and open forest	open savannas and semi-deciduous terra-firme forest	terra-firme forest
Tree basal area DHB > 1cm (m^2/hectare)	20.17(9.45)	27.65 (3.96)	32.07 (2.79)
Soil characteristics (percentage)[a]			
Clay	19.8 (16.8)	8.6 (3.3)	42.6 (36.3)
Silt	17.5 (5.9)	11.4 (5.3)	3.1 (1.8)
Sand	62.7 (18.7)	80.0 (7.4)	54.4 (36.8)
Mean annual rainfall (mm)	1,682[b]	1,718[c]	2,507[d]
Number of dry months (<100 mm)	7	6	0
Rainfall intensity in the 3 drier months	48.6	50.9	116.5
Number of wet months (>300 mm)	0	2	2
Rainfall intensity in the 3 wettest months	284.6	303.5	329.4
Stream density			
Number of temporary streams	3	5	0
Number of perennial streams	0	0	7
Seasonal flooded area (%)	~60	~5	0

[a] soil data from 2004 for Reserva Ducke, and 2007 for Maracá and Viruá sites

[b] based on time series of 1984-2004

[c] based on time series of 1979-2005

[d] based on time series of 1979-2008

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: generalized dolichoderines, formicines, and myrmicines” following the guild classification suggested by Silva & Brandão (2010).

		Occurrence		
		Bait	pitfall	Winkler
Azteca	sp. 01	+	+	+
Blepharidatta	*brasiliensis*	+	+	+
Brachymyrmex	*heeri*	+	+	+
Camponotus	*atriceps*		+	
Camponotus	*crassus*	+	+	
Camponotus	*femoratus*	+		
Camponotus	*latangulus*	+		
Camponotus	*leydigi*		+	
Camponotus	*novogranadensis*	+	+	+
Camponotus	*rapax*	+	+	+
Camponotus	*retangularis*		+	
Camponotus	*sericeventris*	+	+	
Camponotus	sp. 02		+	
Camponotus	sp. 04	+	+	
Camponotus	sp. 05	+	+	
Camponotus	sp. 06		+	+
Camponotus	sp. 08		+	
Camponotus	sp. 10		+	
Camponotus	sp. 11		+	+
Camponotus	sp. 14		+	
Crematogaster	*curvispinosa*	+		
Crematogaster	*erecta*	+	+	+
Crematogaster	*evallans*		+	

Crematogaster	*flavomicrops*		+	
Crematogaster	*flavosensitiva*	+	+	+
Crematogaster	*jardineiro*	+		
Crematogaster	*levior*			+
Crematogaster	*longispina*		+	
Crematogaster	*nigropilosa*		+	+
Crematogaster	*sotobosque*	+	+	+
Crematogaster	sp. 01	+	+	
Crematogaster	sp. 06		+	+
Crematogaster	*stollii*		+	
Crematogaster	*torosa*		+	
Dolichoderus	*bispinosus*	+	+	
Dolichoderus	*cf. atelaboides*	+	+	
Dolichoderus	sp. 01		+	
Dolichoderus	sp. 02		+	
Dolichoderus	sp. 03		+	+
Dolichoderus	sp. 05		+	
Dolichoderus	sp. 07	+		
Dolichoderus	sp. 08		+	
Dolichoderus	sp. 09		+	
Dolichoderus	sp. 10		+	
Dolichoderus	sp. 11		+	+
Dolichoderus	sp. 12		+	
Dolichoderus	sp. 13		+	
Ectatomma	*brunneum*	+	+	
Ectatomma	*edentatum*	+	+	+
Ectatomma	*lugens*	+	+	+
Ectatomma	*tuberculatum*	+	+	
Gigantiops	*destructor*	+	+	
Linepithema	fm-01	+		

Megalomyrmex	*balzani*	+	+	
Megalomyrmex	*drifti*		+	+
Megalomyrmex	*leoninus*	+	+	
Megalomyrmex	sp. 02	+	+	+
Megalomyrmex	sp. 04		+	+
Megalomyrmex	sp. 06		+	
Nylanderia	sp. 01	+	+	+
Nylanderia	sp. 02	+	+	+
Nylanderia	sp. 03	+	+	+
Nylanderia	sp. 04	+	+	
Ochetomyrmex	*semipolitus*	+	+	+
Odontomachus	*bauri*	+	+	+
Odontomachus	*brunneus*		+	
Odontomachus	*caelatus*	+	+	+
Odontomachus	*haematodus*	+	+	
Odontomachus	*laticeps*		+	
Odontomachus	*meinerti*	+	+	+
Odontomachus	*opaciventris*		+	+
Odontomachus	*scalptus*		+	+
Pachycondyla	*apicalis*	+		
Pachycondyla	*arhuaca*		+	
Pachycondyla	*commutata*		+	
Pachycondyla	*constricta*	+	+	+
Pachycondyla	*crassinoda*	+	+	
Pachycondyla	*harpax*	+	+	+
Pachycondyla	*impressa*		+	
Pachycondyla	JL01	+		
Pachycondyla	*obscuricornis*	+	+	
Pachycondyla	sp. 01		+	
Pachycondyla	sp. 02		+	

Pachycondyla	sp. 03		+	
Pachycondyla	sp. 04		+	
Pachycondyla	*villosa*	+		
Pheidole	*arachnion*		+	
Pheidole	*cephalica*	+	+	+
Pheidole	*cramptoni*	+	+	+
Pheidole	ES	+		
Pheidole	*exigua*	+		
Pheidole	*fracticeps*	+	+	+
Pheidole	JL	+		
Pheidole	*meinerti*	+	+	+
Pheidole	*prolixa*		+	+
Pheidole	sp. 01	+	+	+
Pheidole	sp. 02	+	+	+
Pheidole	sp. 04	+	+	
Pheidole	sp. 05	+	+	
Pheidole	sp. 07	+	+	
Pheidole	sp. 08	+		+
Pheidole	sp. 11	+	+	+
Pheidole	sp. 14	+	+	
Pheidole	sp. 15	+	+	+
Pheidole	sp. 16			
Pheidole	sp. 17		+	+
Pheidole	sp. 18	+		
Pheidole	sp. 19	+	+	+
Pheidole	sp. 21	+	+	
Pheidole	sp. 22		+	+
Pheidole	sp. 23	+	+	
Pheidole	sp. 24	+		+
Pheidole	sp. 25	+		+

Pheidole	sp. 26	+	+	
Pheidole	sp. 27	+	+	
Pheidole	sp. 28		+	+
Pheidole	sp. 29	+	+	+
Pheidole	sp. 30		+	
Pheidole	sp. 31	+	+	+
Pheidole	sp. 32	+	+	+
Pheidole	sp. 33		+	
Pheidole	sp. 34	+		+
Pheidole	sp. 36	+	+	
Pheidole	sp. 37	+	+	+
Pheidole	sp. 38	+	+	+
Pheidole	sp. 39	+	+	+
Pheidole	sp. 40	+		
Pheidole	sp. 41		+	
Pheidole	sp. 56			+
Pheidole	sp. 57	+		+
Pheidole	sp. 59		+	
Pheidole	sp. 60	+	+	
Pheidole	sp. 61		+	
Pheidole	sp. 62		+	
Pheidole	sp. 63		+	+
Pheidole	sp. 64		+	
Pheidole	sp. 70	+	+	
Pheidole	sp. 71	+	+	
Pheidole	sp. 73	+		
Pheidole	sp. 75		+	+
Pheidole	sp. 76			
Pheidole	sp. 77	+		
Pheidole	sp. 78	+	+	

Pheidole	sp. 79		+	
Pheidole	sp. 85			
Solenopsis	sp. 01	+	+	+
Solenopsis	sp. 02	+	+	+
Solenopsis	sp. 03		+	+
Solenopsis	sp. 04	+	+	+
Solenopsis	sp. 05	+	+	+
Solenopsis	sp. 06	+	+	
Solenopsis	sp. 07	+		+
Solenopsis	sp. 08	+		
Solenopsis	sp. 09	+	+	+
Solenopsis	sp. 10		+	+
Solenopsis	sp. 11	+		
Solenopsis	sp. 12	+	+	
Solenopsis	sp. 13		+	+
Wasmannia	*iheringi*		+	
Wasmannia	*rochai*		+	+
Wasmannia	*scrobifera*		+	

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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.

Variable	Effect	d*f*	MS	*F*	*P*
Subordinate species (baits)	Abundance of dominant^2	1	42.1	6.505	**0.012**
	Site	2	24.1	3.734	**0.028**
	Abundance of dominant^2 X Site	2	1.2	0.189	0.828
	Residuals	83	6.4		
Subordinate species (pitfall)	Log (Abundance of dominant)	1	4111.7	70.843	**> 0.001**
	Site	2	256.5	4.419	**0.014**
	Log (Abundance of dominant) X Site	2	76.5	1.317	0.273
	Residuals	84	58		
Subordinate species (Winkler)	Log (Abundance of dominant)	1	3466.7	179.681	**> 0.001**
	Site	2	275.4	14.274	**> 0.001**
	Log (Abundance of dominant) X Site	2	33.3	1.726	0.184
	Residuals	79	19.3		
Subset of subordinate species (pitfall and Winkler)	Log (Abundance of dominant)	1	2075.1	69.87	**> 0.001**
	Site	2	632.8	21.306	**> 0.001**
	Log (Abundance of dominant) X Site	2	27	0.909	0.407
	Residuals	79	29.7		

Capítulo 3

Baccaro, F.B., Machado, J.P., Evans, H., Souza, J.L.P, Magnusson, W.E., & Hughes, D. Complex behavioral manipulation drives mismatch between host and parasite diversity. Manuscrito em preparação para *Biology Letters*.

