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Determinants of Termite Species Taxonomic, Phylogenetic, and Functional Diversity in the Amazonian Forest

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DETERMINANTS OF TERMITE SPECIES TAXONOMIC, PHYLOGENETIC, AND FUNCTIONAL DIVERSITY IN THE AMAZONIAN FOREST

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ABSTRACT

The distribution of species in space is determined by the species dispersal capacity, adaptation to environmental conditions, and response to predators and competitors. To determine the importance of dispersal limitation, environmental filtering, and species interactions on the distribution of species in the Brazilian Amazonian forest, I sampled termites in a large area of Brazil. I investigated patterns in species occurrence that could indicate competition and predation structuring termite communities, and analyzed the association of termite abundance and species richness with the density of ant predators. The spatial distribution of termites, and their association with climatic and edaphic conditions were also used to infer about the effects of dispersal limitation and environmental filtering. A total of 271 termite species and 4,389 colonies was found in the 148 transects sampled. Predator density was the strongest predictor of termite abundance and species richness at small spatial scales, but the turnover in termite species composition was mostly associated with measures of soil texture. At broad spatial scales, soil chemistry, climate, and isolation by distance were associated with termite abundance, species richness, and species composition. These results suggest that both species interactions, their association with the environment, and their dispersal capacity determine their distribution. Nevertheless, dispersal limitation seem to be stronger over large areas, whereas environmental filtering can act both at small and large geographic scales.

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Introduction

The presence of a species in a given area depends on the ability of individuals to disperse from a previously established population (source limitation; Chave, 2004), and to survive and reproduce in the local environment (establishment limitation; Clark *et al.*, 2007, 2013). In small geographic areas, species are not usually limited by dispersal: given that an established population exists, all nearby areas are likely to receive at least some immigrants over long periods of time. Because limiting conditions for establishment controls population, and ultimately community dynamics, species occurrence can be strongly associated with local environmental conditions (Hubbell, 2005; Clark *et al.*, 2007, 2013), or with the presence of predators (Janzen, 1971) and competitors (Hutchinson, 1957).

Over large geographic areas, evolutionary and dispersive processes can also affect species distribution. Geographical barriers to dispersal can isolate populations and promote diversification (Nagylaki, 1980; Morlon, 2014), creating differences in species identity in isolated communities (Hubbell, 2001; Chave, 2004). Geographical barriers to dispersal can be represented by clear boundaries to species movement, such as mountain chains (Smith *et al.*, 2014), but small barriers, such as rivers (Smith *et al.*, 2014; Boubli *et al.*, 2015), and geographical distance *per se*, can also limit the dispersal of individuals (Nathan *et al.*, 2011). Despite the known effects of dispersal limitation and of species association with the environment (Ricklefs, 1987), ecological studies are historically conducted in small geographic scales (Hubbell, 2001; Mcgill, 2010), and emphasize the effects of the environment or species interactions (Hutchinson, 1957; MacArthur & Levins, 1967).

Fifteen years ago, the publication of *The Unified Neutral Theory of Biodiversity* – UNTB (Hubbell, 2001) triggered an intense debate about the importance of species adaptation to the environment (*niches*) *vs* random processes on community organization (Adler, 2004; Bell, 2005; Jabot & Chave, 2011; Ricklefs & Renner, 2012; and many citations hereafter). This debate led to the development of new techniques to disentangle effects of dispersal limitation and environmental control in species composition (Dray *et al.*, 2006; Diniz-Filho *et al.*, 2012), and boosted the use of species phylogeny and trait data in community ecology (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2009; Kembel, 2009). Recent studies using these techniques have found evidence for both niche and neutral processes, depending on the geographical scale of investigation (Hubbell, 2005), the dispersal capacity and environmental requirements of the species being studied (Thompson & Townsend, 2006), and on the specific environmental conditions of the study region.

Tropical forests are not strongly affected by the seasonal effects that influence the distribution of species in temperate regions, and some studies have suggested that the species association with the environment are weak in tropical regions (Algar *et al.*, 2011). Despite the evidence for the effects of dispersal limitation and stochastic processes in plant (Hubbell, 2001; Kembel, 2009) and animal (Gómez *et al.*, 2010) communities, several studies have demonstrated that neutral processes cannot predict the decay in species similarity with geographic distance in Amazonia (Condit *et al.*, 2002; Tuomisto *et* *al.*, 2003, 2014; Higgins *et al.*, 2011). Indeed, many studies have found strong associations of species composition with soil texture and chemistry, but not with geographical barriers to dispersal (Higgins *et al.*, 2011; Pomara *et al.*, 2014; Tuomisto *et al.*, 2014, 2003; but see Dias-Terceiro *et al.*, 2015). However, many of these studies are conducted over a limited geographic area, and the study area often do not encompass large rivers (eg. Gascon *et al.*, 2000) – the major barriers to dispersal of species in Amazonia (Smith *et al.*, 2014; Boubli *et al.*, 2015). Finally, the effect of other processes that can cause changes in species composition, such as predation and competition, are rarely investigated.

In this study, I investigated how termite communities are distributed in space over large areas of the Brazilian Amazonian forest, and attempted to separate the effects of isolation by distance and the environment in species distribution. At a small geographic area, I also investigated patterns in species occurrence that could indicate effects of competition and predation structuring termite communities. Termites were sampled in 198 transects, representing the largest sampling effort of a termite study to date. In 30 transects, environmental variables, such as soil nutrients, the density of potential predators, and vegetation structure were also measured in previous studies (Castilho *et al.*, 2006; Souza *et al.*, 2012). This unique dataset allowed me to investigate in detail the association of termites with environmental conditions, and with the presence of predators in a relatively small geographic area (Chapter 1). I also measured the phylogenetic relatedness and the trait similarity in co-occurring termite species in order to investigate whether trait similarity imposed a limit on species coexistence, or if termites with certain defense mechanisms were especially affected by the presence of predators (Chapter 2). In order to determine the importance of environmental control in termite distribution over large areas of Amazonia, I quantified the broad scale spatial variation in termite diversity and composition that could be explained by differences in climate, soil conditions, and tree cover (Chapter 3). In my last chapter, I simulated the distribution of species using models of dispersal, and of species association with the environment. The predictions from these simulations were then compared with empirical observations of species distributions. The comparison of several models allowed me to determine how dispersal limitation and the species association with the environment affect species richness and species composition (Chapter 4).

Termites are among the most ecologically important organisms in tropical forests. Along with ants they are the most abundant animals in tropical forests (Fittkau & Klinge, 1973; Watt *et al.*, 1997), and are termed ecosystem engineers for their important role in nutrient cycling (Jones *et al.*, 1994; Jouquet *et al.*, 2006). Termites have strong associations with soil nutrients (Davies *et al.*, 2003) and are limited by the amount of available wood and litter (Pequeno *et al.*, 2013). Nevertheless, termites are relatively sessile, and might be more affected by dispersal limitation than other organisms with high dispersal capacity (Thompson & Townsend, 2006), such as small-seeded plants, and migratory birds. These properties make termites an ideal model for comparing neutral and niche predictions.

Although this study filled many gaps in the sampling of termites in Amazonia, the sampling coverage of termites and other organisms in this region is still low compared to other South American forests. This limitation prevented me from developing and testing the dispersive and environmental models used in Chapter 4. Because small mammals have been extensively sampled in a bounded domain, the Brazilian Atlantic Forest, we used a small-mammal dataset for model simulation and comparison in Chapter 4.

Description of studies performed in individual chapters

In the first two chapters of this dissertation, I describe the association of termites with soil conditions and the density of ant predators in small geographic scales. In the first chapter I explore several patterns of termite community structure along these gradients, and compare them with expectations of the effects of generalist versus specialist predators. In the second chapter, I compare the phylogenetic relatedness and trait similarity in co-occurring termite species. Co-occurrence of closely-related and similar species may indicate that environmental control is important structuring communities, whereas competition may reduce the coexistence of closely-related species and species with similar traits (Webb *et al.*, 2002). In the second chapter I also explored how predators affect the co-occurrence of termite species, which could suggest their effect as generalist or specialist predators. Most ecological studies of termites (Bandeira, 1991; Davies *et al.*, 2003; Roisin & Leponce, 2004; Ackerman *et al.*, 2009), and other taxa (Gascon *et al.*, 2000; Costa *et al.*, 2009; Boelter *et al.*, 2014) are conducted in geographic scales similar to those investigated in Chapter 1 and 2. These similarities make our results comparable to other studies conducted in Amazonia with several taxa.

In the third chapter, I associate changes in termite community structure with differences in climate, soil conditions, vegetation structure, and geographic distance between areas in a vast region of the Amazonian forest. Despite the large extent in which the data were collected, I explore the patterns of species distribution both at large and small spatial scales, making a link between species distribution in large and in small areas. Some previous studies have found that species are associated with different environmental gradients at small and large spatial scales. For example, Costa *et al.* (2009) have found strong changes in palm species composition along a gradient of soil texture in a small area of central Amazonia, whereas Kristiansen *et al.* (2012) found soil chemistry to be more important in a larger area of western Amazonia. In Chapter 3, I found that soil texture is in fact more important than soil chemistry at small spatial scales, and that soil chemistry and climate are more important at large spatial scales. These results suggest that different factors control species distribution in large and small spatial scales, and that differences observed in previous studies are not a result of differences in sampling method or region.

Finally, I devoted the fourth and final chapter to compare some methods commonly used to tease apart dispersal limitation and environmental control in species distribution. I showed that dispersive models, such as the neutral model and the mid-domain effect model, produce a steep decay in species similarity as study areas get farther apart from each other. In Chapter 3, a decay in species similarity with geographic distance was found for termites in Amazonia, but only over large geographic scales. Moreover, at the small scale investigated in Chapter 1 and 2, the similarity in species composition was associated only with environmental conditions. Collectively, these results suggest that dispersal limitation is more important at large geographic scales, and that species distribution is strongly associated with the environment at small spatial scales.

