



Association of Ant Predators and Edaphic Conditions with Termite Diversity in an Amazonian Rain Forest

Cristian S. Dambros^{1,4}, José W. Morais², Alexandre Vasconcelos³, Jorge L. P. Souza², Elizabeth Franklin², and Nicholas J. Gotelli¹

¹ Department of Biology, University of Vermont, 05405, Burlington, VT, U.S.A.

² Coordenação de Biodiversidade, National Institute of Amazonian Research, CP 2223, 69067-375, Manaus, AM, Brazil

³ Departamento de Sistemática e Ecologia, Laboratório de Termitologia, Universidade Federal da Paraíba, CCEN, 58051-900, João Pessoa, PB, Brazil

ABSTRACT

Predation is a key determinant of prey community structure, but few studies have measured the effect of multiple predators on a highly diverse prey community. In this study, we asked whether the abundance, species richness, and species composition of a species-rich assemblage of termites in an Amazonian rain forest is more strongly associated with the density of predatory ants or with measures of vegetation, and soil texture and chemistry. We sampled termite assemblages with standardized hand-collecting in 30 transects arranged in a 5 km × 6 km grid in a *terra firme* Amazonian rain forest. For each transect, we also measured vegetation structure, soil texture, and soil phosphorus, and estimated the density of predatory ants from baits, pitfall traps, and Winkler samples. Seventy-nine termite species were recorded, and the total density of predatory ants was the strongest single predictor of local termite abundance ($r = -0.66$) and termite species richness ($r = -0.44$). In contrast, termite abundance and species richness were not strongly correlated with edaphic conditions ($|r| < 0.01$), or with the density of non-predatory ants ($r_{\text{abund}} = -0.27$; $r_s = -0.06$). Termite species composition was correlated with soil phosphorus content ($r = 0.79$), clay content ($r = -0.75$), and tree density ($r = -0.42$). Assemblage patterns were consistent with the hypothesis that ants collectively behaved as generalist predators, reducing total termite abundance, and species richness. There was no evidence that ants behaved as keystone predators, or that any single termite species benefited from the reduction in the abundance of potential competitors.

Key words: environmental gradients; predator–prey interaction; species composition; species richness; top-down effect; tropical rain forest.

TERMITES AND ANTS ARE AMONG THE MOST ABUNDANT AND ECOLOGICALLY IMPORTANT ANIMALS IN TROPICAL FORESTS (Hölldobler & Wilson 1990). Termites are important for nutrient cycling (Jones *et al.* 1994, Jouquet *et al.* 2006), and ants can affect soil properties (Jones *et al.* 1994), and function as seed dispersers (Bennett & Krebs 1987), herbivores (Vasconcelos & Cherrett 1997), and predators (Sheppe 1970). In spite of the importance of both ants and termites in tropical forests, little is known about the interactions between these taxa.

Termites are frequently preyed upon by ants in tropical forests (Sheppe 1970, Gonçalves *et al.* 2005), and most termite species are likely to be affected by ant predators (Gonçalves *et al.* 2005). Termites exhibit several adaptations for avoiding predation, including chemical defense (*e.g.*, *Nasutitermes*), mandible-snapping (*e.g.*, *Neocapritermes*), and fighting with large, smashing mandibles (*e.g.*, *Syntermes*; Prestwich 1984, Hölldobler & Wilson 1990, Legendre *et al.* 2008). Nevertheless, it is not known how effective these mechanisms are at the population level, or whether some termite species are more vulnerable to ant predators than others (Mertl *et al.* 2012). Quantitative sampling of hyper-diverse tropical arthro-

pods is challenging (Longino & Colwell 1997), and no study has examined the association of an entire ant predator community with the species abundance, richness, and composition of termites. Moreover, both ant and termite abundance can be associated with soil nutrients (Davies *et al.* 2003, Roisin & Leponce 2004, Kaspari *et al.* 2014). This correlation makes it hard to tease apart the direct association of termites and ants from their independent responses to soil nutrients and other environmental covariates.

Termite abundance and diversity can also be associated with the quantity and quality of their food. Termites consume plant material in several stages of decomposition (Donovan *et al.* 2001, Bourguignon *et al.* 2011), and termites can be limited by the amount of nitrogen in their diet (Morales-Ramos & Rojas 2003). Although no termite study has investigated the effects of phosphorous limitation on termite colony growth and survival, this nutrient is usually limiting for consumers and decomposers (Anderson *et al.* 2005). Phosphorus is particularly scarce in the soils of tropical forests (Vitousek 1984), and the concentration of soil phosphorus has been associated with the distribution of several species of plants and animals in the Amazonian forest (López-Hernández 2001, Costa *et al.* 2005, Boelter *et al.* 2014).