Complex behavioral manipulation drives mismatch between host and parasite diversity

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Short title: Mismatch between host and parasite diversity

Abstract

Parasites and hosts are intimately associated such that changes in the diversity of one partner are thought to lead to changes in the other. We investigated this linked diversity hypothesis in a specialized ant-*Ophiocordyceps* system in three forests across 750 km in Central Amazonia. All species belonging to the fungal genus *Ophiocordyceps* associated with ants have evolved some degree of host-control behavior to increase their own transmission, but the leaf-biting behavior is the most complex form of host manipulation. Such a system requires control of the mandibular muscles and a distinct shift in behavior, from climbing vegetation to walking on leaves to rasping leaf veins in the seconds before death. The need to induce complex behavior may represent a constraint on parasite diversity, limiting host availability. The consequence for community structure is that complex behavioral manipulation leads to in a mismatch between ant hosts and their fungal parasites diversity.

Keywords: ants, behavior manipulation, interaction, Ophicordyceps, tropical forests.

Introduction

Species diversity varies considerably between habitats and regions [1]. The factors driving such heterogeneity typically depend on the scale of the analysis [2]. At the local level, interactions among species are known to play an important role in structuring communities [3,4]. This is especially the case when the interacting species occupy different trophic levels, which leads to a stronger link between the diversity of consumers and the diversity of resources [5–7]. Parasite-host interactions are examples of such trophic effects. Parasites tend to be host specific with hosts serving as both the habitat and the dispersal agents for parasites [8,9]. This implies that changes in host abundance often lead to changes in parasite abundance. Such specificity is considered to lead to arms races that promote overall diversity at the community level [10].

Within the framework of linked diversity in host-parasite systems, the sub-set of parasites that manipulate behavior has not been considered. The effect of parasites on their hosts is not only to reduce host fitness but in some cases also involves a manipulation of host behavior that directly increases parasite fitness [11]. In these cases, other constraints related to the need to control behavior as a life-history strategy may affect the coupling of diversity across scales. The interaction between ants and the ascomycete fungus *Ophiocordyceps* provides a convenient model for understanding the roles of behavioral manipulation on host and parasite diversity patterns. Ants infected by *Ophiocordyceps* species die in specific locations outside the nest where the microenvironment is ideal for fungal sporulation and subsequent dispersal to new hosts. Dying outside the nest is considered adaptive for the fungus, because it avoids the cleaning behavior of ant workers that may prevent the completion of the fungal lifecycle inside the colony [12]. Depending on which fungal species is involved, infected ants may die attached to stems (Fig. 1C), buried in the leaf-litter or in the ground, attached to tree bark (Fig. 1D) or biting leafs (Fig. 1E). Biting leaf veins or leaf tissue is the most complex form of manipulation and maintains the ant in situ after death giving the fungus the necessary 24-48 hours to grow adhesive mycelia that bind the ant to the plant [13]. This behavioral manipulation is ancient with vein biting occurring at least since the Eocene [14]. Recent evidence has shown that this host-parasite relationship is highly specific with each host species examined having its specific parasite species [15]. Here, we worked with a large dataset of more than 340 ant species and over 2,700 samples to investigate the community-level patterns of infected and non-infected ants in three different forests types in Brazilian Amazonia (Fig. 1A). We specifically compare the composition of infected and non-infected ants species among sites and how the complex behavioral manipulation by the fungus *Ophiocordyceps* can affect the parasite assemblage structure.

Materials and Methods

We sampled ants and their fungal parasites in three Amazonian forests. Two of them (Maracá Ecological Station, 3° 22’N, 6° 127’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 (Ducke Reserve, 2° 57’S, 59° 56’ W) is situated 25 km north of Manaus, Central Amazonia (Fig. 1A). The sites cover a latitudinal gradient (~ 750 km) in Amazonian forests and encompass wide environmental heterogeneity, including areas of open and dense forests, and areas subject to different degrees of seasonal flooding [16]. We sampled both, parasitized and non-parasitized ants in 9 randomly selected plots per site covering approximately an area of 9 km^2. In each plot, we carefully searched for infected ants buried in soil/litter, and attached to vegetation and tree trunks: habitats where the infected ants are most commonly found. The three-dimensional volume sampled per plot was ~ 500 m^3: 250 m length, 1 m wide and 2 m in height, resulting in 13,500 m^3 in total. Two persons sampled each plot for at least 1.5 hours (~

40 hours/person over the three sites); one focusing on all infected ants and the other on non-infected ants belonging to the genera infected by *Ophiocordyceps*. In the Upper Amazon, this and previous research [17] has shown that the 7 following ant genera are infected: *Camponotus*, *Cephalotes*, *Daceton*, *Dolichoderus*, *Ectatomma*, *Pachycondyla* and *Paraponera* genera. To contrast the assemblage of infected ants with the whole ant community, we used a comprehensive ant survey of 30 plots per site. This survey included 900 1 m^2 litter samples (Winkler sacks), 900 pitfall-traps and 900 sardine baits regularly distributed among the three sites to describe the ant assemblage composition (see [16,18] for additional details).

The data were organized in three matrices: 1) all ant species collected at the three sites, 2) all species from the genera known to be suitable hosts (i.e. *Camponotus*, *Cephalotes*, *Daceton*, *Dolichoderus*, *Ectatomma*, *Pachycondyla* and *Paraponera* genera) and 3) only the species we discovered to be infected. This last category was erected because not all species in a genus are infected. Across our three sites the percent of species infected/genus was 37% ranging from 11–100% in monotypic genera such as *Paraponera* (Fig. 1B). To provide further understanding of the role of complex behavioral manipulation on ant community-level patterns, we also constructed matrices of ant species according to the type of manipulation (Fig. 1B). We reduced the dimensionality of all matrices using Principal Coordinate Analysis (PCoA) based on the Sørensen dissimilarity index. Occurrence data (presence/absence) were used to avoid over estimation of species with larger nests. We compared assemblage composition between the three areas using non-parametric multivariate analysis of variance [19]. The statistical significance of each analysis was based on 9,999 Monte Carlo permutations. We also individually regressed the number of plots were an ant species was found infected against the number of plots were the host species were found according to the type of manipulation.

Results

For all species from all the ant genera recorded, we found that the ant assemblage composition was markedly different between areas ($p < 0.001$; Fig. 1F). We found very little overlap of species between areas and only 72 out of 343 ant species belonging to 24 genera (~20%) were sampled in the three sites. The same pattern holds with only the ant species from the 7 genera, *Camponotus*, *Cephalotes*, *Daceton*, *Dolichoderus*, *Ectatomma*, *Pachycondyla* and *Paraponera* known to be host genera of *Ophiocordyceps* ($p < 0.001$, fig. S1). However, the assemblage of species we discovered to be infected did not mirror the community structure, either of all ants from all genera or all ants from the genera known to be infected. Unlike both, the assemblage composition of infected ants was not different between sites ($p = 0.109$; Fig. 1G). This is despite the fact that ~18% of the hosts' species were shared among the three locations. We expected that different areas would have different infected species assemblages reflecting the general pattern of ant diversity across three sites. The linked diversity in this host-parasite system only matched when the infected ants that are manipulated to bite into plant tissue are removed from the analysis ($p < 0.001$, Fig. 1H). The mismatch between hosts and parasite species composition may be driven by an increase in infection prevalence caused by complex behavior manipulation. The number of plots with infected species by *O. unilateralis* was much higher (Fig. 2A) compared with other groups of *Ophiocordyceps* (Fig. 2B).

Discussion

To infect an ant worker, *Ophiocordyceps* fungus needs to overcome several barriers. The high hiperparasitism levels on *Ophiocordyceps* keeps the number of reproductive individuals relatively low, which makes the infection of new workers by direct contact with dead ant corpses unlikely [20]. The spores of this fungus are very large, with a relative thin cell wall and devoid of pigmentation [17], which probably makes them very sensitive to dehydration and UV radiation. Therefore, to complete its life cycle, an ant must pass over the spores scattered on the forest floor at correct time of the day to be infected. In addition of fungal requirements, the parasite must overcome the host population structure to complete their life cycle. Ants are very interactive organisms, and the competition between colonies of the same species at local scale is frequently demonstrated [21]. This characteristic posits an additional barrier for the transmission between colonies of a specialized parasite. However, the complex behavior manipulation by *O. unilateralis* seems to circumvent these barriers by creating a relative large minefield areas (~ 100 m^2, [13]) where the foraging ants can be infected by their spores. Virtually, in all the plots we find a potential host, it was infected and over the 750 km the same group of *Camponotus* species was infected. Other groups of *Ophiocordyceps* that infect species with large colonies, such as *Cephalotes* and *Dolichoderus* (both included in this study) also create graveyards, but in a smaller area. In the latter case, the dead ants died attached in one tree trunk [22], and sites whitout infected ants were more common.

Biting behavior requires a control of the mandibular muscles that involves a reduction in muscle organelle abundance [14]. It also requires a distinct shift in behavior in the seconds before biting as infected ants shift from a wandering behavior to rasping of either the major veins or leaf edges. Other complexes of *Ophiocordyceps* cause ants to die on leaves (*O. lloydii*, 17) but in no case do ants rasp the plant tissues or choose sites to anchor their mandibles. We suggest that the nature of complex manipulation and the necessary additional control of the host's phenotype that is entailed, limit the potential host range of fungi investing in manipulation. Transmission requires this complex control of behavior, which in turn requires multiple effects at the physiological and neuronal level. The consequence for community structure is that even across large geographical areas, complex behavioral manipulation results in a mismatch between host and parasites diversity patterns.

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Figure legends

Figure 1. (A) Map of study area. (B) Relative infection levels by ant genera showing where the ants died and the seven more specious non-infected genera sampled in 27 plots (note that *Pheidole* bar is at different scale). Black bar shows the number of infected species and gray bars the number of non-infected species. (C) *Pachycondyla inversa* infected by *Ophiocordyceps kniphofioides* var. *ponerinarum* (see [22] for taxonomy of this species complex) attached to a stem. (D) *Cephalotes atratus* killed by *O. kniphofioides* var. *kniphofioides* buried in the mosses of a tree trunk. (E) *Camponotus atriceps* parasitized by *O. unilateralis s.l.* biting a leaf edge. PCoA ordination plots indicating (F) the differences in species composition among the three sites using all data, (G) congruence in species composition of all infected ant species found in 25 out of 27 plots and (H) different assemblage composition of non-biting infected ants. Some plots are stacked in the last two figures, because had the same infected ant species composition.