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CHAPTER 1: ASSOCIATION OF ANT PREDATORS AND EDAPHIC CONDITIONS WITH TERMITE DIVERSITY IN AN AMAZONIAN RAINFOREST

Abstract

Predation is a key determinant of prey community structure, but few studies have measured the association of multiple predators on a highly diverse prey community. In this study, we asked whether the species richness, composition, and turnover of a species-rich assemblage of termites in an Amazonian rainforest is more strongly associated with the abundance of predatory ants or with measures of vegetation and soil chemistry. We sampled termite assemblages with standardized hand-collecting in 30 transects arranged in a 5 km × 5 km grid in a Terra-Firme Amazonian rainforest. For each transect, we also measured vegetation structure and soil chemistry, and estimated the density of predatory ants from baits, pitfall traps, and Winkler samples. 79 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 correlated with edaphic conditions ($r < 0.01$). Turnover in species composition among transects was not correlated with ant predator density ($r = 0.01$), but was correlated with soil phosphorus content ($r = 0.79$), nitrogen content ($r = –0.46$), 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 termite species benefited from the reduction in the abundance of potential competitors.

Key-words: Environmental gradients, predator-prey interaction, species richness, species turnover, tropical rainforest.

Introduction

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), whereas ants can be important 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), and most termite species are likely to be affected by ant predators (Hölldobler & Wilson 1990, Gonçalves et al. 2005). Termites exhibit several adaptations for avoiding predation, including chemical defence (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 arthropods 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 (Kaspari et al. 2014, Davies et al. 2003, Roisin & Leponce 2004). 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 and phosphorus in their diet, as commonly observed for other herbivores 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 (Costa et al. 2005, Boelter et al. 2014, López-Hernández 2001).

In this study, we quantified the association of ant predator density, vegetation, and soil chemistry with the abundance, species 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. However, 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 (3º05'S, 60º00'W), a tropical forest reserve of 10,000-ha in central Amazonia, Brazil (Fig. 1). 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 rainforest (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 less than 20 cm, and the undergrowth is dominated by palms in the genera *Astrocarium* and *Attalea* (Chauvel et al. 1987, Ribeiro et al. 1999). The site has never been logged or burned, and a total of 1,200 tree species have been recorded in the area (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 allows access to a grid of 30 transects located 1 km apart (Fig. 1). 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.

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 3 trained investigators for 20 minutes, yielding 1 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. 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 dug down to a 50 cm depth or until the upper layer of humus was thoroughly searched. 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 Apicotermitinae, 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 m^2 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 sections). Ants were extracted for 48 h from Winkler bags through a 1 cm^2 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 hours. 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 minutes, 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. As with termites, ants were sampled during both the dry season and the wet season.

We classified 158 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). Predator density was quantified as the incidence of predatory ants in the sections within each 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 nutrients [nitrogen (%) and phosphorus (mg/dm^3 of soil)]. Other variables were correlated in some degree with soil nitrogen and phosphorus, and their relation with termite community structure is shown as a Supplementary Material (Table S3; Fig. S1). These data are available at http://ppbio.inpa.gov.br/Port/inventarios/ducke/pterrestre/solosb. 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 incidence 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.

Species turnover among transects was measured by the Bray-Curtis dissimilarity index in species composition between all possible pairs of transects. We used 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 density, termite richness, termite PIE, and turnover of termite species composition (response variables) versus ant predator density, tree density, and soil phosphorus and nitrogen (predictor variables). For termite density and species richness, we used Generalized Linear Models (GLMs) with log-link functions, and a Poisson distribution of errors in the residuals. 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 be both affected by the same spatial and environmental variables, which could result in a 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 nitrogen and phosphorus, tree density, ant predator density, and termite abundance and species richness.

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 (Fig. 2, left and right panels). In contrast, if predators are generalists, ant predator density should not be strongly associated with termite PIE (Fig. 2, 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. Termite samples were randomly subsampled 1000 times for each transect, and standard deviations were calculated as Standardized Effect Sizes (SES; Gotelli & McCabe 2002).

Before beginning analyses, we tested for potential collinearity of independent variables across the sampling grid by calculating pairwise correlations among all possible independent variables. Soil phosphorus, nitrogen, and tree density were not correlated with one another 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 Fig. S1). 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 Fig. S1, 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; z = –4.34; *P* < 0.001; Fig. 3A) and termite species richness (r = –0.44; z = –2.93; *P* = 0.003; Fig. 3B; Table 1) but was not significantly related to PIE (r = –0.15; t = –1.39; *P* = 0.17; Table 1) or turnover in termite species composition (r = 0.004; t = –1.39; *P* = 0.52 and r = –0.37; t = 0.64; *P* = 0.11 for the first and second ordination axes respectively; Table 1; S3). The multiple regression models for termite abundance and species richness explained 50 and 33 percent of the variation in the data, respectively.

For PIE (Fig. 4A) and termite species richness (Fig.4B), 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. Turnover in termite species composition (first ordination axis of species composition) was correlated with soil phosphorus (r = 0.79, t = 6.28; *P* < 0.001), soil nitrogen (r = –0.48, t = –3.66; *P* = 0.007), and tree density (r = –0.42, t = –2.83; *P* = 0.02; Fig. 5). The density of trees per transect was also negatively correlated with the PIE index of termite species diversity (r = –0.44, t = –2.92; *P* = 0.01). The multiple regression model for PIE explained 28 percent of the variance. The explained variance for termite species composition was 77 and 4 percent for the first and second ordination axes, respectively.

Deviations from rarefaction curve for the termite PIE index were related to soil nitrogen ($r = -0.25$, $t = -2.32$; $P = 0.03$) and tree density ($r = -0.43$, $t = -2.72$; $P = 0.01$; Table 1). Deviations from the rarefaction curve in termite 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 ($P = 0.009$ for soil nitrogen) than on termites ($P = 0.05$ for soil nitrogen), and a strong direct effect of ant predators on termites ($P < 0.001$ for density and richness; Fig. 6). The SEM was able to explain 19 percent of the variation in ant predator density, and 51 and 30 percent of the variation in termite abundance (Fig 6A-C) and species richness (Fig 6D-F), respectively.

The use of a PCA axis of environmental variables as a predictor in multiple regression models (Table S3) and SEMs (Fig. S1) generated similar results.

Discussion

The single strongest predictor of both termite abundance and termite species richness was the density of ant predators (Fig. 3; Table 1). Based on the calculated regression slopes, an increase in ant predator density of 4 ants/m^2 corresponded to an approximate decrease in termite density of 2 termites/m^2 and a decrease in termite species richness of 1 species/m^2. 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 suggest that ant predator density was directly and negatively associated with termite abundance and species richness (Fig. 2A-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 nitrogen, soil phosphorus (Table 1), and to other environmental covariates (Table S3). The direct association of termites and ant predators was also supported by the results of the SEM analyses (Fig. S1).Hi

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 density matched the predictions of a simple random draw from the local pool of termite species. These results are consistent with the hypothesis that ants effectively rarefied the termite assemblage (Fig. 2), leading to progressive losses of rare termite species (Fig. 3B). Alternatively, it is possible 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 behaviour 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. 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 5A). 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 soil-dwelling termites that depend on these resources. In contrast, wood-feeding termites can be strongly limited by the nutrient content of their food (Morales-Ramos & Rojas 2003). In the soils of the Amazonian forest, phosphorus is a scarce nutrient (Vitousek 1984), and the amount of phosphoros in the soil is usually correlated with phosphorus content in plant tissues (Stark 1970).

The correlative evidence presented here for strong 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 homogenous systems, there may be stronger effects of bottom-up control through changes in productivity and habitat diversity. For example, Kaspari et al. (2000) showed that overall ant density and species richness decreased along a productivity gradient from deserts to rainforests. In Amazonia, both termite and ant densities are much lower in savannas than in rainforests, 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). 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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Tables

Table 1.1 Slope coefficients for multiple regressions of termite community structure against predictor variables.
Generalized Linear Models with Poisson distributed errors were used for abundance and richness. R^2 values for abundance and richness were calculated using Cox and Snell's (1968) method. P: Phosphorus; N: Nitrogen.

Response variable	Intercept	Predator density	P	N	Tree density	df	χ^2	*F*	R^2
Abundance	3.609***	-0.024***	0.009	-0.079†	-0.021	25	20.907		0.502***
Richness	3.013***	-0.021**	-0.03	-0.105†	-0.085	25	11.948		0.329*
PIE	0.951***	-0.002	-0.006	-0.03*	-0.032**	25		3.805	0.279*
NMDS1	-0.037	0.002	0.155***	-0.09**	-0.067*	25		24.19	0.762***
NMDS2	0.14	-0.007	-0.017	0.004	-0.033	25		1.35	0.046
SES_{PIE}	0.333	-0.041	-0.116	-0.738*	-0.847*	25		3.119	0.226*
$SES_{Richness}$	0.083	-0.029	-0.274	-0.357	-0.538†	25		1.211	0.028

$^{***}P < 0.001$ $^{**}P < 0.01$ $^{*}P < 0.05$ $^{\dagger}P < 0.1$.

Figure legends

FIGURE 1. Location of the Reserva Ducke and grid system in South America. Gray dots on the trail system indicate the location of the 30 sampling transects. Shading indicates elevation within the grid.

FIGURE 2. Predictions for relative abundance distributions and the PIE index (Probability of Interespecific Encounter) for three hypothetical termite species under random versus non-random predation by ants. The expectation of the termite PIE index and termite species richness was quantified by simulating a random removal of termite species (center column), preferential removal of the most common species (left column), and preferential removal of the most rare species (right column).