In this study, we quantified the association of ant predator density, vegetation, and soil chemistry with the abundance, species

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⁴Corresponding author; e-mail: cristian.dambros@uvm.edu

richness, and species composition of termites. We constructed a set of statistical models to tease apart the association of termites and ants from their simultaneous association with environmental variables. We also compared the association of termites and ants with a null expectation based on random predation. These analyses suggest that termite abundance and termite species richness are more strongly associated with the density of predatory ants than with measures of vegetation and soil chemistry. In addition, there was little evidence at the community level for non-random predation of termite species by ants.

METHODS

STUDY AREA.—Sampling was conducted between December 2008 and May 2009 at Reserva Ducke (3°05'S, 60°00'W), a tropical forest reserve of 10,000 ha in central Amazonia, Brazil (Figure S1). Elevation within the reserve varies from 39 to 110 asl (PPBio 2009), with a moderate decrease in soil nutrient content along this gradient. The vegetation consists of relatively uniform dense evergreen tropical rain forest (*terra firme* forest; Chauvel *et al.* 1987) that is not subjected to periodic flooding (Hopkins 2005). The leaf litter depth varies among transects, but is typically <20 cm, and the undergrowth is dominated by palms in the genera *Astrocaryum* and *Attalea* (Chauvel *et al.* 1987, Ribeiro *et al.* 1999). There is no record of logging or burning in this area, and a total of 1200 tree species have been recorded (see <http://ppbio.inpa.gov.br> for more information).

SAMPLING DESIGN AND DATA COLLECTION.—In 1998, a permanent array of 9°N–S and 9 E–W perpendicular trails was established in the reserve as part of the Program on Biodiversity Research (PPBio) of the Brazilian government (Magnusson *et al.* 2005). The PPBio survey strategy aims to make the sampling effective and efficient for a diversity of taxa from soil invertebrates to canopy trees (Magnusson *et al.* 2005). The minimum distance between the trails and the forest edge is 1 km. The trails allow access to a 5 km × 6 km grid of 30 transects, with 1-km spacing (Figure S1). Each transect is 250-m long and follows an elevation isocline to minimize variation in exposure and soil composition. Transects were established at least 10 m away from the nearest walking trail.

Termite sampling was performed using a modification of the standard sampling protocol developed by Jones and Eggleton (2000). To sample termites, we established 10 'sections' (5 m × 2 m) at 25-m intervals along each transect. Every section was actively searched for termites by three trained investigators for 20 min, yielding 1-man hour of search time per section, and 10 hours total for each of the 30 transects. We searched for termites in soil, leaf litter, rotting logs, and tree and shrub roots. However, nests higher than 2 m above ground level were not surveyed, and our results do not include termites living exclusively in the canopy. The upper layer of soil was completely dug down to a 50-cm depth or until the upper layer of humus was thoroughly searched. Most termite colonies were found in the soil, small branches, and inside dry leaves of *Astrocaryum* and *Attalea* palms. Termites were sampled in the wet season (December

2008) and in the dry season (May 2009), and the data were combined for analyses.

Termites were collected and preserved in 95 percent EtOH and were identified to genus using Constantino (1999). Individuals were then sorted to morphospecies and to species whenever possible by comparison with museum collections at the Federal University of Rio Grande do Norte and the National Institute of Amazonian Research (INPA), Brazil. For termites in the taxonomically problematic subfamily Apicotermatinae, we dissected worker guts for species identification based on diagnostic characters of the enteric valve (Noirot 2001), and compared our specimens with descriptions from Bourguignon *et al.* (2010). Voucher specimens from this survey were deposited in the Entomological Collection of the National Institute of Amazonian Research. Termite data are included in Table S1.

We analyzed termite community structure with predictor variables of ant density, tree density, and soil variables that were measured by other investigators for each transect. Ant data at the transect level were taken from Souza *et al.* (2012), who used pitfall traps, sardine baits, and litter samples extracted by the Winkler method. Sifted leaf litter samples of 1 m² surface area were collected from sampling stations located at 25-m intervals along the center line of each transect. Pitfall traps and sardine baits were placed at the same stations after litter collection, giving 10 sections for each method per transect (10 sections × 30 transects × 3 techniques resulted in 900 samples). Ants were extracted for 48 h from Winkler bags through a 1 cm² mesh sieve (Bestelmeyer *et al.* 2000).