Figure 2. Relatioship between number of plots with infected individuals against number of plots with non infected individuals for (A) *O. unilateralis* complex and (B) other *Ophiocordyceps*. Each point represents a different species. The dotted line indicates a perfect ratio between infected and non-infected plots. The full line represent the model prediction of the regression for *O. unilateralis* complex ($r^2 = 0.95, F_{1,12} = 257, p < 0.001$). The regression analisys for other *Ophiocordyceps* were not significat ($r^2 = 0.18, F_{1,11} = 3.57, p = 0.085$).

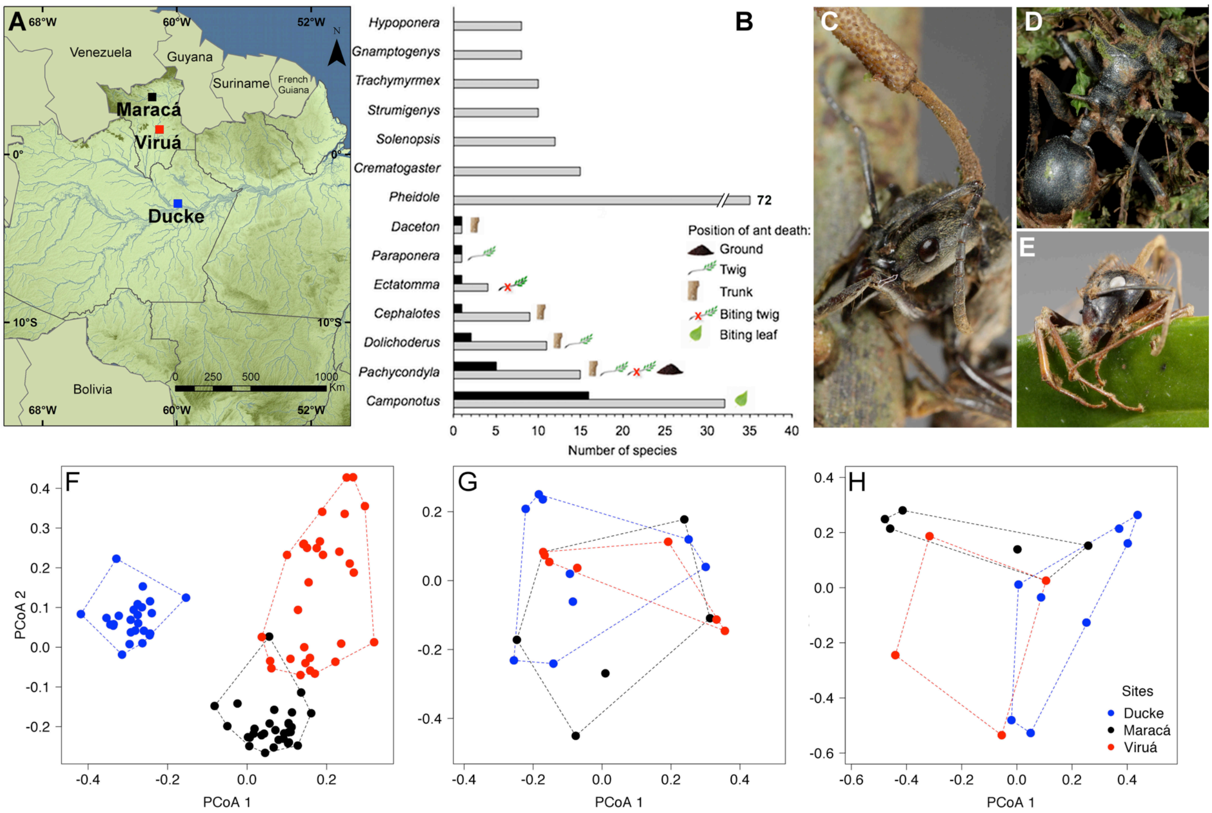
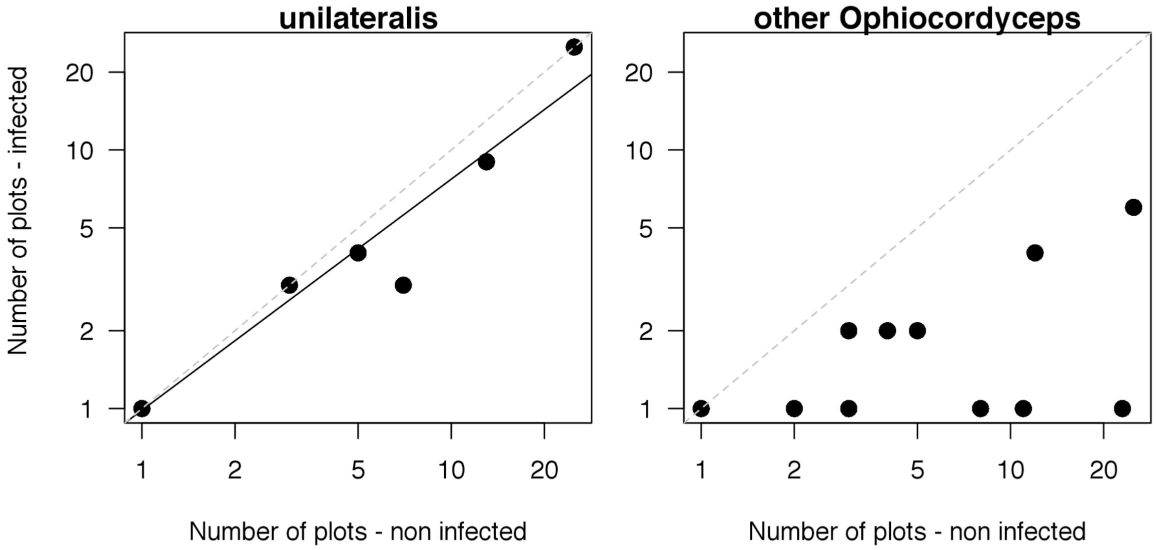

A
68°W
60°W
52°W
N
Venezuela
Guyana
Suriname
French Guiana
Maracá
Viruá
Ducke
0°
10°S
Bolivia
0 250 500 1000 Km
B
Hypoponera
Gnamptogenys
Trachymyrmex
Strumigenys
Solenopsis
Crematogaster
Pheidole
72
Daceton
Paraponera
Ectatomma
Cephalotes
Dolichoderus
Pachycondyla
Camponotus
Position of ant death:
Ground
Twig
Trunk
Biting twig
Biting leaf
0 5 10 15 20 25 30 35 40
Number of species
C
D
E
F
PCoA 2
0.4 0.3 0.2 0.1 0.0 -0.1 -0.2
-0.4 -0.2 0.0 0.2
PCoA 1
G
0.2 0.0 -0.2 -0.4
-0.4 -0.2 0.0 0.2 0.4
PCoA 1
H
0.4 0.2 0.0 -0.2 -0.4 -0.6
-0.6 -0.4 -0.2 0.0 0.2 0.4
PCoA 1
Sites
Ducke
Maracá
Viruá

Figure 1


unilateralis
other Ophiocordyceps
Number of plots - infected
20
10
5
2
1
20
10
5
2
1
1
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5
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20
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2
5
10
20
Number of plots - non infected
Number of plots - non infected

Figure 2

Supplementary Materials

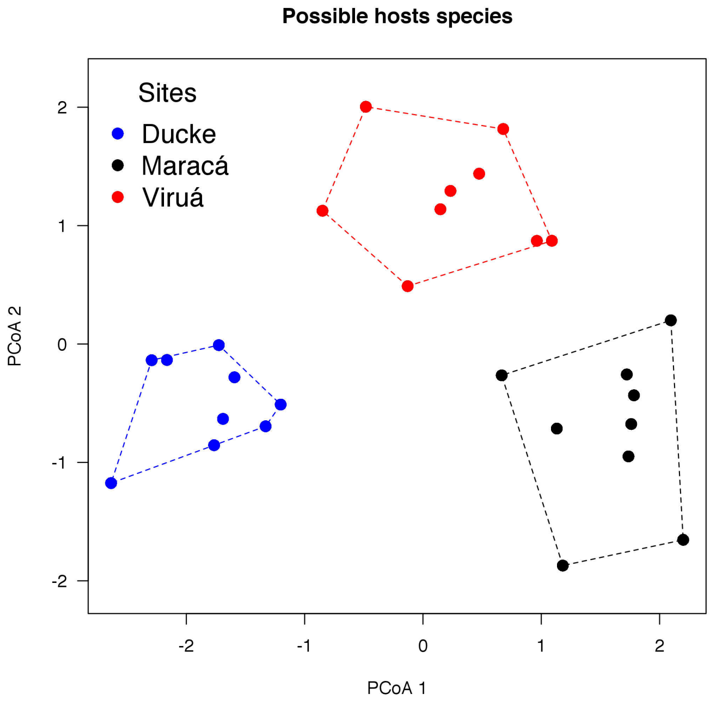

Figure S1. PCoA ordination plots based on Bray-Curtis similarity distance, indicating the differences in species composition among the three sites using possible ant hosts species (all ant species from the genera *Camponotus*, *Cephalotes*, *Daceton*, *Dolichoderus*, *Ectatomma*, *Pachycondyla* and *Paraponera* known to be host genera of *Ophiocordyceps*).

Capítulo 4

Baccaro, F.B., Rocha, I.F., Águila, B.E.G. del, Schietti, J., Emilio, T., Pinto, J.L.P. daV., Lima, A.L., & Magnusson, W.E. Changes in ground-dwelling ant functional diversity are correlated with water table level in an Amazonian terra firme forest. Submetido a *Biotropica*.