FIGURE 3. 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 = $e^{(3.54820 - 0.02088 \times \text{predator density})}$. Termite species richness = $e^{(2.94704 - 0.01784 \times \text{predator density})}$.

FIGURE 4. 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 values were calculated by comparison of observed PIE and species richness with the expectation from

a null model of random removal of termite colonies from a regional species pool. $SES_{PIE} = 0.02142 - 0.02550 \times$ predator density. $SES_{Richness} = -0.04859 - 0.02243 \times$ predator density.

FIGURE 5. Changes in termite species composition along soil phosphorus (A), soil nitrogen (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. $NMDS1 = -0.2548 + 0.0637 \times$ phosphorus. $NMDS1 = 0.2397 - 1.2919 \times$ nitrogen. $NMDS1 = 0.4503594 - 0.0001002 \times$ tree density.

FIGURE 6. Structural equation models (SEMs) with regressions between environmental variables, the density of ant predators, and the termite density (A-C) and termite species richness (D-F). A and D: Direct effects of environmental variables on predator and termite density and richness. B and E: Direct effect of environmental variables on predator density and direct effect of predator density on termite density and richness. C and F: Direct effect of environmental variables on predator density and on termite density and termite species richness, and direct effects of predator density on termite density and termite species richness. The solid, dashed, and dotted lines represent significant, marginally significant, and non-significant correlations at $P < 0.05$, respectively. All variables were standardized before analysis.

Figures

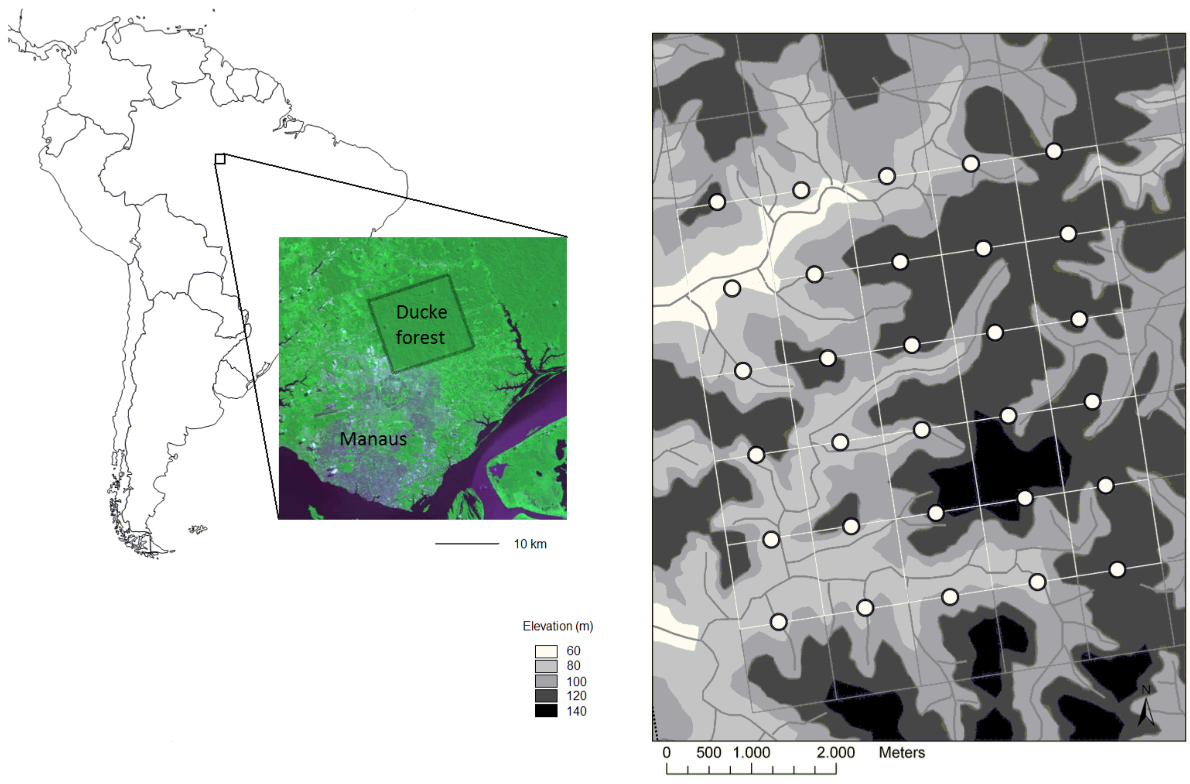

Figure 1.1 Location of the Reserva Ducke and grid system in South America.

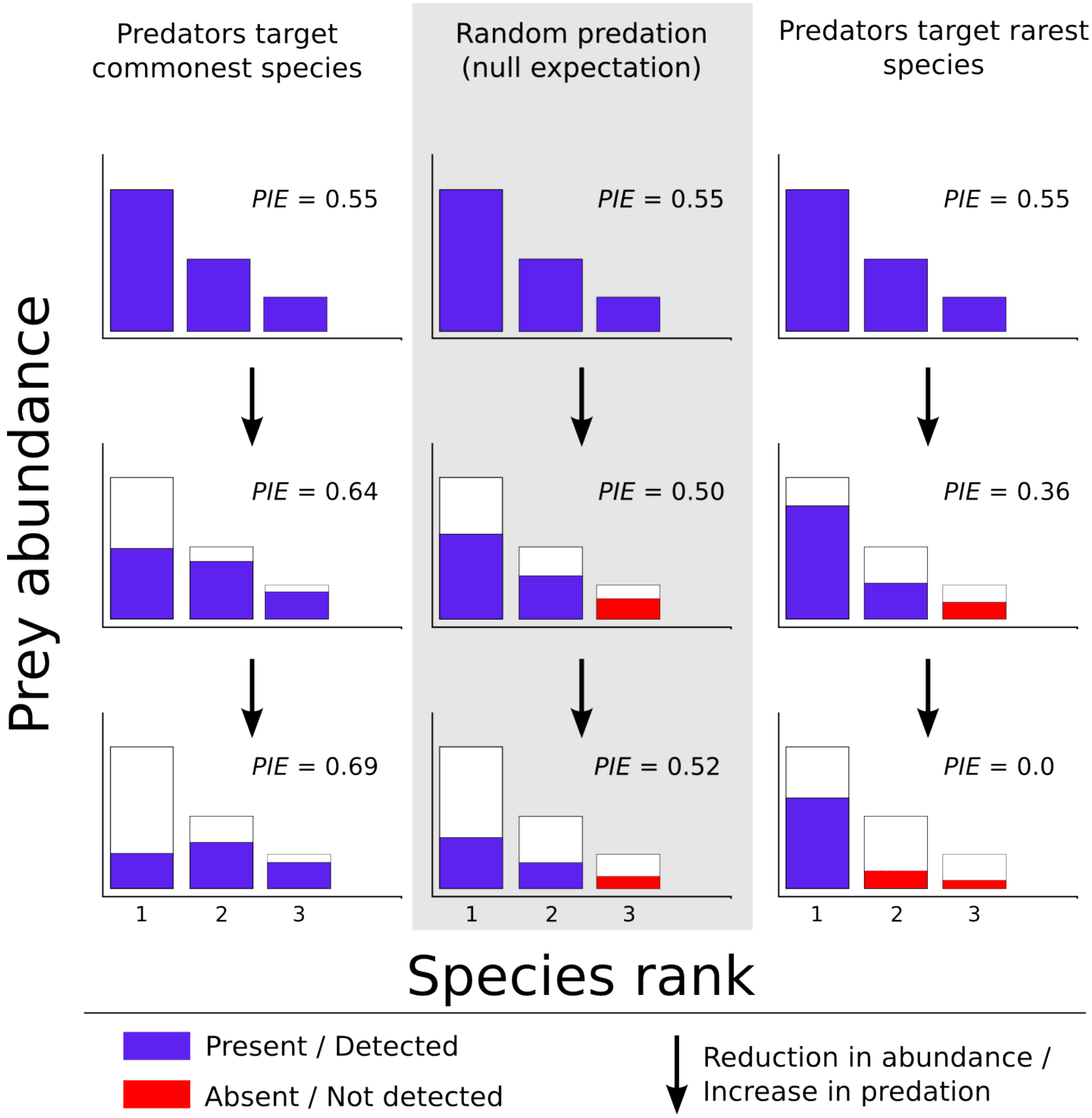

Figure 1.2 Predictions for relative abundance distributions and the PIE index (Probability of Interespecific Encounter) for three hypothetical termite species under random versus non-random predation by ants.

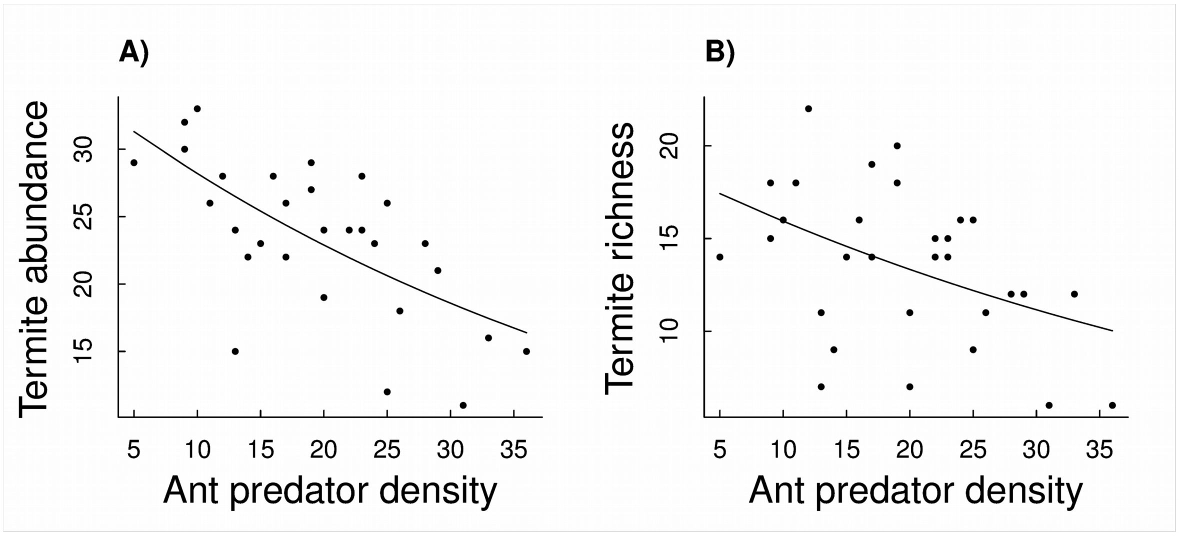

Figure 1.3 Relationship between ant predator density and termite abundance, and termite species richness.