The pitfall traps (95 mm diameter; 8 cm depth; 500 ml volume) were partially filled with water and detergent, buried with the rim at ground level, and left for 48 h. After removal of the pitfall traps, approximately 5 g of canned sardine was placed on a plastic card (10 cm × 7 cm) on the litter surface; after 45 min, all ants on the plastic card were collected and preserved in 90 percent EtOH. The baiting and litter-sampling were conducted between 0800 h and 1700 h. Ant data used in our study were collected in September 2006, but a recent survey from September 2012 demonstrates that ant density and species composition remained nearly constant during this period (*unpublished data*). Stations for ant sampling were adjacent to the sections where termites were collected.

We classified 71 of the 242 ant species represented in the transects *a priori* as either a potential 'predator' or 'non-predator' of termites based on published details of their feeding habits (Silva & Brandão 2010, see Table S2 for details). When data on ant feeding habit were not available at the species level, data at the genus level were used. Ant species not classified exclusively as predators by Silva and Brandão (2010) were not included as potential predators. Some predatory ants could potentially be misclassified as 'non-predators' of termites (*e.g.*, *Solenopsis* ants). However, the lack of information about the interaction of ants and termites as predator and prey prevented a precise classification of all ant species. To standardize our classification of predatory ants, we maintained the original classification of Silva and Brandão (2010) (see discussion for the implications of our classification). To confirm our classification of ants, we ran all analyses using

both ant predator and non-predator density as predictor variables. Ant density was quantified as the total number of ant nests detected per transect.

Tree data at the transect level were taken from Castilho *et al.* (2006), who measured the number of trees and palm trees per transect at breast height (dbh) using transects of 0.5-ha (20 m × 250 m) and 0.1-ha (4 m × 250 m) to sample trees with dbh of 10–30 cm and 1–10 cm, respectively.

From a previous survey, we obtained measures for each transect of soil phosphorus (mg/dm³ of soil) and soil clay (%). Other variables were correlated in some degree with soil phosphorus and clay content, and their relation with termite community structure is shown in Table S3; Figure S3. These data are available at <http://ppbio.inpa.gov.br>. For the measurements of soil nutrients and texture, five soil samples were collected at a depth of 5 cm at 50-m intervals along each transect. The five samples from each transect were pooled for texture and chemical analyses. Before analysis, samples were cleaned of roots, air-dried, and sieved through a 2-mm sieve. Soil texture analyses were conducted at the Soil Laboratory of the Agronomy Department at INPA and chemical analyses at the Soil Laboratory of the Brazilian Enterprise of Research of Livestock and Agriculture, Manaus (Embrapa 1997).

DATA ANALYSIS.—In each transect, we counted the number of sections (0–10) in which a termite species occurred and treated these data as a measure of termite abundance. We quantified species diversity by using Hurlbert's (1971) Probability of an Interspecific Encounter (PIE; also known as Simpson's Diversity Index). The PIE index measures the probability that two randomly chosen individuals represent two different species. The PIE index is unbiased by sample size (Gotelli & Ellison 2012), and is an estimate of the slope of the individual-based rarefaction curve at its base (Olszewski 2004). We calculated the PIE index using the total abundance of each termite species recorded in a transect.

The dissimilarity in species composition among transects was measured by the Bray–Curtis dissimilarity index between all possible pairs of transects. We used the scores of the first two axes of a Non-Metric Multidimensional Scaling (NMDS; Faith *et al.* 1987) to summarize the changes in overall species composition among transects.

Using multiple regression models, we tested for the relationship between termite abundance, termite species richness, termite PIE, and termite species composition (response variables) versus ant predator density, tree density, and soil phosphorus and clay content (predictor variables). Because termite density and species richness represent count data and cannot take negative values, we used Generalized Linear Models (GLMs) with log-link functions, and a Poisson distribution of errors in the residuals for termite abundance and species richness. For the remaining analyses, we used multiple ordinary least squares regression models (OLS), which assume normally distributed errors in the residuals.

Ants and termites could both be affected by the same spatial and environmental variables, which could result in a spurious correlation between ants and termites that does not reflect a cause-and-effect relationship. Structural Equation Models (SEMs) can

be used to test for associations between variables, while controlling for potential confounding effects (Rosseel 2012). To disentangle the direct association of ant predator density with termite abundance and species richness from the simultaneous association of termite and ants with measured environmental variables, we created a set of Structural Equation Models (SEM). The models were created including direct and indirect links among soil phosphorus, clay content, tree density, ant predator density, and termite abundance and species richness. Finally, we also tested for the association of termite abundance, species richness, and species composition with the density of non-predatory ants. The results from the analyses using non-predatory ants are described in the Supplementary Material (Tables S4 and S5; Figures S4 and S5).