Changes in Ground-dwelling Ant Functional Diversity are Correlated with Water Table Level in an Amazonian Terra Firme Forest

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ABSTRACT

Areas with shallow water tables comprise a significant portion of tropical forests, and have distinctive forest structure and plant-assemblage composition. However, it is not clear how the water-table regime shapes distributions of other organisms. Here, we evaluated the influence of water-table level on terrestrial-ant assemblage richness, abundance and composition in a terra firme forest, in Central Amazonia. We sampled ants in ten 250 m-long transects, regularly distributed over 5 km^2 by extracting ants from 100 1-m^2 litter samples, 100 pitfall traps and 100 sardine baits. During one year, the water table level in each transect was monitored every 15 days with a 6-m deep dipwell. The relative abundance of individuals was lower in areas where the water table was closer to the surface (≤ 1 m depth) for longer periods (~ 5.5 months). However, the number of ant species was higher in transects where the water table was close to the surface more frequently. Changes in number of species were mainly a result of an increase in generalist species associated with a decrease in the number of specialist predators and small hypogaeic generalist foragers. Although disturbance by the water-table may increase ant diversity at larger scales, it reduces the ant assemblage functional diversity locally.

Key words: disturbance, flooding, functional group, guild, hydrology, tropical forest, riparian zone, species distribution.

RESUMO

Áreas com lençol freático superficial compreendem uma grande parte das florestas tropicais e essa condição hidrológica afeta a estruturada da vegetação e a composição de plantas. No entanto, não está claro como a variação do nível do lençol freático afeta a distribuição de espécies de outros organismos. Neste estudo, nós avaliamos a influência do nível do lençol freático na abundância, riqueza e composição de formigas, em dez transectos de 250 m de comprimento regularmente distribuídos em 5 km^2 em uma floresta de terra-firme na Amazônia Central. A assembléia de formigas foi amostrada pela extração de formigas em 100 amostras de folhiço de 1 m^2, 100 armadilhas de solo (pitfall) e 100 iscas de sardinha enlatada. Durante um ano, o nível do lençol freático em cada transecto, foi monitorado a cada 15 dias em poços de 6 m de profundidade. A abundância relativa de formigas foi menor em áreas onde o lençol freático ficou superficial (≤ 1 m de profundidade) por longos períodos (~ 5,5 meses). No entanto, o número de espécies de formigas foi maior em transectos onde o lençol freático chegou mais perto da superfície mais frequentemente. Embora a perturbação causada pela variação do lençol freático próximo da superfície possa aumentar a diversidade alfa, ela reduz a diversidade funcional da assembléia de formigas. O aumento no número de espécies pode ser atribuído principalmente ao aumento de espécies generalistas associado com a diminuição do número de espécies de formigas predadoras especialistas e generalistas pequenas que forrageiam no solo.

THE SPATIAL AND TEMPORAL DISTRIBUTION OF SOIL WATER IS AN IMPORTANT DESCRIPTOR IN MANY TERRESTRIAL ecosystems (Sanchez *et al.* 1998, Jansson *et al.* 2007). In tropical forests, seasonal changes in rainfall and spatial differences in soil properties create gradients of soil moisture, and determine forest structure and plant species distributions (Rodriguez-Iturbe 2000). Sandy and frequently waterlogged soils in valleys generally harbour different plant species than sites on plateaus with clay soils and relatively deeper water-tables (Kinupp & Magnusson 2005, Costa *et al.* 2005, Drucker *et al.* 2008, Zuquim *et al.* 2008, Schietti *et al.* in press). Although some environmental variables are correlated along the soil-water gradient, several herbs and palms species are confined to the bottomlands, suggesting incapacity to withstand the water stress in the upland clayey soils (Costa *et al.* 2005, 2008). Like plants, terrestrial ants are relatively sessile organisms and may experience stress caused by local changes in soil-water availability. Once established, ant nests tend to relocate locally (McGlynn *et al.* 2004), with relatively longer distances travelled only by inseminated winged females during the reproductive phase (Perfecto & Vandermeer 2002). Thus, areas with shallow water table may limit the distributions of ground-dwelling ant species by drowning established nests or preventing the foundation of new colonies.

Changes in ant-assemblage structure related to spatial distribution of soil water are evident in areas subjected to seasonal flooding. In those areas, terrestrial ants avoid drowning by evacuating nests to higher sites or vegetation (Wilson 1986, Adis & Junk 2002). During high-water periods, the colonies need to survive on stored energy sources or subsist on suboptimum energetic resources until floodwaters recede (Adis 1983, Adis & Junk 2002). Such disturbance limits the establishment of species that are not adapted to inundation, changing ant-assemblage composition (Majer & Delabie 1994, Ballinger *et al.* 2007, Mertl *et al.* 2009). Specialist and predatory species appear to have low tolerance to flooding, probably as a response to the reduction in prey availability (Adis *et al.* 1984, Adis & Junk 2002), while generalist and omnivorous species may be favoured (Milford 1999, Ballinger *et al.* 2007). Despite the fact that major changes in ant assemblage composition and richness are related with high degree of flooding, disturbance caused by low flood frequency and low flood intervals can also impact ant assemblage structure (Mertl *et al.* 2009). Therefore, seemed reasonable that disturbance caused by vertical changes in the water table may also be operating even in sites not subject to flooding. In contrast to flooding, the effect of water-table fluctuation may be more subtle, limiting the soil volume available for ant colonies, which in turn may limit the spatial distribution of ant species (Seal & Tschinkel 2010).

Studies that have investigated the effect of water-table fluctuations on ant community structure are restricted to the subtropics (Seal & Tschinkel 2010, Tschinkel 1988, Tschinkel *et al.* 2012). This is surprising, given that areas with potentially shallow water table comprise a large part of tropical forests (Sombroek 2000, Renno *et al.* 2008), and are normally under high human pressure (Tockner & Stanford 2002). Here, we evaluate the influence of water-table level on terrestrial-ant richness, abundance and species composition in a tropical forest that is not subject to periodic flooding. To examine ecological correlates of ant distribution patterns, we used a functional group approach, based on diet, nesting habits, external morphology and phylogeny (Delabie *et al.* 2000, Silvestre *et al.* 2003, Silva & Brandão 2010), which provides a useful framework to describe and analyze ant-assemblage structure. Based on previous studies, we predicted that species occurrence and richness would be lower in areas with relatively shallow water table. We also predicted that changes in community composition would be mediated principally by decrease in occurrence and number of hypogaeic and specialist species in areas where the water table is closer to the surface.

METHODS

STUDY SITE AND SAMPLING DESIGN.—

The study was conducted at Manaquiri module, a Brazilian Biodiversity Research Program (PPBio) site established by the State of Amazonas PRONEX program located between the Purus and Madeira Rivers, Brazil (03°41' S, 60°34' W). The terrain is flat to gently undulating (elevation 37-45 m asl. based on Shuttle Radar Topography Mission – SRTM images), and characterized by seasonally waterlogged soils with small intermittent streams. The site is covered by relatively undisturbed dense forest, but small areas show evidence of human disturbance, such as selective logging and extraction of non-timber forest products. The area receives an average of 2225 mm of rain annually (based on interpolated rainfall gauges data from 1970 to 2011 available from CPTEC web site http://bancodedados.cptec.inpe.br/downloadBDM), which is distributed seasonally. The rainy season occurs between November and April and a drier period between May and October.

As the terrain is predominantly flat and the soils are silty and poorly-drained, some areas located near intermittent streams may be flooded. However, those flooded areas are not equivalent to varzea and igapó forests, which receive a predictable and regular flood pulse from overflow of large rivers. Flooded areas in the Manaquiri module are more unpredictable and normally related to heavy rains, especially during the rainy season. Those floods create temporary small water bodies (1-3 m diameter), submerging the soil and litter for relatively short periods (10-12 h) after rain. However, depending on the rainfall regime, some areas may remain with shallow water-table for several days.

We sampled ten 250m-long transects that were regularly distributed over 5 km^2. Sampling was done along the center lines of RAPELD plots (Costa & Magnusson 2010), which follow terrain contours, located at 1 km intervals along two 5 km-long trails (Fig. S1). As plot center lines follow the topographic contours, variation in water-table depth within transects was minimized.

ANT SAMPLING.—

Ten sampling stations were established at 25-m intervals along each transect, avoiding small depressions with may be filled with water after heavy rains during the rainy season. Each sampling station consisted of a pitfall trap, a 1m2 litter sample (Winkler sacks) and a bait sample. These methods are often combined to describe tropical ant assemblages (Souza *et al.* 2012). At each sampling station, 1 m2 of litter was sifted through a 1 cm2 mesh, placed in Winkler sacks and hung in a field camp at ambient temperature (about 28 ± 8°C) for 48 h to extract the ants. A 9.5 cm internal-diameter pitfall trap, partially filled with 96 percent alcohol and a drop of detergent, was established adjacent (~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 white paper (10 cm by 7 cm) on the litter surface. After 45 minutes all ants on the paper were collected and preserved in 96 percent alcohol. The baiting and litter-sampling procedures were undertaken between 0800 h and 1700 h. The site was sampled in October 2009, during the dry season.

The ants from the Winkler sacks, pitfall traps and bait samples were identified to morphospecies or species whenever possible. Voucher specimens were deposited in the Entomological Collection of the Instituto Nacional de Pesquisas da Amazônia (INPA, Manaus, Brazil). The raw data and metadata describing collection protocols can be downloaded from PPBio web site http://ppbio.inpa.gov.br/Port/inventarios/br319/km100.

Species were placed into functional groups based on classifications for Neotropical ants (Delabie *et al.* 2000, Silvestre *et al.* 2003, Silva & Brandão 2010) and on our observations of their foraging behavior, food choice and nesting ecology. This functional-group scheme is based on microhabitat distribution, natural history information, eye size, body size and shape, and phylogeny; grouping species with potentially similar life styles. We followed the nomenclature proposed by Silva and Brandão (2010): (1) Large-sized epigaeic generalist predators; (2) Medium-sized epigaeic generalist predators; (3) Dacetini predators (specialist predators with kinetic mandible and cryptic behavior); (4) Hypogaeic predators; (5) Small-sized hypogaeic generalist foragers; (5) Generalists; and (7) Litter-nesting fungus growers. We grouped the Medium-sized hypogaeic generalist predators, Hypogaeic generalist predators with vestigial eyes and specialists predators living in soil superficial layers into a single Hypogaeic predators functional group, because these three functional groups represent species from the same trophic position and have relatively large overlap in morphological space (Silva & Brandão 2010). Arboreal species that occasionally forage in soil/litter, army ants and subterranean mealy-bug specialists were not included in analyses. These functional groups are not adequately sampled with the sampling methods used and may increase the noise in analyses. A list of species membership for each functional group can be found in Table S1.