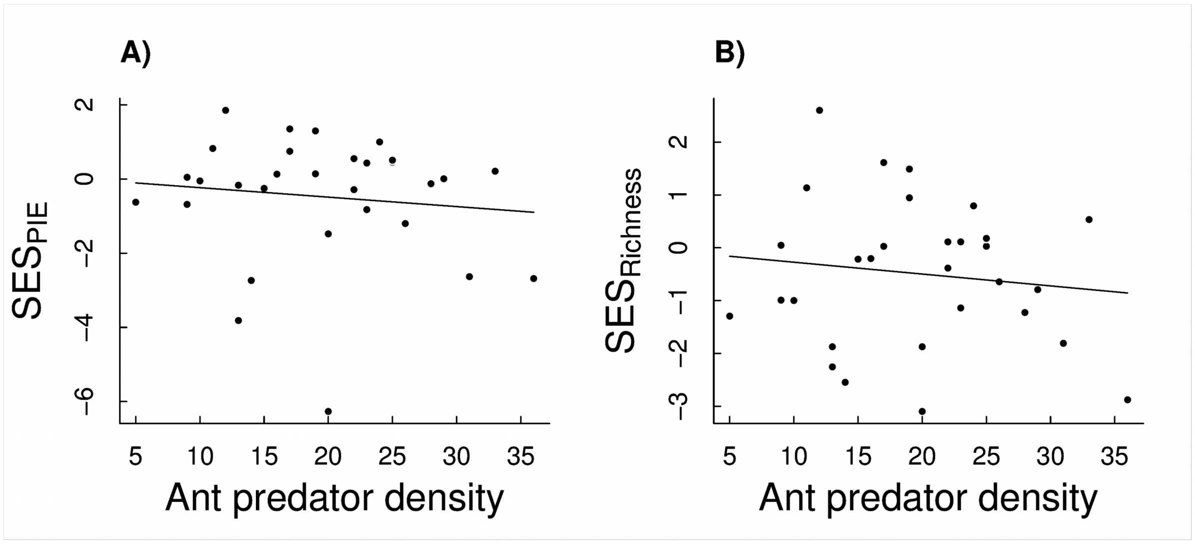

Figure 1.4 Relationship between ant predator density and the Standardized Effect Size (SES) for the Probability of an Interspecific Encounter (PIE), and termite species richness.

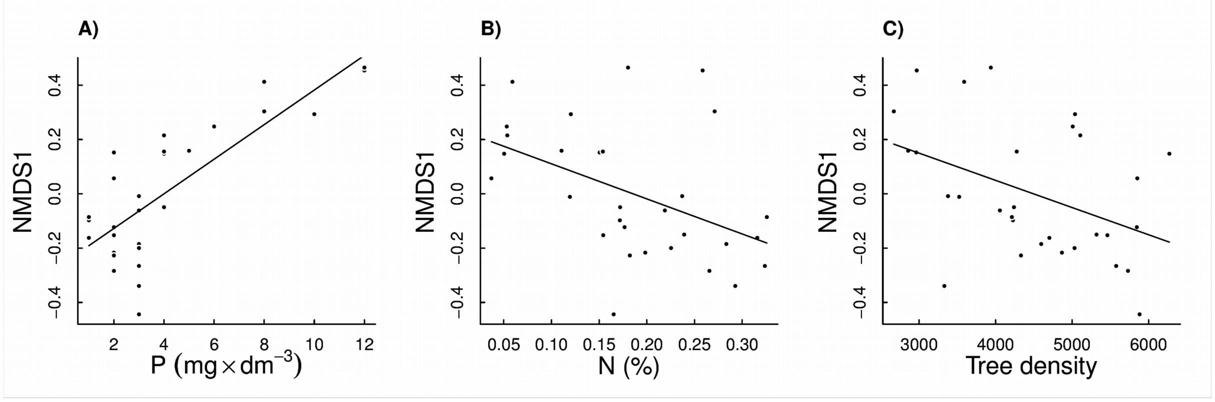

Figure 1.5 Changes in termite species composition along soil phosphorus, soil nitrogen, and tree density gradients.

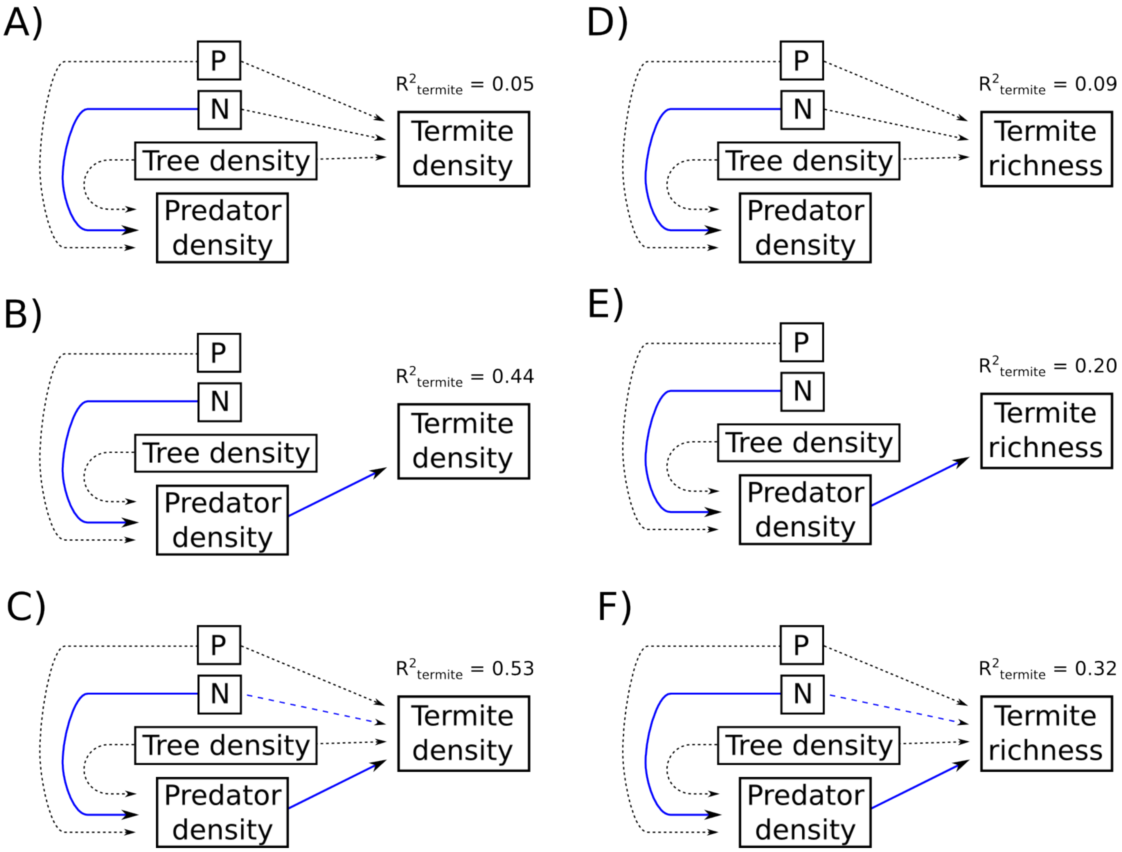

Figure 1.6 Structural equation models (SEMs) with regressions between environmental variables, the density of ant predators, and the termite density and termite species richness.

CHAPTER 2: CHANGES IN TERMITE SPECIES COMPOSITION IN CENTRAL AMAZONIA ARE DETERMINED BY SPECIES FEEDING STRATEGY, BUT NOT BY DEFENSE AGAINST PREDATORS.

Summary

1. Interspecific competition may limit the coexistence of species with similar traits, whereas environmental filters may promote the coexistence of species adapted to similar conditions. Many studies have investigated the net effects of competition and environmental filtering on community structure by testing for phylogenetic patterns of *overdispersion* or *clumping*. Until recently, most studies of community phylogenetics have not related these patterns to continuous environmental gradients that may act as filters, nor have they considered the role of biotic filters, such as predation pressure.

2. We measured the occurrence of 79 termite species in 30 local assemblages in central Amazonia. Each termite species was classified into one of three feeding groups and into one of seven predator defense strategies. We analyzed the association between the phylogenetic and functional structure of each termite assemblage, and soil nutrients, tree density, and total density of 158 species of predatory ants.

3. In sites with high phosphorous content (P), the numerical dominance of wood-feeding termites reduced the functional and phylognetic diversity of termite assemblages. In spite of a strong negative correlation between ant predator density and termite abundance, ant predator density was not associated with termite phylognetic diversity or the diversity and composition of termite defense strategies.

4. Our results might indicate that soil P is the most important environmental filter affecting the phylogenetic and functional structure of termite assemblages even though ant predators strongly reduce termite abundance and species richness. These results suggest that drivers of phylogenetic and functional community structure may be decoupled from the drivers of abundance and species richness.