PREDICTIONS OF EFFECTS OF PREDATION BY ANTS.—To disentangle the potential effects of random versus selective predation of ant species on termite diversity, we examined the relationship between ant predator density and termite PIE.

If ant predators specialize on some termite species, ant predator density should be strongly associated with termite PIE (Figure S2, left and right panels). In contrast, if predators are generalists, ant predator density should not be strongly associated with termite PIE (Figure S2, middle panel). Although ant predators may reduce termite abundance, PIE will remain nearly constant when samples are randomly rarefied (Chao *et al.* 2014). The constancy arises because PIE is determined primarily by the relative abundance of the most common species in the assemblage, and these relative abundances are almost invariant to sample size effects.

As a further check, we rarefied the observed termite samples by random subsampling, and calculated standardized deviations of species richness and PIE from the rarefaction curve. We then tested whether those deviations were correlated with ant predator density.

To rarefy the termite community, we first quantified the number of termite colonies (abundance) found in each transect. We then selected a termite colony at random from the set of pooled transects. This random selection of termites was repeated until the number of selected colonies matched the number of colonies observed in the transect. For each transect, the randomization procedure was repeated 1000 times (30 transects × 1000 randomizations = 30,000 randomizations). For each randomization, we recalculated termite PIE and termite species richness.

Deviations of observed termite PIE and termite species richness from the expectations of PIE and richness in the rarefaction were quantified as a standardized effect size (SES; Gotelli & McCabe 2002):

$$SES = \frac{x - \mu}{\sigma},$$

where x represents the observed PIE or richness in a given transect, and μ and σ represent the mean and standard deviation of PIE or richness in a transect in 1000 randomizations. Values of SES less than approximately -1.96 indicate that the observed ter-

mite PIE or termite species richness are significantly smaller than expected by chance, whereas values >1.96 indicate that the observed values of PIE or richness are significantly larger than expected. If ants are selective predators on the rarest termite species, ants should lead to a reduction in termite PIE and species richness that is greater than predicted by the rarefaction curve (negative SES values). In contrast, if predators target the commonest termite species, ants should reduce termite species richness less than predicted by the rarefaction curve (positive SES values).

Before beginning analyses, we tested for potential collinearity of independent variables across the sampling grid by calculating pairwise correlations among all possible independent variables. Ant predator density, soil phosphorus, clay content, and tree density were not correlated with each other and were therefore used as independent predictors in the regression analysis. Among the remaining variables included in the supplementary analysis, only 20 percent of the pairwise comparisons were statistically significant ($P < 0.05$), mostly for associations of nutrient concentrations and elevation (see Figure S3). These variables were combined with a principal components analysis (PCA), and the PCA scores were used as predictor variables of termite community structure. The results of regression and SEM analyses using these PCA axes as predictor variables are presented in Table S3 and Figure S3, respectively.

For both independent and dependent variables, there could be spatial trends or spatial autocorrelation in the grid of sampled transects. To detect spatial trends, we regressed each variable against the x - and y -coordinates of the sample grid. To detect spatial autocorrelation, we binned the data into 1.5 km distance classes and calculated Moran's I for each variable. None of these analyses were significant ($P > 0.05$), so we used each transect within a grid as an independent sample in regression models.

All statistical analyses were performed in R (R Development Core Team 2013), using the *vegan* (Oksanen *et al.* 2008) and *lavaan* (Rosseel 2012) packages. The randomization functions and all the tests performed in this paper are available as an annotated

R script (Appendix S1). Termite data are publicly available at <http://figshare.com/download/file/1320575/1> under CC-BY licence.

RESULTS

Among the 30 censused transects, we recorded 702 termite occurrences and a total of 79 termite species. Ant predator density was negatively correlated with termite abundance ($r = -0.66$; $\chi = -3.92$; $P < 0.001$; Fig. 1A) and termite species richness ($r = -0.44$; $\chi = -2.93$; $P = 0.003$; Fig. 1B; Table 1) but was not significantly related to PIE ($r = -0.15$; $t = -0.80$; $P = 0.42$; Table 1) or termite species composition ($r = 0.004$; $t = -1.02$; $P = 0.32$ and $r = -0.37$; $t = -1.60$; $P = 0.12$ for the first and second ordination axes, respectively; Table 1; Table S3). The multiple regression models for termite abundance and species richness explained 49 and 32 percent of the variation in the data, respectively.