MEASURING WATER-TABLE VARIATION.—

A 6m-deep dipwell was installed in each transect. Approximately 5.5 m was below and 0.5 m above ground level. The dip well consisted of a 5 cm diameter plastic pipe with holes drilled in the lower portion (30 cm) to permit water flow. The holes were covered with a thin polyester mesh to avoid obstruction by mud, and the dip wells were capped to prevent entry of rainwater and litter. A lateral orifice equilibrated the air pressure in the pipe. Between January 2010 and January 2011, the water-table level was manually monitored every 15 days using a measuring tape.

We used the number of 15-day periods in which the water table was ≤ 1 m from the surface as a measure of probable disturbance caused by water-table level on ant assemblages. When the water table is less than 1 m, vertical water percolation decreases (Fan & Miguez-Macho 2010), favoring short-term flooding of shallow depressions which normally do not flood during the dry season (F. B. Baccaro, pers. obs.). Therefore, periods with water table less than 1 m deep represent potential disturbance and relatively less vertical soil available for ant colonies.

DATA ANALYSIS.—

The number of 15-day periods in which the water table was ≤ 1 m from the surface was used as a predictor variable for changes in ant abundance, species richness and composition. The overall ant abundance and total number of ant species per transect were regressed against the frequency of water-table depth < 1m. To avoid overestimation of large colonies, we used the number of occurrences of each species as a measure of ant abundance per transect. Therefore, the abundance for each species varied from 0 to maximum of 10 per transect.

We used non-metric multidimensional scaling (NMDS), to evaluate the relationship between the water-table gradient and overall ant-assemblage composition. NMDS analysis was done with frequency standardizations per plot and the Bray-Curtis index as dissimilarity measurement. The adjusted r^2 of the original ant dissimilarity matrix regressed against the dissimilarity in the two-dimensional NMDS was used to evaluate the adequacy of the ordination (McCune & Grace 2002). We fitted the water-table gradient (frequency of water-table depth < 1m) to the NMDS ordination using the envfit-function of the R package vegan. The significance of the correlation of point projections (ant species composition in each plot) onto the predictor vector (frequency of water-table depth < 1m) was estimated with 999 permutations.

To describe and interpret the major pattern in detail, the abundance and number of ant species in each functional group was also individually regressed against the frequency of water-table depth < 1m. Residual analyses were used to check the error distribution and the suitability of the regression models. The analyses were undertaken with R software (R Development Core Team 2011) using the package vegan (Oksanen *et al.* 2011).

RESULTS

We collected 185 ant species/morphospecies representing 42 genera in nine subfamilies. Strictly arboreal, subterranean mealy-bug dependent species and army ants, which were not included in analyses, comprised 25 species distributed in 10 genera (Acropyga, Azteca, Cephalotes, Camponotus, Crematogaster, Dolichoderus, Eciton, Labidus, Platythyrea and Pseudomyrmex). The most specious genus of ground-dwelling ants was Pheidole with 36 species, followed by Solenopis and Strumigenys with 11 species each. At least one of these three genera were collected in 20 percent of baits, 32 percent of pitfall traps and 29 percent of

Winkler samples, and were recorded in all sampling stations (300). Solenopsis sp.1 and Strumigenys cf. denticulata were the most abundant species, sampled in 35 and 25 percent of sampling stations, respectively. However, 31 percent of species were recorded in only one sampling station.

Water-table level showed marked variation between seasons. Two transects had water in the dipwell throughout the year (Fig. 1). However, during the dry season, the water-table level in the remaining eight transects was below our dipwells. The number of 15-day periods when the water table was ≤ 1 m ranged from zero to 11 (approximately 5.5 months) among transects (Fig. 1). Transect T1 and T6 had some small depressions with water after heavy rains during the rainy season. These small ponds (varying from 1 to 3 m diameter) typically dried up between 10 and 12 h after rainfall, but the litter and the soil remained saturated with water for longer periods. During the rainy season, the same small pounds may be filled with water for several days (specially in T1 transect).

The abundance of ant species, measured by the total number of stations occupied by each species per transect (Fig. 2A), was lower in areas with shallow water table ≤ 1 m ($r^2 = 0.44$, $b = -4.58$, $p = 0.038$). However, contrary to our prediction, the total number of ant species (Fig. 2B) increased in areas where the water table was close to the surface for longer periods ($r^2 = 0.47$, $b = 0.54$, $p = 0.029$).

The ant assemblage composition was also related to the water-table gradient. The major pattern of ant assemblage composition captured by the NMDS analysis (Fig. 3) showed a strong correlation with the frequency of water-table depth < 1m ($r^2 = 77.62$, $p = 0.008$). The final configuration of the NMDS with two axes (stress 0.13) explained ~ 73 percent of the variance in differences in ant species composition.

All functional groups, except generalist species, decreased in abundance with increase in frequency of water-table depth < 1m (Table 1), but this pattern was more evident for the large-sized epigaeic predators (Fig. 4A) and the small-sized hypogaeic generalist foragers (Fig. 4B). However, the number of species per functional group did not show a similar trend. The overall increase in species richness was mainly caused by an increase of nearly 40 percent in generalist species in areas where the peaks of shallow water table were more frequent (Fig. 4C). Conversely, specialized species, represented by small-sized hypogaeic species (Fig. 4D) and Dacetini predator species (Fig. 4E) decreased as the number of periods with water table ≤ 1 m depth increased. The number of species of large-sized epigaeic generalist predators, medium-sized epigaeic generalist predators, hypogaeic generalist predators and litter-nesting fungus growers were not correlated with the gradient of water-table level (Table 1).

DISCUSSION

Water-table level was strong correlated with changes in abundance, richness and assemblage composition of ground-dwelling ants at our site in Central Amazonia. As hypothesized, the overall abundance of ants was lower in areas with shallow water table (≤ 1 m depth). However, contrary to our prediction, the number of terrestrial ant species increased along the gradient of water-table level. Changes in species richness were mainly due to an increase in generalist species associated with a decrease in the number of specialist predators and the small-sized hypogaeic generalist foragers. The different responses among ant functional groups suggest that the effects of water table in this forest are more subtle than in tropical seasonally-flooded environments.

A shallow water table means less soil volume available for ant colonies (Seal & Tschinkel 2010, Tschinkel 1988), but also means relatively higher soil moisture and therefore less desiccation risk. Soil/litter moisture can favor some species and also modify the activity of terrestrial ant species even in tropical ecosystems. Overall, ant activity and species richness tend to be higher in more humid seasons and habitats (Levings 1983, Kaspari & Weiser 2000). Therefore, the moisture gradient may explain why we found more species in areas with relatively superficial water table. However, this process is hard to conciliate with the decrease in overall ant abundance in these areas, suggesting that another mechanism may be operating.

More generalist species associated with less specialized species suggests that water table is a source of disturbance for ant species rather than a simple moisture gradient. Shallow water table may favor lateral water percolation and temporary flooding, which is a recurrent disturbance event near small streams (Pazin *et al.* 2006). However, the scale and level of disturbance caused by water-table fluctuations are more subtle compared with areas subjected to a regular flood pulse from overflow of large rivers. The periodic flooding in varzea and igapó forests may shape ant communities regionally, reducing diversity in large and continuous areas close to river margins (Adis & Junk 2002). On the other hand, temporary water bodies created after rain or superficial water table may disturb ant assemblages locally, leaving small patches of relatively well-drained soil available. Therefore, disturbance mediated by changes in water table level in terra firme ant assemblages, may be similar to low flooding intensity areas in floodplains (Mertl *et al.* 2009), favoring generalist species and limiting colony establishment and growth of specialized species (i.e. specialist and hypogaeic species).

The Dacetini-predator functional group is a relatively well studied set of cryptic specialist predators that live and forage in the leaf litter and rotten wood (Bolton 1999). Although, little information about small-sized hypogaeic generalist foragers is available, their morphology (small ants with very small or vestigial eyes), suggest that these species live and forage in the soil (Brown 2000). Both groups show specialized foraging and nesting habitats, which are expected to be more sensitive to disturbance caused by soil water compared to other functional groups (Majer & Delabie 1994). In our study site, during the rainy season, four of ten transects had water-table levels around 1 m depth during at least three months. In this period, recurrent disturbance events caused by temporary flooding, or by increase in water table level may force nest relocation to avoid drowning and/or limit the establishment of colonies of these species.

The absence of changes in abundance and number of species observed in litter-fungus growers and medium-sized epigaeic generalist predators indicates that species in these functional groups may be tolerant to disturbance mediated by changes in water-table level. As the life styles of medium-sized epigaeic generalist predator species have some overlap with generalist species (Silva & Brandão 2010), it is possible that nesting and foraging habits also allow them to recolonize or persist during the rainy season in more disturbed transects. However, the lack of evidence of a decrease in frequency and richness of litter-fungus growers in more disturbed transects was surprising. The fungus-gardening ant species feed the developing brood and, to a lesser extent, adult workers on symbiotic fungus (Bass & Cherrett 1995). The symbiotic fungus has narrow humidity and temperature requirements and, consequently, adequate conditions for fungus growth in the soil layer are limited (Roces & Kleineidam 2000, Bollazzi *et al.* 2008, Seal & Tschinkel 2010). Our results suggest that, unlike fungus-growing species that nest in the soil, litter fungus-growers have broader microhabitat tolerances. Some of litter fungus-growers species can also take advantage of litter trapped by tree trunks and palms above ground using as complementary nesting sites during the rainy season. Moreover, as litter receives unpredictable input of vegetable and animal detritus and its organic material is constantly subject to decomposition (Facelli & Pickett 1991), a broader microhabitat tolerance for symbiotic-fungus growth may be an evolutionary adaptation to higher disturbance and more variable environment.