Key-words: Amazonian Rainforest; Ants; Competition; Phylogenetic Community Structure; Predation; Species Abundance; Species Composition; Termites.

Introduction

Many studies of community phylogenetics and functional trait diversity argue that competition for limited resources will reduce the coexistence of closely-related species with similar traits (Webb *et al.* 2002; Cavender-Bares *et al.* 2009; Cadotte, Albert & Walker 2013). Alternatively, environmental filtering will increase the coexistence of closely-related species with similar traits that allow for persistence in harsh environments (Webb *et al.* 2002; Cavender-Bares *et al.* 2009; Cadotte *et al.* 2013). These recent studies recapitulate an old set of arguments about competition and habitat specialization, and their opposing effects on species/genus ratios and other taxonomic diversity indices (eg. Simberloff 1970).

In spite of widespread interest in community phylogenetics, there are relatively few studies of the relationship between predator density and the phylogenetic and functional structure of prey communities. In host-parasite systems, shared parasites can cause extinctions of closely-related species and lead to phylogenetic overdispersion (Webb, Gilbert & Donoghue 2006). Similarly, specialized predators can cause phylogenetic overdispersion of prey communities if closely-related related prey species have similar defensive traits (Cavender-Bares *et al.* 2009).

In tropical rainforests, diverse communities of termites and their ant predators are a model system for studying community phylogenetics. Ants are the main predators of termites (Sheppe 1970; Hölldobler & Wilson 1990) and termites have several defense mechanisms that probably evolved as a response to ant predation (Prestwich 1984). Generalist ant predators reduce the overall abundance and species richness of termites, although termite species composition is more strongly correlated with soil phosphorous than with ant predator density (Dambros *et al.*, 2015).

In this study, we asked whether ant predator density, soil nutrients, and tree density were associated with the phylogenetic structure, and the distribution of feeding and defensive traits of termites. We tested whether certain termite defense strategies were more common in areas of high ant predator density, and whether the turnover in termite species composition along soil nutrient gradients was accompanied by a turnover in termite feeding strategies.

Methods

Study area

The study was conducted at Ducke Reserve, a 10,000 ha tropical rainforest located at Manaus, Brazil. Elevation in the reserve varies from 39 m to 110 m asl. Sandy soils in the bottomlands are usually poorer in nutrients than clayey soils in uplands (Chauvel, Lucas & Boulet 1987). Vegetation consists of dense evergreen forest, with average canopy height above 40 m (Hopkins 2005). The understory is mostly open, with dominance of palms in the genera *Attalea* and *Astrocarium* (Ribeiro *et al.* 1999). The sampling area is not subject to periodic flooding, and the site has never been logged or burned.

Sampling design and data collection

Termite data were obtained from Dambros *et al.* (2015), who sampled termites at Ducke Reserve between December 2008 and May 2009 during the rainy and dry seasons. Termites were sampled in 30-250 m long transects regularly spaced in a 5 × 6 km grid (Fig. 1). The transects were at least 1 km apart from each other, and each transect followed an elevation contour line to minimize variation in edaphic conditions within each transect. Transects were established at least 10 m away from the nearest walking trail.

Along the central line of each transect, 10 equally spaced 5 x 2 m sections were surveyed for termites. In each section, three investigators searched for termites for 20 min. Each section was thoroughly searched for termites in the soil, fallen logs, small branches, standing trees, and nests. Nests in trees above 2 m were not surveyed. Termite soldiers and workers were hand-collected and stored in 4 ml containers filled with 95% EtOH. Voucher specimens of all species are deposited in the Entomological Collection of the National Institute of Amazonian Research (INPA), Manaus, Brazil. Termite data are publicly available at http://ppbio.inpa.gov.br/ and http://files.figshare.com/1922298/Dambros2009_Isoptera.RFAD.csv under Creative Commons – BY license.

We assigned each termite species to one of three feeding guilds following Davies *et al.* (2003): Wood, soil or leaf-litter feeders. We also classified each termite species by defense strategy into eight groups based on mandibular shape and presence of chemical defense in the soldier caste (Prestwich 1984; Scholtz, Macleod & Eggleton 2008): 1) Bitting mandibles (BM); 2) Asymmetrical snapping (ASN); 3) Symmetrical snapping (SSN); 4) Piercing (PI); 5) Daubing brush (DB); 6) Glue-squirting (GS); 7) Crushing mandibles (CM); and other types of defense (OT; only for Apicotermitinae). When termite species had more than one defense strategy, and for termite species with differentiation within the soldier caste; we used the most common defense strategy to characterize the species.

We analyzed termite community structure with predictor variables of ant predator density, tree density, and soil phosphorous (P) and nitrogen (N), which were also measured in each transect by other investigators.

Ant data at transect level were taken from Souza *et al.* (2012), who used pitfall traps, sardine baits, and litter samples extracted by the Winkler method. Similar to termite sampling, ants were sampled in 10 equally spaced sections *per* transect during the rainy and dry seasons. More details of ant sampling can be found in Souza *et al.* (2012) and Dambros *et al.* (2015).

Of the 242 ant species found, we classified 158 ant species *a priori* as potential termite predators based on previously published information on feeding habits for ant species or genera (Silva & Brandão 2010). We used incidence of ant predators per transect as a measure of ant predator density.

Tree data at 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 nutrients [N (%) and P (mg/dm^3 of soil)]. These data are available at http://ppbio.inpa.gov.br/Port/inventarios/ducke/pterrestre/solosb. For these measurements, 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).

Termite phylogeny

We used a previously published termite phylogeny by Legendre *et al.* (2008), which was constructed using only molecular data (12S, 16S, 18S, 28S, COI, COII, and Cytb). Using Mesquite (Maddison & Maddison 2011), we incorporated into the Legendre *et al.* (2008) tree termite clades represented in this study that have not yet been sequenced but that have well-defined characters or a previously proposed phylogeny. We represented poorly characterized species or taxa as polytomies in our phylogeny (Fig. 2). Due to the inclusion of poorly characterized taxa, quantitative branch lengths were not available for this phylogeny, so we used the number of nodes separating two species as a pairwise measure of phylogenetic distance (patristic distance). Previous studies have demonstrated that polytomies on terminal branches of a phylogeny do not have strong effects on the phylogenetic metrics used in our study (Swenson 2009). Similarly, the use of patristic distances in previous phylogenetic studies provided similar results to quantitative measures of branch length (eg. Freitas *et al.* 2014).

Data analysis

Phylogenetic signal on traits

One common assumption of phylogenetic analyses in community ecology is that closely-related species are more similar to each other in their traits than distantly-related species (Webb *et al.* 2002). Although this is usually the case (Wiens *et al.* 2010), some important traits might be convergent between distant lineages, or very labile (Blomberg, Garland & Ives 2003; Losos 2008), so it is important to first test for phylogenetic signal in measured traits before analyzing the relationship between species relatedness and co-occurrence (Crisp & Cook 2012).

Due to the categorical nature of the feeding and defense strategy traits, we were not able to test if species are more similar to each other in their traits than it would be expected under a random evolutionary model, (ie. phylogenetic niche conservatism strictu sensu; Blomberg *et al.* 2003; Crisp & Cook 2012). However, we compared the distribution of species traits in the phylogeny against a null expectation based on the reshuffling of terminal branches of the termite phylogeny (phylogenetic signal). We created a pairwise similarity matrix between all pairs of species. The matrix was filled with 1s and 0s, representing species pairs sharing (1) or not sharing (0) a particular trait. We then calculated a pairwise matrix of phylogenetic distances between all pairs of species. These distances represented classes from 2 (same genus) to *n*, the maximum phylogenetic distance between two species in the phylogeny. For each phylogenetic distance class, we averaged the trait values from all the species pairs in that class. The resulting metric represented the proportion of species sharing a given trait in a phylogenetic distance class.

We next calculated the Moran's *I* to test for the presence of phylogenetic autocorrelation in species traits. Additionally, we calculated Pearson's correlations between trait distance and phylogenetic distance in several classes of phylogenetic distance ([2,3.69); [3.69,5.38); [5.38,7.08); [7.08,8.77); [8.77,10.5); [10.5,12.2); [12.2,13.8); [13.8,15.5); [15.5,17.2); [17.2,18.9); [18.9,20.6); [20.6,22.3); [22.3,24]). Mantel correlogram tests were used to investigate the significance of the Pearson's correlations. Both Moran's *I* and Mantel correlograms were performed independently for feeding and defense strategy traits.

Phylogenetic and functional diversity

To determine the importance of species phylogenetic relatedness and trait similarity on species co-occurrence, we calculated the species phylogenetic and functional diversity in each transect.

Phylogenetic diversity was calculated by using three metrics: Phylogenetic Distance (PD; Faith 1992), Mean Pairwise Distance (MPD), and Mean Nearest Taxon Distance (MNTD) (Webb *et al.* 2002). PD is a general metric of phylogenetic distance among all species co-occurring in a given transect (total number of nodes), whereas MPD and MNTD measure phylogenetic distances between pairs of species. MPD and MNTD give more weights for basal or terminal branches of a phylogeny, respectively (Webb *et al.* 2002). PD, MPD, and MNTD are usually correlated with species richness (more species = more phylogenetic branches). To quantify phylogenetic diversity independently from species richness, we compared the observed values of phylogenetic diversity against an expectation generated from a null model.

The null model was created by 999 randomizations of the terminal branches (species labels) in the phylogeny. For each randomization, PD, MPD, and MNTD were recalculated. This procedure generated a null distribution of PD, MPD, and MNTD under the assumption of no phylogenetic signal in species distribution. Because only the species positions in the phylogeny are randomized, the null model retained the original number of species per transect. We then calculated deviations of the observed metrics from their null expectation as Standardized Effect Sizes (SES):

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

where x represents the observed phylogenetic metric in a given transect, and μ and σ represent the mean and standard deviation of the phylogenetic diversity per transect in 999 randomizations. Values of SES lower than zero indicate phylogenetic clustering, whereas values higher than zero indicate phylogenetic overdispersion (Kembel 2009). The SES of MPD and MNTD corresponds to -1 × the Net Relatedness Index (NRI) and -1 × the Nearest Taxon Index (NTI) of Webb *et al.* (2002). We used SES values for each metric as response variables representing phylogenetic diversity (hereafter only referred as PD, MPD, and MNTD).