For PIE (Fig. 2A) and termite species richness (Fig. 2B), the declines in diversity with abundance matched those that would be expected with random predation by ants, based on rarefactions of the pooled termite transect data. Termite species composition (first ordination axis of NMDS) was correlated with soil phosphorus ($r = 0.79$, $t = 3.81$; $P < 0.001$), and soil clay content ($r = -0.75$, $t = -2.82$; $P = 0.009$; Table 1; Fig. 3). The density of trees per transect was weakly correlated with the PIE index of termite species diversity ($r = -0.44$, $t = -2.00$; $P = 0.056$). The multiple regression model for PIE explained 26 percent of the variance. The explained variance for termite species composition was 76 and 13 percent for the first and second ordination axes, respectively.

Deviations from the rarefaction curve in termite PIE and species richness were not associated with any measured environmental variable ($P > 0.07$; Table 1).

For both termite abundance and termite species richness, the Structural Equation Models (SEMs) indicated a much stronger effect of edaphic variables on ants (slope coefficient $b = -0.40$; $P < 0.001$ for soil clay content) than on termites

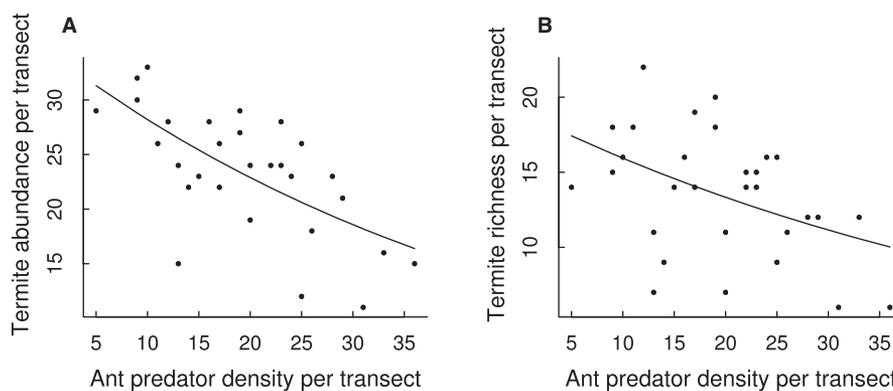


FIGURE 1. Relationship between ant predator density and termite abundance (A), and termite species richness (B). Each point represents a different transect within the grid. Termite abundance = $e^{(3.548 - 0.021 \times \text{predator density})}$. Termite species richness = $e^{(2.95 - 0.02 \times \text{predator density})}$.

TABLE 1. Slope coefficients for multiple regressions of termite community structure against predictor variables. Generalized linear models with Poisson distributed errors were used for abundance and species richness. R^2 values for abundance and richness were calculated using Cox and Snell's (1968) method. $df = 25$.

Response variable	Intercept	Predator density	Phosphorus	Clay content	Tree density	χ^2	F	R^2
Abundance	3.554***	-0.021***	0.015	-0.023	-0.003	18.038	NA	0.452***
Richness	2.939***	-0.018**	-0.022	-0.031	-0.061	8.985	NA	0.259*
PIE	0.937***	-0.001	-0.01	-0.021	-0.024†	NA	2.195	0.26*
NMDS1	-0.067	0.003	0.124***	-0.092**	-0.039	NA	20.076	0.763***
NMDS2	0.157	-0.002	0.002	0.024	-0.048	NA	0.946	0.131
SES _{PIE}	-0.012	-0.024	-0.237	-0.534	-0.638	NA	1.99	0.241
SES _{Richness}	-0.161	-0.017	-0.259	-0.14	-0.449	NA	0.821	0.116