Disturbance can reduce overall ant diversity, but may also favor the increase of adapted species (Gibb & Hochuli 2003). Most of the generalists in this study are species of

Solenopsis, Wasmannia and Pheidole. In general, these species are omnivores with varied nesting habitats and aggressive behavior against co-occurring species at artificial resources (Delabie *et al.* 2000, Baccaro *et al.* 2010, 2012). Aggressive behavior and competitive traits favor nest relocation and/or colony maintenance under stress, facilitating establishment in disturbed areas (King & Tschinkel 2008, Vonshak *et al.* 2009, Krushelnycky & Gillespie 2010). Mertl *et al.* (2010) found that approximately 60 percent of 39 Pheidole species were not affected or showed some degree of tolerance to periodic flooding in an Ecuadorian tropical forest. Our results suggest that disturbance created by a relatively shallow water table may also favor the occurrence of other generalists species, such as Solenopsis and Wasmannia. However, to what extent the increase in the number of generalist species is a result of colonization/competition abilities or disturbance resistance requires further scrutiny.

Our results suggest that changes in water-table level can lead to changes in ant species richness, abundance and composition even in locations with little or no superficial flooding. Disturbance mediated by the water table appears to increase species richness, but also decreases the functional diversity, with proportionally less specialists and hypogaeic species than generalist species. The relationship between ant diversity and local water table has important implications for conservation, given that areas with shallow water table, in most cases riparian zones, are among the most threatened ecosystems in tropical forests (Tockner & Stanford 2002). As ants comprise a large part of the animal biomass (Fittkau & Klinge 1973) and are among the most ubiquitous tropical-forest predators, scavengers and seed dispersers (O’Donnell *et al.* 2005, Manzaneda & Rey 2008), human modification of the water-table dynamics may lead to changes in ant-assemblage functional diversity that could affect many other elements in the ecosystem.

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Table 1. Results of regression models between number of fortnights with water table ≤ 1 m depth and abundance and number of ant species per functional group. Ant abundance was estimated as the total number of sampling stations occupied by each species per transect. Statistically significant models ($p \leq 0.05$) are indicated by asterisks.

	Abundance			Richness		
Ant functional groups	r^2	*b*	*p*	r^2	*b*	*p*
Dacetini predators	0.33	-0.69	0.080	0.62	-0.25	0.007*
Generalists	0.01	0.36	0.781	0.60	1.06	0.009*
Hypogaeic generalist predators	0.02	-0.20	0.676	0.13	-0.09	0.297
Large-sized epigaeic generalist predators	0.76	-0.99	0.001*	0.01	0.06	0.758
Litter-nesting fungus growers	0.18	-0.51	0.221	0.01	0.06	0.788
Medium-sized epigaeic generalist predators	0.12	-0.25	0.328	0.02	-0.08	0.672
Small-sized hypogaeic generalist foragers	0.43	-0.72	0.040*	0.45	-0.22	0.035*

Figure legends

FIGURE 1. Water table level monitored fortnightly between January 2010 and January 2011 in 10 transects. Gray triangles represent samples in which the water-table depth was ≤ 1 m, open circles samples with water-table depth > 1 m, and the "x" represents samples in which no water was observed in the dip well. Transects were ordered by number of fortnights with water table ≤ 1 m depth. Transects labels are the same as on Fig. S1.

FIGURE 2. Relationships between number of fortnights with water table ≤1 m depth and (A) ant abundance, measured as the sum of the number of stations occupied by each species per transect, and (B) number of ant species.

FIGURE 3. The water-table gradient vector fitted onto the NMDS scores of the ant assemblage composition. The symbol size is proportional to the number of fortnights with water table ≤ 1 m depth. Transects labels are the same as on Fig. S1.

FIGURE 4. Relationships between number of fortnights with water table ≤ 1 m depth and (A) frequency of large-sized epigaeic predators, (B) frequency of small-sized hypogaeic generalist foragers, (C) number of Generalists species, (D) number of Hypogaeic generalist predators species and (E) number of Dacetini predator species.

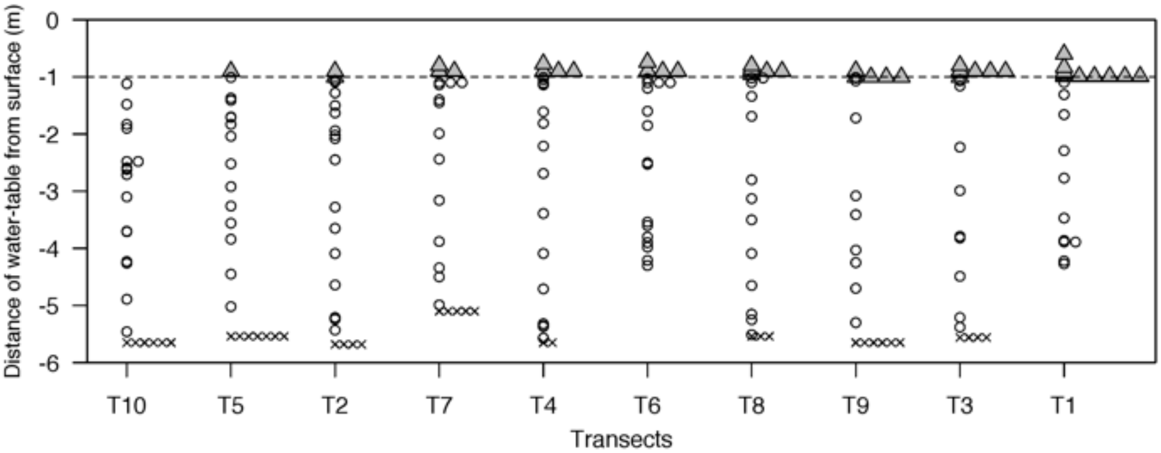
Distance of water-table from surface (m)
0
-1
-2
-3
-4
-5
-6
T10
T5
T2
T7
T4
T6
T8
T9
T3
T1
Transects

Figure 1

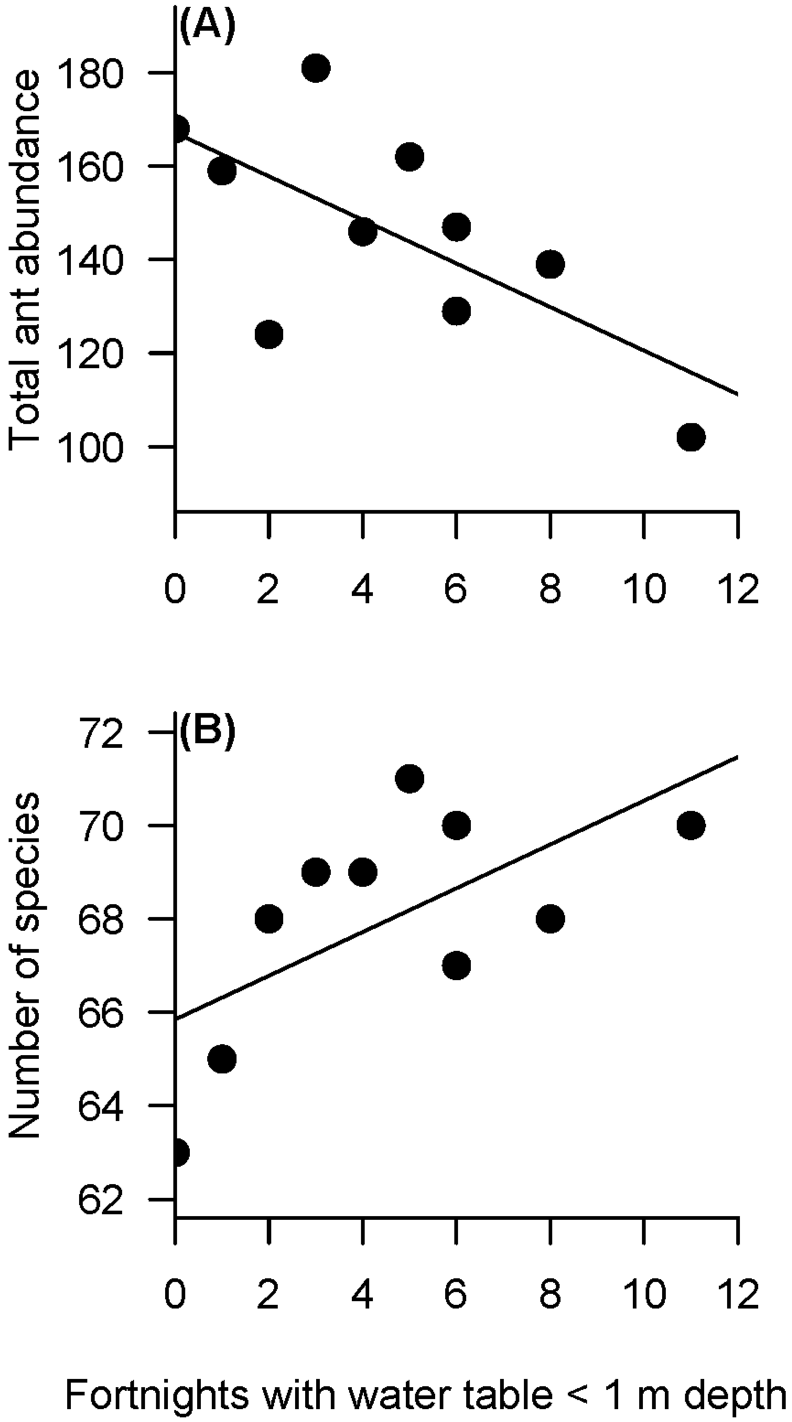
(A)
Total ant abundance
180
160
140
120
100
0
2
4
6
8
10
12
(B)
Number of species
72
70
68
66
64
62
0
2
4
6
8
10
12
Fortnights with water table < 1 m depth