Termite phylogenetic diversity was calculated using all termite species and independently for wood- and soil-feeding termites. The number of litter-feeding species, as well as the number of species with specific defense strategies was too small for meaningful analyses of these groups separately.

Functional diversity was calculated using the Functional Dispersion metric (FDis; Laliberté & Legendre 2010). FDis is calculated as the mean trait distance of individual species to the centroid of all species in trait space. FDis was calculated independently for feeding and defense strategy and weighted by species abundances. FDis is by definition independent of species richness (Laliberté & Legendre 2010), and the use of a null model to remove the correlation of richness and FDis generated similar results (not shown).

Phylogenetic and functional composition

Commonly used metrics of species composition are based on taxonomic information (eg. number of shared species between pairs of assemblages). Although taxonomic metrics can be used to investigate turnover in species composition along environmental gradients, taxonomic metrics do not provide information about species traits associated with species turnover, and cannot be used to detect phylogenetic patterns in species composition (eg. family level turnover along environmental gradients).

To determine if the turnover of termite species previously reported along the P gradient (Dambros *et al.* 2015) was associated with a phylogenetic turnover along P, we calculated the phylogenetic Sørensen metric (Psor; Bryant *et al.* 2008) and the UniFrac metric (Lozupone & Knight 2005). Psor and UniFrac are phylogenetic counterparts of standard Sørensen and Jaccard metrics (Chiu, Jost & Chao 2013) quantify the phylogenetic overlap in pairs of transects by comparing the shared phylogenetic branches represented in the transects. Differently from conventional metrics of species similarity, pairs of transects with no shared species might still have a high degree of phylogenetic similarity by sharing other clades, such as genera or families. We summarized the pairwise phylogenetic similarity matrices of Psor and UniFrac into ordination axes by using a Principal Coordinates Analysis (PCoA). We then used the first ordination axis as a measure of phylogenetic composition in multiple regression analyses against ant predator density, tree density, P, and N.

To test for changes in the composition of feeding and defense traits along environmental gradients, we grouped termite species in each transect according to their feeding and defense strategies. We then summarized changes in species feeding and defense strategies across transects by conducting a Principal Component Analysis (PCA) on the traits × transects matrix. The first ordination axis of the PCA was used as a response variable in multiple regression analyses against ant predator density, tree density, P, and N.

The similarity measures and the PCA ordination technique used in our analyses cannot be used to distinguish changes in trait composition caused by the replacement of species (turnover) or changes in the number of species sampled (nestedness; Baselga 2010). To test if changes in the composition of feeding traits was associated with a the replacement of species with particular feeding strategies, we conducted individual regression analyses of wood and soil feeding termite density against the predictor variables. Turnover in feeding strategy would be represented by an increase in the species abundances from a feeding group and a simultaneous decrease in the abundance of species from the other feeding group.

We conducted all analyses in the R program (R Development Core Team 2013), using the packages vegan (Oksanen *et al.* 2008), picante (Kembel *et al.* 2010), and FD (Laliberté & Shipley 2011). Annotated R scripts with all analyses necessary to replicate our results are provided in Supporting Information S1 and S2. The scripts also include links for downloading all data used in our study.

Results

Closely-related species were significantly more similar in their traits than distantly-related species, both considering feeding and defense strategy traits (P for Moran's $I < 0.001$; Table S1; Fig. 3). However, the phylogenetic signal of feeding and defense strategy was much stronger on small phylogenetic distance classes, and was not significant at large phylogenetic distances (Table S1; Fig. 3).

The phylogenetic diversity of termites, as measured by PD and MNTD, was highest in areas with low P, but PD and MNTD were not associated with ant predator density, tree density, or N, either considering all termite species or by feeding group (Table 1; Fig. 4). The phylogenetic diversity measured by MPD was also negatively correlated with P, but only when wood and soil feeding species were analyzed separately

(Table 1). The multiple regression model including all predictor variables explained 28% and 43% of the variation in PD and MNTD, respectively (Table 1). The explained variance of PD and MNTD was 42% and 51% for wood feeding termite species, and 16% and 14% for soil feeding species, respectively. All models had a poor fit to MPD ($r^2<0.10$).

The functional diversity, as measured by the diversity of feeding strategies, was negatively correlated with P (Table 1). The diversity of defense strategies was not associated with any measured predictor variable (Table 1).

There was not significant phylogenetic turnover in species composition along any measured predictor variable (Table 1). The first PCA axis representing the turnover of feeding strategies was strongly associated with ant predator density and P (Table 1).

The abundance of soil feeders was negatively correlated with P, whereas the abundance of wood feeders was positively correlated with P (Table 1; Fig. 5). The abundance of both soil- and wood-feeding termites was negatively correlated with ant predator density (Table 1; Fig. 6).

Discussion

Predators can reduce the functional diversity of prey communities by eliminating a subset of prey species (Cavender-Bares *et al.* 2009). Different termite species have different potential defensive mechanisms against ants, ranging from species that deliver liquid chemical defenses through nozzle-headed soldiers to species with no soldier caste that stay hidden from predators (Prestwich 1984; Scholtz *et al.* 2008). We hypothesized that, in areas of high ant density, termite species with weak defense mechanisms would be missing, resulting in termite assemblages with low functional and phylogenetic diversity.

Although termite abundance and species richness decrease sharply in areas of high ant density (Dambros *et al.* 2015), we could not detect any association between ant predator density and the defense mechanisms of different termite species (Table 1). Similarly, ant predator density was not associated with termite phylogenetic diversity and phylogenetic composition. When closely related species share similar traits, phylogenetic diversity can be used as a proxy for functional diversity (Cadotte *et al.* 2013). Legendre *et al.* (2008) showed that many morphological traits are more similar between closely-related termite species than between distantly-related species. Collectively, these results suggest that other *unmeasured* defensive traits, such as termite foraging behavior or nest defense, are also unlikely to be related to ant predator density.

Although some termite species may be effective at defending themselves against particular ant species, the high species diversity of ants in the Amazonian rainforest might prevent any termite species from escaping ant predators (Sih, Englund & Wooster 1998). Moreover, ant predation may be highest during initial stages of termite colony formation, when soldiers are absent; or during foraging, nest construction, and nest repair, when termite workers are more vulnerable. For example, Sheppe (1970) demonstrated that even the smallest ant species can be highly efficient at preying on termite workers and alates outside of their nests. Although ant predator density was the strongest predictor of termite density, other environmental variables could be a stronger selective force favoring termite species with particular traits. Termite colony growth can be constrained by food quality and quantity (López-Hernández 2001; López-Hernández *et al.* 2006), and termite species strongly compete for highly nutritious patches of wood (Shellman-Reeve 1994).

Unlike predator density, soil P was strongly associated with termite phylogenetic diversity and composition. P is the most limiting nutrient in tropical forests, especially in Amazonia (Vitousek 1984; Quesada *et al.* 2010), where the composition of other animals (Tarli *et al.* 2014) and plants (Costa, Magnusson & Luizao 2005; Boelter *et al.* 2014) also changes along P gradients. In a Venezuelan rainforest, species composition of termites also changed from wood-feeders to soil-feeders in high-P versus low-P areas (Salick, Herrera & Jordan 1983).

In this study, closely-related termite species with similar traits co-occurred less in areas with low P than in areas with high P (Fig. 4a), which might suggest that termite species compete when P is scarce (Fig. 4b-c). In low P areas, wood-feeding termites were also more phylogenetically dispersed than soil-feeding termites. This result would be expected if wood-feeding termites were more P limited than soil-feeding termites. Moreover, the change in termite species composition along P was associated with changes in species feeding strategies. Wood-feeding termites were more common in high P areas, whereas soil-feeding termites were more common in low P areas (Fig. 5). Collectively, these results indicate that termite feeding strategies are more strongly associated with changes in termite species composition along environmental gradients than are species defense mechanisms against predators.

Organisms feeding exclusively on plant material are usually constrained by the low availability of nutrients in their food (Anderson *et al.* 2005). Wood is especially poor in nutrients compared to other plant parts, such as leaves and flowers (Stark 1970; Kerkhoff *et al.* 2006). Wood-feeding termites usually seek food in the most nutritious parts of the vascular cambium, and nutrient content in the cambium can strongly limit termite colony growth and survival (López-Hernández 2001). Soil-feeding termites have a distinct physiology from wood feeding-termites, and soil-feeding termites might not depend on cellulose digestion, as do wood-feeding termites (Brauman 2000). The strong correlation between soil and plant nutrient content (Stark 1970) could explain why wood-feeding termites were less abundant in low P areas than in high P areas.

Many recent studies have interpreted phylogenetic and functional patterns in communities as evidence of competition and environmental filtering (Webb *et al.* 2002), but other important factors, such as predation, are usually not considered. Despite the strong reduction in prey abundance and richness in areas of high predator density in our study area (Dambros *et al.* 2015), we found strong evidence for environmental control on species phylogenetic and functional composition. Although environmental filtering might have a stronger effect in communities with low trophic complexity (Cavender-Bares *et al.* 2009), our results suggest that environmental filters are also more important than trophic interactions in highly diverse and complex predator and prey communities.

Acknowledgements

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Data accessibility

R functions, environmental data, and data on termite species occurrence, phylogeny, and species traits are available at: http://dx.doi.org/10.6084/m9.figshare.1316563. Termite data and R functions are publicly available for use, distribution, and modification given that credit is provided. See http://ppbio.inpa.gov.br for environmental and ant data use.