*** $p < 0.001$ ** $p < 0.01$ * $p < 0.05$ † $p < 0.1$.

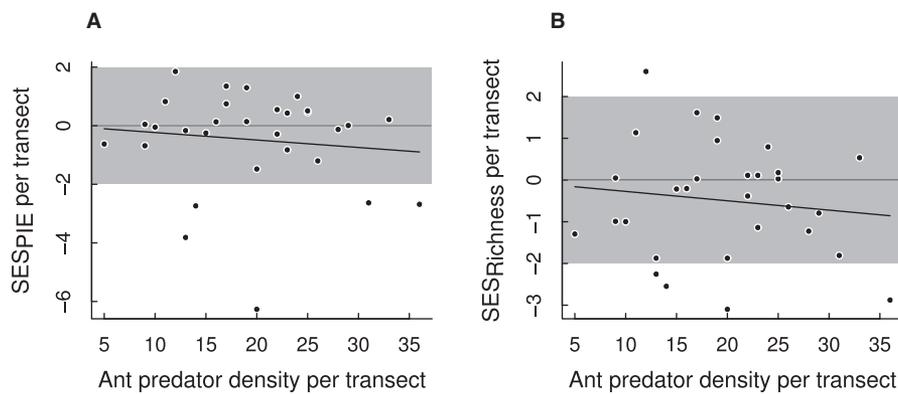


FIGURE 2. Relationship between ant predator density and the standardized effect size (SES) for the probability of an interspecific encounter (PIE) (A), and termite species richness (B). Each point represents a different transect within the grid. $SES_{PIE} = 0.021 - 0.025 \times \text{predator density}$. $SES_{Richness} = -0.049 - 0.022 \times \text{predator density}$. Shaded area represents the null expectation based on a rarefaction curve.

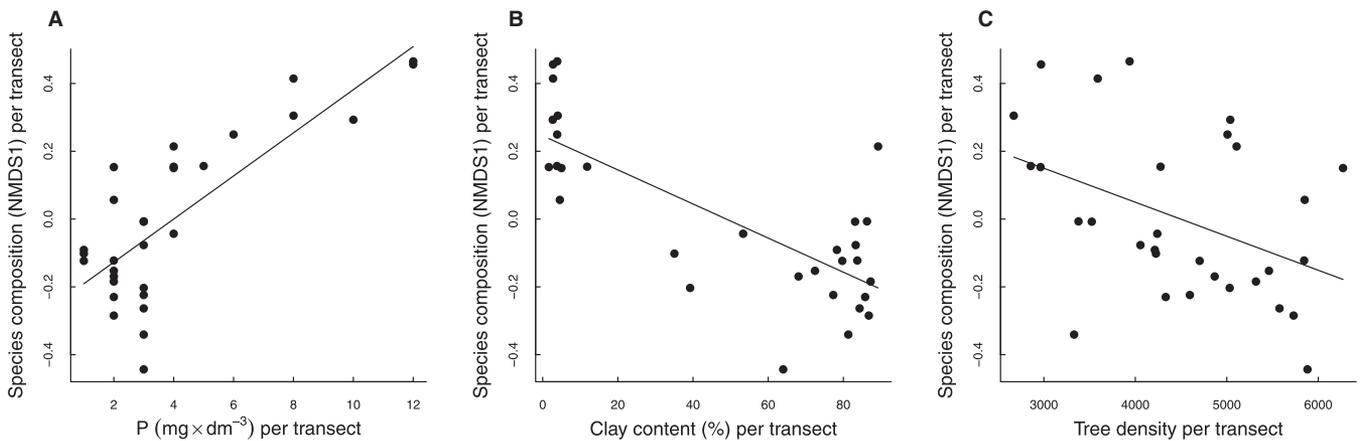


FIGURE 3. Changes in termite species composition along soil phosphorus (A) soil clay content (B), and tree density (C) gradients. The Y-axis represents termite species composition measured as the first non-metric multidimensional scaling (NMDS) axis of the Bray-Curtis similarity metric. $NMDS1 = -0.2548 + 0.0637 \times \text{phosphorus}$. $NMDS1 = 0.2397 - 1.2919 \times \text{clay content}$. $NMDS1 = 0.4503594 - 0.0001002 \times \text{tree density}$. Tree density was only associated with termite species composition when analyzed in isolation from other variables.

($b = 0.25$; $P = 0.30$ for soil phosphorus; Fig. 4A), and a strong direct effect of ant predators on termites ($b < -0.43$; $P < 0.001$ for abundance and species richness; Fig. 4). The SEM was able

to explain 19 percent of the variation in ant predator density, and 46 and 24 percent of the variation in termite abundance (Fig. 4C) and species richness (Fig. 4F), respectively.