Figure 2

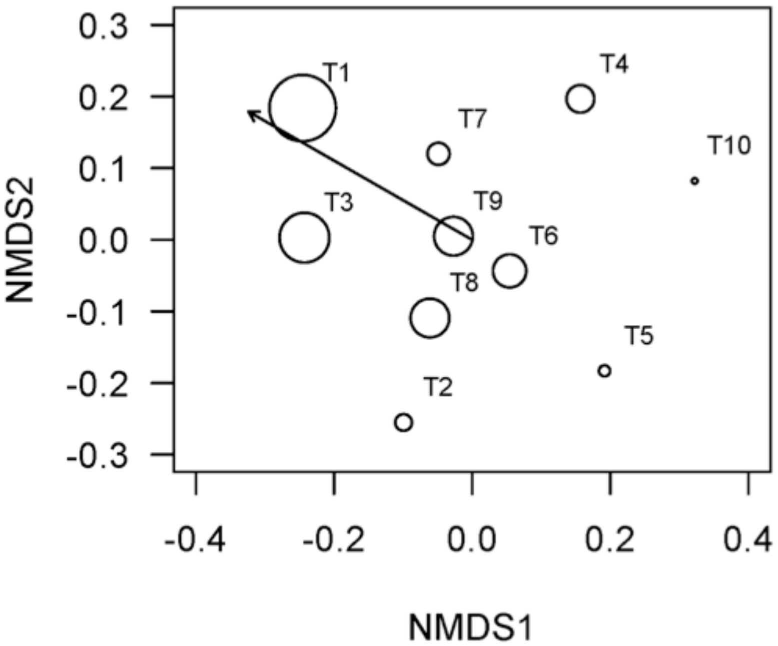
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
NMDS2
-0.4
-0.2
0.0
0.2
0.4
NMDS1
T1
T2
T3
T4
T5
T6
T7
T8
T9
T10

Figure 3

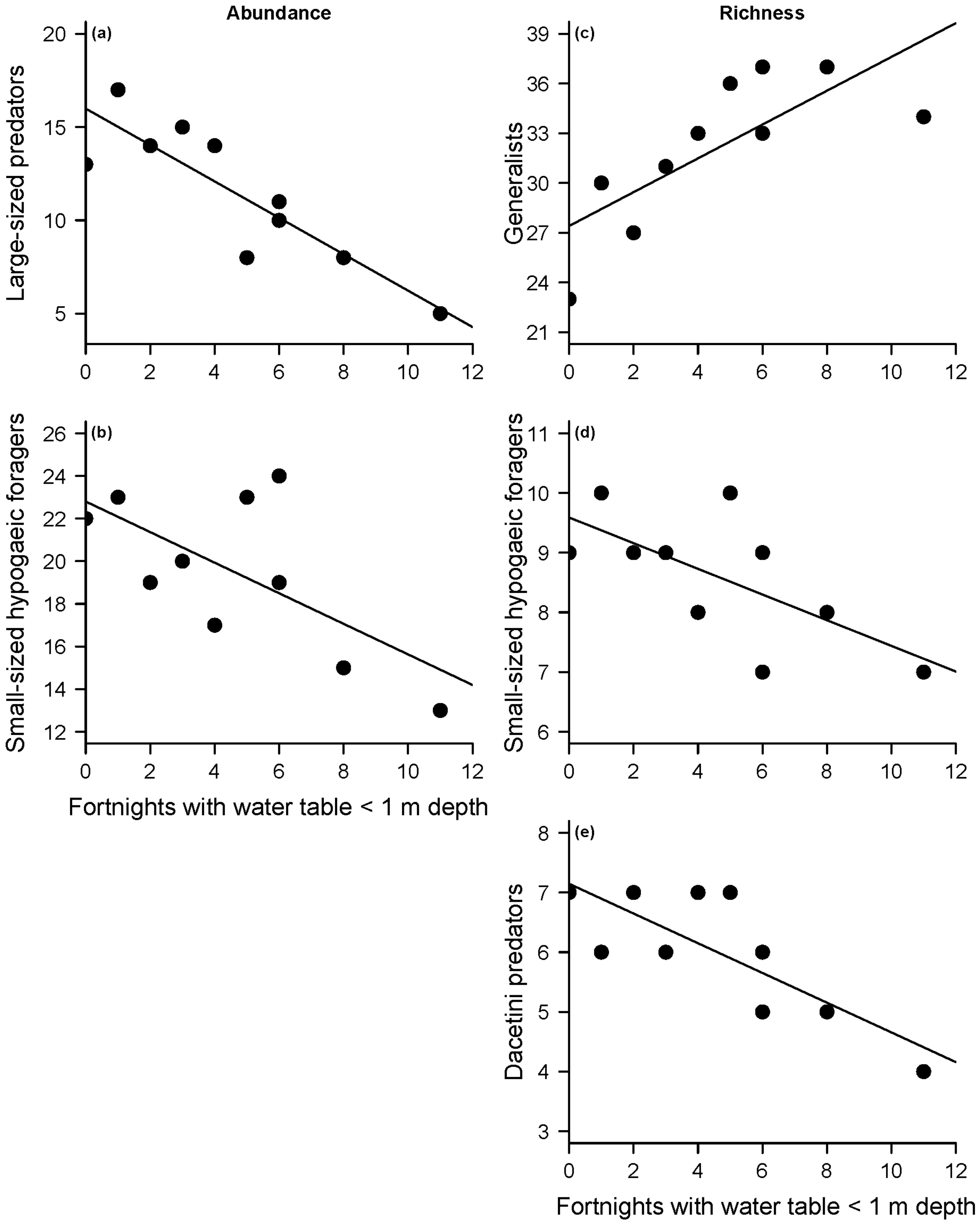
Abundance
Richness
(a)
(b)
(c)
(d)
(e)
Large-sized predators
Small-sized hypogaeic foragers
Generalists
Small-sized hypogaeic foragers
Dacetini predators
20
15
10
5
26
24
22
20
18
16
14
12
39
36
33
30
27
24
21
11
10
9
8
7
6
8
7
6
5
4
3
0
2
4
6
8
10
12
Fortnights with water table < 1 m depth
Fortnights with water table < 1 m depth

Figure 4

Supporting Information - Biotropica

Changes in Ground-dwelling Ant Functional Diversity are Correlated with Water Table Level in an Amazonian *Terra Firme* Forest

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FIGURE S1. Map of the study region using LandSat image from GeoCover/NASA. Black circles represent the locations of 250 m transects in the 5 x 1 km rectangular grid. Magenta indicates deforested areas and green shades indicate forested areas (dark green shows mature forests and light green areas of forest regrowth).

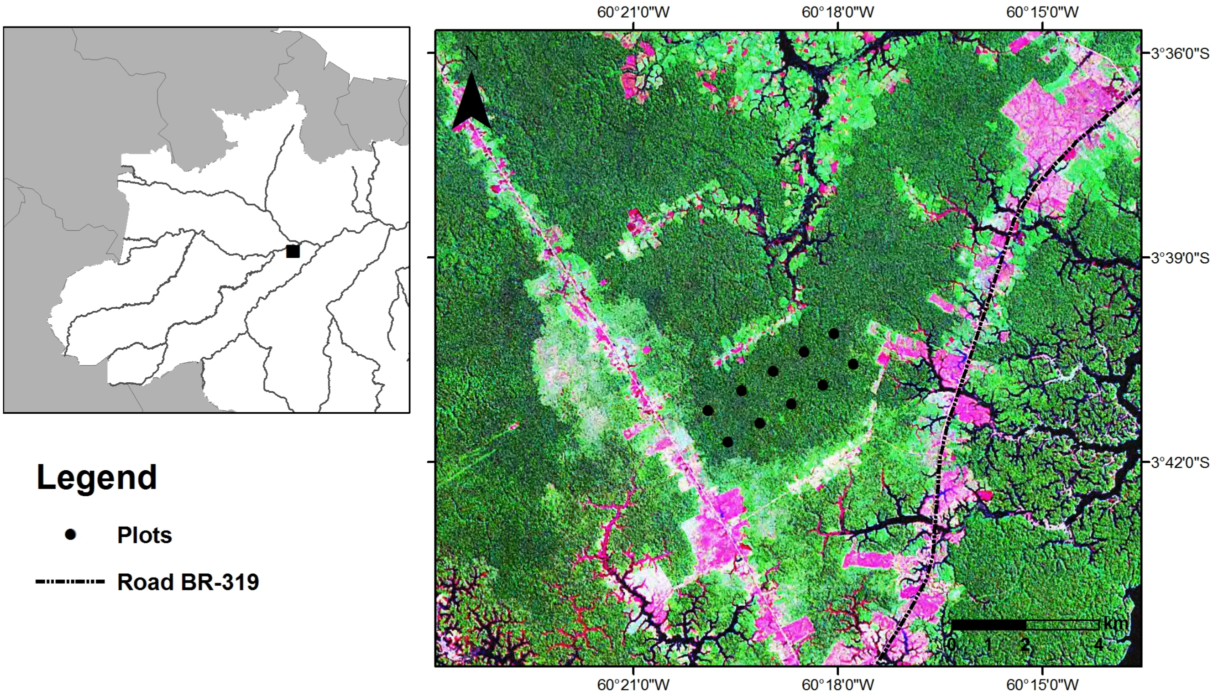

TABLE S1. Frequency of occurrence by sampling method (% occurrence in 100 sampling stations) and functional group classification following Silva & Brandão (2010) of ant assemblages in a terra-firme forest, Central Amazonia, Brazil

	Frequency (%)		
Functional groups	Bait	Pitfall	Winkler
Dacetini predators			
Basiceros balzani	-	0.03	0.97
Strumigenys beebei	-	-	1.00
Strumigenys cf. denticulata	-	0.05	0.95
Strumigenys sp.01	-	0.14	0.86
Strumigenys sp.03	-	-	1.00
Strumigenys sp.04	-	0.09	0.91
Strumigenys sp.05	-	-	1.00
Strumigenys sp.06	-	-	1.00
Strumigenys sp.07	-	-	1.00
Strumigenys sp.08	-	-	1.00
Strumigenys trudifera	-	-	1.00
Generalists			
Blepharidatta brasiliensis	-	-	1.00
Brachymyrmex heeri	-	1.00	-
Brachymyrmex sp.01	0.05	0.15	0.80
Brachymyrmex sp.02	-	-	1.00
Brachymyrmex sp.03	-	1.00	-
Camponotus femoratus	0.40	0.49	0.11
Camponotus rapax	0.57	0.43	-
Creamtogaster brasiliensis	0.21	0.21	0.59
Creamtogaster carinata	-	0.38	0.63
Creamtogaster erecta	-	-	1.00
Creamtogaster flavosensitiva	-	0.27	0.73
Creamtogaster limata	0.35	0.43	0.22
Creamtogaster sotobosque	-	0.33	0.67
Creamtogaster tenuicula	-	0.60	0.40