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Tables

Table 2.1 Association of termite phylogenetic and functional community structure with ant predator density, soil phosphorous (P), soil nitrogen (N), and tree density.
PD, MPD, and MNTD: Standardized effect sizes measured as deviations from the null expectation of Phylognetic Distance (PD; Faith, 1992), Mean Pairwise Distance (MPD), and Mean Nearest Taxon Distance (MNTD; Webb *et al.*, 2002); PCoA.sor, PCoA.psor, and PCoA.ufrac: First ordination axis of a Principal Coordinates Analysis (PCoA) using the Sorensen, Phylogeneric Sørensen (Bryant *et al.*, 2008), and UniFrac (Lozupone & Knight, 2005) distance matrices; TG.FD and DEF.FD: Functional dispersion (Laliberté & Legendre, 2010) of feeding and defensive traits; PCA.TG and PCA.DEF: First ordination axis of a Principal Component Analysis (PCA) using the trait × transect matrix for feeding and defensive traits.

	Predator density	P	N	Tree density	df	*F*	Explained variance (%)
All termites							
PD	0.075	-0.485***	0.203	-0.003	25	3.983	29.153*
MPD	-0.026	-0.159	-0.06	-0.049	25	0.427	0
MNTD	-0.005	-0.719***	0.21	-0.014	25	6.557	43.39***
PCoA.sor	0.026	0.133***	-0.039	-0.036	25	13.059	62.453***
PCoA.psor	-0.039	0.016	0.004	0.032	25	0.969	0
PCoA.ufrac	-0.03	-0.088*	-0.025	-0.033	25	2.055	12.7
Wood feeders							
PD	0.281†	-0.624***	0.239	0.079	25	6.703	44.03***
MPD	0.026	-0.3*	0.021	-0.075	25	1.659	8.329
MNTD	0.064	-0.802***	0.324†	-0.002	25	7.959	48.976***
PCoA.sor	-0.022	-0.132***	0.034	0.052†	25	10.611	57.001***
PCoA.psor	0.006	-0.016	-0.024	-0.029	25	0.401	0
PCoA.ufrac	0.002	0.036	0.029	0.052	25	0.647	0
Soil feeders							
PD	0.099	0.344*	0.243†	0.019	24	2.391	16.573†
MPD	-0.009	0.385*	0.162	0.154	24	1.648	8.475
MNTD	0.08	0.554*	0.196	0.152	24	2.256	15.211†
PCoA.sor	0.061	-0.059†	0.038	0.038	25	1.777	9.678
PCoA.psor	-0.002	-0.032	-0.003	-0.022	25	0.423	0
PCoA.ufrac	-0.054	0	0.014	0.03	25	0.598	0
Functional structure							
TG.FD	-0.037	-0.06**	-0.034	-0.023	25	3.765	27.607*

	Predator density	P	N	Tree density	df	*F*	Explained variance (%)
DEF.FD	-0.03	-0.015	-0.031†	-0.026†	25	2.371	15.906†
PCoA.TG	2.49***	-1.368**	0.933†	0.086	25	9.185	53.03***
PCoA.DEF	0.371	0.459	-0.48	-0.508	25	0.709	0

$^{***}P < 0.001$ $^{**}P < 0.01$ $^{*}P < 0.05$ $^{\dagger}P < 0.1$.

Figure legends

Figure 1. Sampling grid in Reserva Ducke (RD), central Amazonia. Open circles represent transects sampled within the grid. Gray colors in the sampling grid represent the altitude gradient from lowlands (light gray) to uplands (dark gray).

Figure 2. Phylogenetic tree topology for termite species of Amazonia. The tree was reconstructed from Legendre *et al.* (2008) and was supplemented with data from other studies. Colors on circles on terminal branches represent abundances of extant species (cool colors = low abundance, hot colors = high abundance). Uncolored branches represent species that were not represented in the sampled transects and species in outgroups.

Figure 3. Relationship between frequency of shared traits and phylogenetic distance between pairs of species for feeding (A) and defense (B) strategies. Regression line in the graphs represent the fit of a Generalized Linear Regression model (GLM) to the data. Both traits were significantly more similar between closely-related species than between distantly-related species ($P < 0.001$).

Figure 4. Relationship between phylogenetic diversity and P content in the soil for the whole termite community (A), wood feeding-termites (B), and soil-feeding termites (C). Phylogenetic diversity was measured as the standardized Mean Nearest Taxon Distance

(MNTD) from a null model as Standardized Effect Sizes (SES). The regression line in the plots was obtained by fitting exponential non-linear least squares (nls) regression to the data. Transects were more phylogenetically dispersed in low P areas than in areas with high P when considering the whole community, and only wood-feeding termites. In contrast, soil-feeding termites were more phylogenetically dispersed in low P areas than in areas with high P.

Figure 5. Diagram of termite species presence against P content in the soil. Species are represented in rows, and species were ordered by their phylogeny. Blue: wood-feeding termites; green: soil-feeding termites; black: litter-feeding termites. Wood-feeding termites were more common in high P areas, whereas soil-feeding termites were more common in low P areas. There was no significant relationship between P in the soil and phylogenetic composition of termites within transects.

Figure 6. Diagram of termite species presence against ant predator density. Species are represented in rows, and species were ordered by their phylogeny. Blue: glue-squirting; dark blue: asymmetrical mandibles; gray: symmetric mandibles; black: bitting mandibles; yellow: piercing mandibles; green: crushing mandibles; orange: others. Although species with piercing mandibles were not present in areas of highest ant predator density, there was no association of ant predator density and the number of defense traits represented within transects. There was also no significant relationship between ant predator density and phylogenetic composition of termites within transects.

Figures

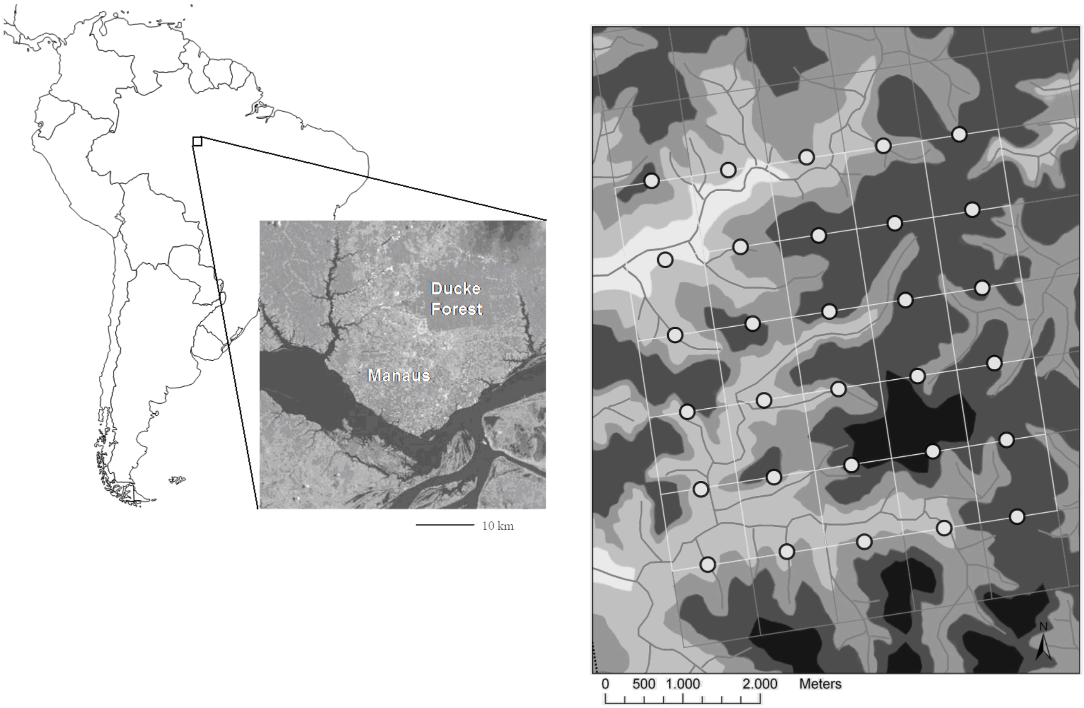

Figure 2.1 Location of the Reserva Ducke and sampling grid within the reserve.