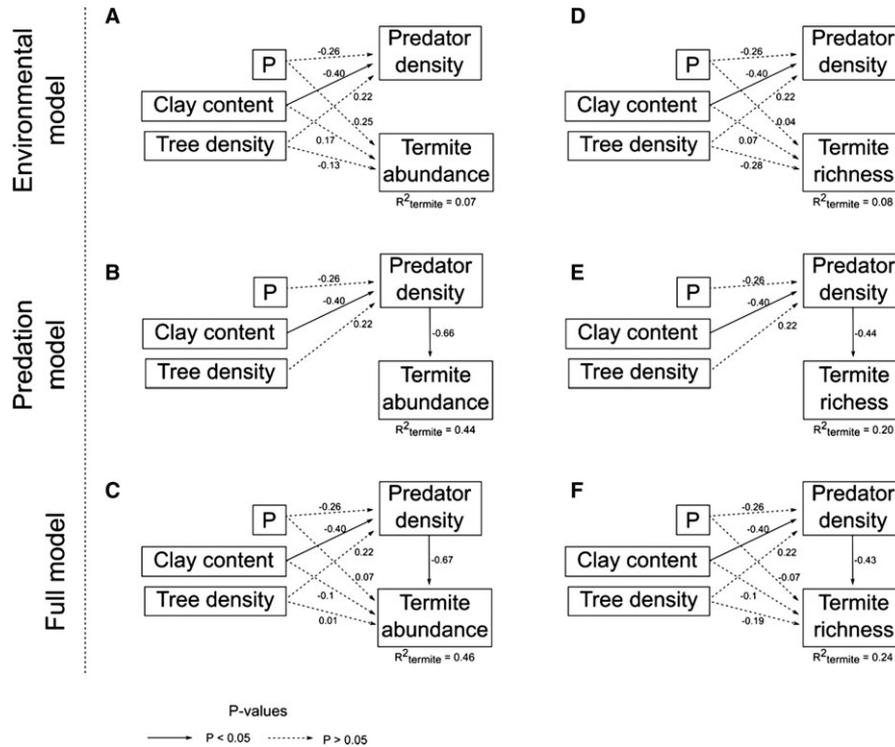


FIGURE 4. Structural equation models (SEMs) with regressions between environmental variables, the density of ant predators, and the termite abundance (A–C) and termite species richness (D–F). A and D: Direct effects of environmental variables on predator and termite abundance and richness. B and E: Direct effect of environmental variables on predator density and direct effect of predator density on termite abundance and species richness. C and F: Direct effect of environmental variables on predator density and on termite abundance and termite species richness, and direct effects of predator density on termite abundance and termite species richness. The solid and dashed lines represent significant and non-significant correlations at $P < 0.05$, respectively. All variables were standardized before analysis.

The density of non-predatory ants was not associated with termite abundance and species richness (Table S4). The density of non-predatory ants alone explained 7 percent of the variance in termite abundance, and <1 percent of the variance in termite species richness.

The use of a PCA axis of environmental variables as a predictor in multiple regression models (Tables S3–S5) and SEMs (Figures S3–S5) generated similar results.

Although most ant species were too rare for individual analyses of their association with termite abundance, the density of most predatory ant species was negatively correlated with termite abundance (60% negative; $P = 0.04$; binomial test; Table S6). For non-predatory ants, positive and negative associations were equally likely (48% negative; $P = 0.62$; Table S6).

DISCUSSION

The single strongest predictor of both termite abundance and termite species richness was the density of ant predators (Fig. 1; Table 1). Based on the calculated regression slopes, an increase in ant predator density of 4 ants/m² corresponded to an approximate decrease in termite abundance of 2 termites/m² and a decrease in termite species richness of 1 species/m². Although

ants are known to be predators of termites (Sheppe 1970, Hölldobler & Wilson 1990) and can have important effects on termite populations (Abe & Darlington 1985), this is one of the few studies to demonstrate that ant predators are strongly associated with species diversity of termites. Our results are consistent with the hypothesis that ants are strong predators of termites and reduce termite abundance and species richness.

Although environmental conditions can also affect termite and ant populations (Davies *et al.* 2003, Kaspari *et al.* 2014), no measured environmental variable was associated with the abundance of both termites and predatory ants (Table 1). Instead, our results might indicate that ant predator density was directly and negatively associated with termite abundance and species richness (Figure S2A–B). This pattern was unlikely to have been caused by indirect effects of environmental variables on both termites and ants, because termite abundance and species richness were only weakly related to tree density, soil clay content, soil phosphorus (Table 1), and to other environmental covariates (Table S3). Moreover, non-predator ants were not strongly associated with termite abundance and species richness (Tables S4–S5; Figures S4–S5). The direct association of termites and ant predators was also supported by the results of the SEM analyses (Figure S3).