Dolichoderus bispinosus	0.57	0.14	0.29
Megalomyrmex sp.02	-	-	1.00
Megalomyrmex sp.03	-	-	1.00
Megalomyrmex sp.04	-	0.50	0.50
Megalomyrmex sp.06	-	-	1.00
Megalomyrmex sp.07	-	-	1.00
Megalomyrmex sp.08	-	-	1.00
Monomorium sp.01	-	-	1.00
Nylanderia sp.01	0.07	0.40	0.53
Nylanderia sp.02	-	0.32	0.68
Ochetomyrmex semipolitus	0.14	0.45	0.41
Pheidole cephalica	-	1.00	-
Pheidole deima	-	1.00	-
Pheidole embolopyx	-	0.86	0.14
Pheidole exigua cf.	0.02	0.19	0.79
Pheidole meinerti	-	0.13	0.87
Pheidole meinerti C.	-	0.88	0.13
Pheidole prox. *exigua*	0.37	0.33	0.30
Pheidole sp.01	0.50	0.17	0.33
Pheidole sp.02	-	1.00	-
Pheidole sp.03	-	0.40	0.60
Pheidole sp.04	0.07	0.49	0.44
Pheidole sp.05	0.32	0.42	0.26
Pheidole sp.06	-	0.67	0.33
Pheidole sp.06 A.	-	1.00	-
Pheidole sp.09	0.55	0.40	0.05
Pheidole sp.10	1.00	-	-
Pheidole sp.11	0.13	0.75	0.13
Pheidole sp.111	-	1.00	-
Pheidole sp.13	0.24	0.44	0.32
Pheidole sp.15	0.14	0.86	-
Pheidole sp.17	-	0.86	0.14
Pheidole sp.20	0.07	0.87	0.07

Pheidole sp.22	-	0.82	0.18
Pheidole sp.24	-	0.31	0.69
Pheidole sp.25	-	0.56	0.44
Pheidole sp.25 G.	0.80	0.10	0.10
Pheidole sp.25 P.	-	0.50	0.50
Pheidole sp.26	-	0.50	0.50
Pheidole sp.33	-	0.29	0.71
Pheidole sp.40	-	-	1.00
Pheidole sp.50	-	0.50	0.50
Pheidole sp.60	-	-	1.00
Pheidole sp.70	-	-	1.00
Pheidole sp.72	-	-	1.00
Pheidole sp.73	-	0.50	0.50
Pheidole sp.77	-	0.50	0.50
Solenopsis geminata	-	-	1.00
Wasmannia auropunctata	0.08	0.29	0.63
Wasmannia scrobifera	-	-	1.00
Hypogaeic generalist predators			
Adelomyrmex sp.01	-	-	1.00
Cryptomyrmex boltoni	-	-	1.00
Hypoponera sp. 01	-	1.00	-
Hypoponera sp. 04	-	-	1.00
Hypoponera sp. 06	-	-	1.00
Hypoponera sp. 08	-	-	1.00
Hypoponera sp. 09	-	0.08	0.92
Hypoponera sp.11	-	-	1.00
Hypoponera sp.12	-	-	1.00
Hypoponera sp.13	-	-	1.00
Hypoponera sp.14	-	0.06	0.94
Rogeria alzatei	-	-	1.00
Thyphlomyrmex sp.01	-	-	1.00
Large-sized epigaeic generalist predators			
Anochetus diegensis	-	0.31	0.69

Anochetus horridus	-	0.09	0.91
Ectatomma brunneum	-	1.00	-
Ectatomma edentatum	-	0.82	0.18
Ectatomma lugens	-	1.00	-
Ectatomma ruidum cf.	-	0.67	0.33
Gnamptogenys haenschi	-	1.00	-
Gnamptogenys tortuolosa	-	1.00	-
Leptogenys sp.04	-	-	1.00
Odontomachus haematodus	-	0.50	0.50
Odontomachus meinerti	-	-	1.00
Odontomachus opaciventris	-	1.00	-
Odontomachus scalptus	-	1.00	-
Odontomachus caelatus	-	-	1.00
Pachycondyla apicalis	-	1.00	-
Pachycondyla arhuaca	-	-	1.00
Pachycondyla commutata	-	1.00	-
Pachycondyla constricta	-	0.75	0.25
Pachycondyla crassinoda	-	1.00	-
Pachycondyla harpax	-	0.88	0.13
Pachycondyla impressa	-	1.00	-
Pachycondyla obscuricornis	-	1.00	-
Pachycondyla sp.02	-	-	1.00
Litter-nesting fungus-growers			
Apterostigma auriculatum	-	-	1.00
Apterostigma gr. pilosum	-	-	1.00
Apterostigma sp.02	-	-	1.00
Cyphomyrmex gr. rimosus	-	0.08	0.92
Cyphomyrmex sp.01	-	-	1.00
Cyphomyrmex sp.02	-	1.00	-
Myrmicocrypta sp.01	-	-	1.00
Myrmicocrypta sp.02	-	-	1.00
Sericomyrmex sp.01	-	0.75	0.25
Sericomyrmex sp.02	-	0.75	0.25

Sericomyrmex sp.03	-	1.00	-
Trachymyrmex cornetzi	-	0.50	0.50
Trachymyrmex diversus	-	1.00	-
Trachymyrmex farinosus	-	-	1.00
Trachymyrmex mandibulares	-	1.00	-
Trachymyrmex sp.01	-	0.50	0.50
Trachymyrmex sp.02	-	0.50	0.50
Trachymyrmex sp.03	-	-	1.00
Trachymyrmex sp.04	-	0.67	0.33
Medium-sized epigaeic generalist predators			
Gnamptogenys horni	-	0.27	0.73
Gnamptogenys horni cf.G	-	-	1.00
Gnamptogenys sp.05	-	-	1.00
Gnamptogenys sp.08	-	-	1.00
Gnamptogenys sp.09	-	-	1.00
Gnamptogenys sp.10	-	-	1.00
Gnamptogenys sp.11	-	1.00	-
Hylomyrma immanis	-	0.17	0.83
Hylomyrma sp.02	-	-	1.00
Megalomyrmex balzani	-	1.00	-
Thaumatomyrmex atrox	-	-	1.00
Small-sized hypogaeic generalist foragers			
Carebara sp.01	-	-	1.00
Carebara sp.02	-	0.13	0.88
Discothyrea sexarticulata	-	-	1.00
Prionopelta modesta	-	-	1.00
Rogeria sp.02	-	-	1.00
Rogeria sp.03	-	-	1.00
Solenopsis sp.01	0.07	0.22	0.72
Solenopsis sp.02	0.33	0.13	0.53
Solenopsis sp.03	0.17	0.33	0.50
Solenopsis sp.04	0.40	0.40	0.20
Solenopsis sp.06	-	0.50	0.50

Solenopsis sp.07	-	0.30	0.70
Solenopsis sp.08	-	0.24	0.76
Solenopsis sp.09	-	-	1.00
Solenopsis sp.12	-	0.40	0.60
Solenopsis sp.13	-	0.36	0.64

Síntese

A estrutura das assembléias de formigas estudadas esteve mais fortemente relacionada com restrições ambientais do que com interações antagonistas, como competição inter-específica e parasitismo. Apesar de algumas espécies apresentarem comportamento agressivo na presença de outras espécies e serem frequentes no ambiente, formigas de solo e folhiço forrageiam em uma área relativamente pequena. Mesmo as espécies dominantes, que recrutam em massa (mais de 100 operárias) e frequentemente monopolizam recursos alimentares, andam em média 2-3 m ao redor do ninho. Consequentemente, o efeito das espécies dominantes em escalas que efetivamente descrevem assembléias de formigas é limitado nessas florestas. Formigas com comportamento agressivo podem controlar o acesso de outras espécies a recursos alimentares efêmeros, mas a maior parte da assembléia de formigas não está correlacionada com a abundância das espécies dominantes.

O papel de parasitas especializados (que alteram o comportamento de seus hospedeiros) na estruturação das comunidades de formigas, também parece ser pequeno. O desacoplamento dos padrões de diversidade de alguns parasitas e seus hospedeiros entre sítios de coleta sugere que o número de espécies de hospedeiros passíveis de manipulação comportamental é relativamente pequeno, limitando o efeito do parasitismo regionalmente. Localmente, o baixo número de indivíduos infectados ao redor dos ninhos, sugere que a presença do parasita também tem pouco efeito sobre a ocorrência das espécies. Para esses parasitas a seleção natural provavelmente favorece linhagens que conseguem se manter no ambiente com abundância relativamente baixa, sem diminuir muito a aptidão de seu hospedeiro. Esse tipo de relação é frequentemente encontrado em sistemas parasita-hospedeiro com longa história co-evolutiva.

Nas florestas amazônicas estudadas, restrições associadas a gradientes ambientais estiveram mais fortemente relacionadas com a estrutura das assembléias de formigas do que interações interespecíficas. Entre essas restrições, a falta ou excesso de água parece ser um fator importante. Regionalmente, menos espécies de formigas foram encontradas em áreas com menor pluviosidade média, mas a pluviosidade interage com fatores edáficos. Os resultados encontrados em um sítio sugerem que a áreas com lençol freático profundo, abrigaram menor número de espécies de formigas, mas favorecerem maior diversidade funcional. O maior número de espécies de formigas encontrado em locais com lençol freático superficial, foi atribuído a maior proporção de espécies generalistas. Locais com lençol freático mais profundo mantém menor número de espécies, mas com maior diversidade funcional, principalmente pela maior proporção de especialistas e formigas hipogéicas. Dado que áreas com lençol freático superficial compreendem uma parte importante das florestas amazônicas, o efeito do lençol freático sobre a comunidade de formigas pode facilitar a co-ocorrência de espécies regionalmente. Uma abordagem promissora é investigar a redundância funcional dentro e entre guildas de formigas e como restrições ambientais, como o disponibilidade de água, podem moldar as características funcionais e promover a co-ocorrência de espécies.

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