Although ant predator density was strongly associated with termite abundance and species richness, ant predator density was not strongly associated with termite composition. Moreover, the number of termite species and their relative abundances in areas with low termite abundance matched the predictions of a simple random draw from the local pool of termite species. Ant predator density was correlated negatively with termite abundance and species richness, but the data matched the predictions of the simulated rarefaction curve. These results are consistent with the hypothesis that ants effectively rarefied the termite assemblage (Figure S2), leading to progressive losses of rare termite species (Fig. 1B). Alternatively, it is possible that ants are selective on both rare and common termite species, or that several specialized ant species might also have caused a net reduction in overall termite abundance. However, many such specialist predators would be needed to achieve this overall reduction, and they would have to be highly efficient at suppressing the abundance of each different termite species.

Our results are consistent with those of Gonçalves *et al.* (2005), who found that the foraging behavior of different termite groups was similarly suppressed by the presence of ant predators. Sheppe (1970) also found that many ant species preyed on a variety of termite species, and that predation rates of termite colonies were proportional to the relative abundance of termite species. Although some genera and families of termites have evolved distinct defensive mechanisms against certain predators (Prestwich 1984, Legendre *et al.* 2008), in our study system, transects with higher ant densities had systematically fewer termite species. Despite the weak association of non-predatory ants with termite abundance and species richness, some ants classified as non-predators, such as *Pheidole* and *Solenopsis* ants, were negatively associated with the termite abundance and species richness. It is thus possible that ant predators have an even stronger effect on termite abundance and species richness than reported in our study. Future experimental studies are required to confirm our results, which suggest that generalist ant predators reduce termite abundance and species richness regardless of the association of termite species with vegetation or soil chemistry.

Despite the weak association of termite abundance and richness with vegetation and soil nutrients, soil phosphorus content was strongly associated with the changes in termite species composition (Fig. 3A). Nutrient availability is known to affect the formation of fine litter, and the allocation of plants to growth and the production of fine roots (Wright *et al.* 2011), all of which may affect termite distribution. In the soils of the Amazonian forest, phosphorus is a scarce nutrient (Vitousek 1984), and the amount of phosphorus in the soil is usually correlated with phosphorus content in plant tissues (Stark 1970).

The correlative evidence presented here for the effects of ant predators on termite diversity comes from a relatively homogeneous landscape in which local productivity does not change drastically among transects. In less homogeneous systems, there may be stronger effects of bottom-up control through changes in productivity and habitat diversity, making it difficult to disentangle the top-down effects of predatory ants from the bottom-up

effects of resources affecting termite distribution. For example, Kaspari *et al.* (2000) showed that overall ant density and species richness decreased along a productivity gradient from deserts to rain forests. In Amazonia, both termite and ant densities are much lower in savannas than in rain forests, probably due to differences in productivity. Moreover, areas subject to chronic seasonal flooding support lower termite densities (Constantino 1992) and ant densities (Mertl *et al.* 2009), and the species composition in disturbed sites may reflect a strong habitat filter. Finally, the effects of predators, productivity, and disturbance regimes on prey species diversity are likely to vary systematically with the spatial scale of measurements (de Roos 1991). At smaller spatial scales, the effects of biotic interactions, such as predation, are likely to be stronger than at the scales investigated in our study. Nevertheless, the results presented here collectively suggest that, in species-rich systems, generalist predators might be associated with an overall decrease in species abundance and richness of prey.

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SUPPORTING INFORMATION

Additional Supporting Information may be found with online material:

TABLE S1. *Incidence of termite species collected in Ducke Reserve, Manaus, AM, Brazil.*

TABLE S2. *Incidence of predatory and non-predatory ant species at Ducke Reserve, Manaus, AM, Brazil, collected at baits, pitfall traps, and in Winkler traps.*

TABLE S3. *Slope coefficients for multiple regressions of termite community structure against predictor variables.*

TABLE S4. *Slope coefficients for multiple regressions of termite community structure against predictor variables using non-predator ant density as a co-variate.*

TABLE S5. *Slope coefficients for multiple regressions of termite community structure against predictor variables using non-predator ant density as a co-variate.*

FIGURE S1. Location of the Reserva Ducke and grid system in South America.

FIGURE S2. Predictions for relative abundance distributions and the PIE index for three hypothetical termite species under

random versus non-random predation by ants.

FIGURE S3. Structural equation models with regressions between the environmental variables, the density of ant predators and the termite abundance and richness.

FIGURE S4. Structural equation models with regressions between environmental variables, the density of non-predatory ants, and the termite abundance and termite species richness.

FIGURE S5. Structural equation models with regressions between the environmental variables, the density of non-predatory ants, and the termite abundance and richness.

APPENDIX S1. Annotated script on the termite analysis.

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