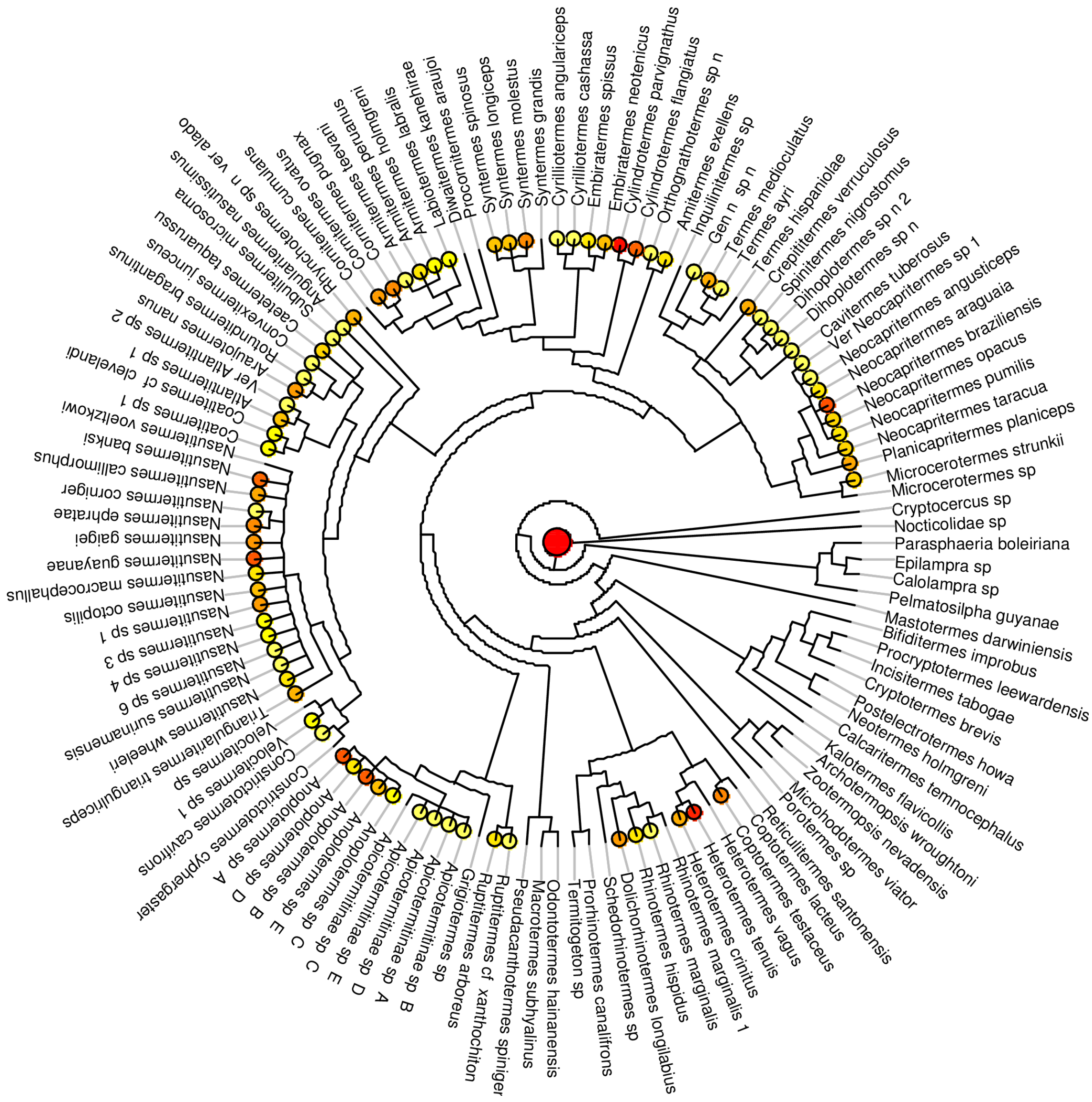

Figure 2.2 Phylogenetic tree topology for termite species of Amazonia.

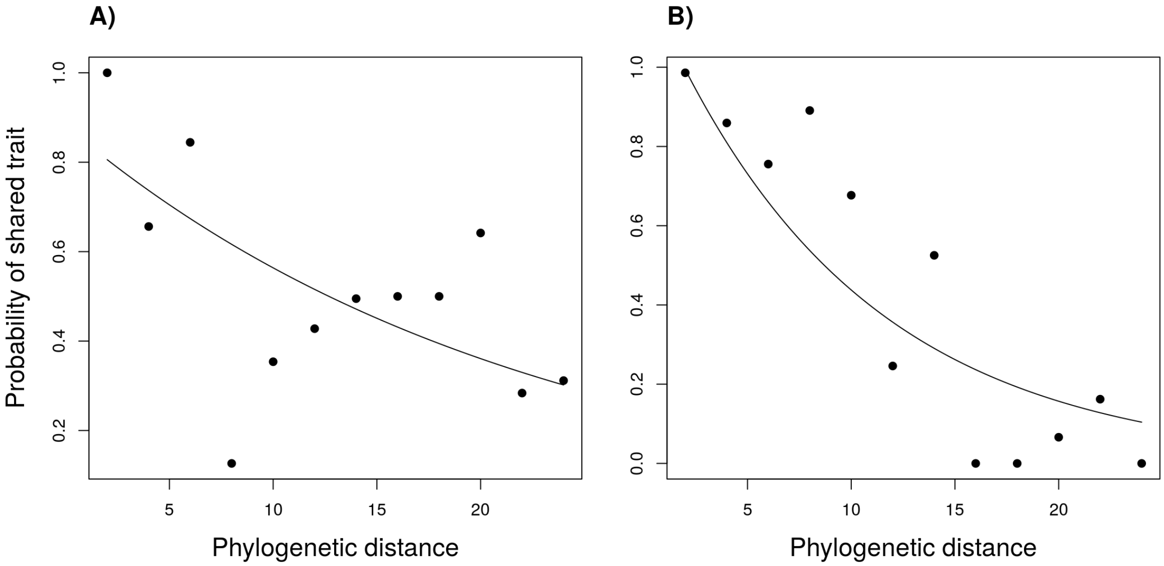

Figure 2.3 Relationship between frequency of shared traits and phylogenetic distance between pair of species for feeding and defense strategies.

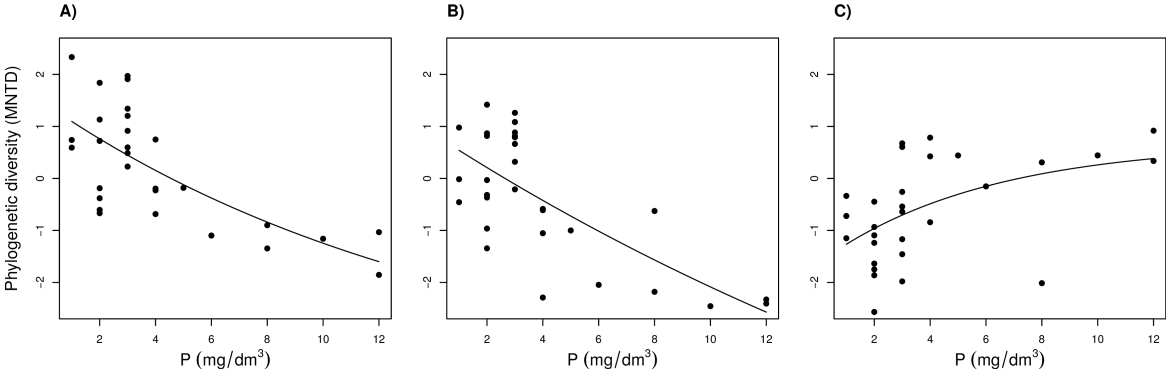

Figure 2.4 Relationship between phylogenetic diversity and P content in the soil for the whole termite community, wood feeding-termites, and soil-feeding termites.

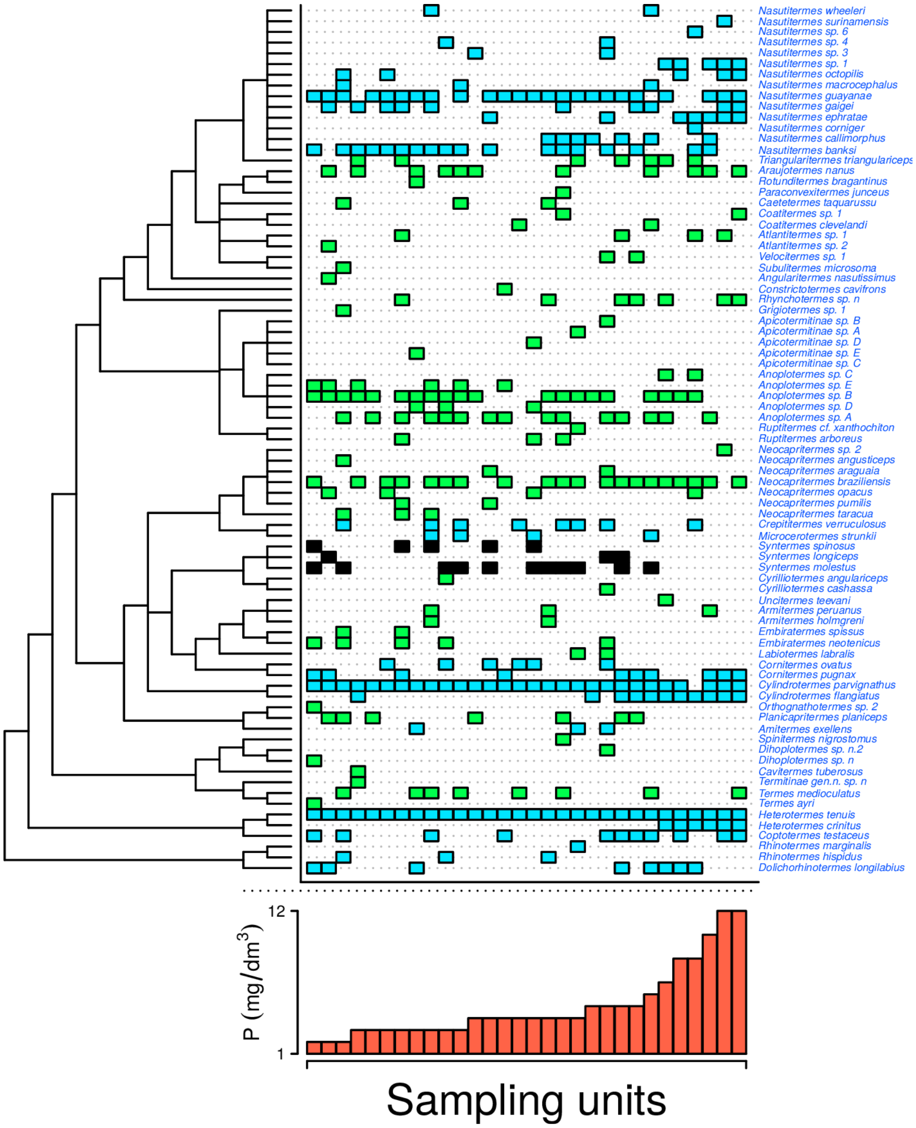

Figure 2.5 Diagram of termite species presence against P content in the soil.

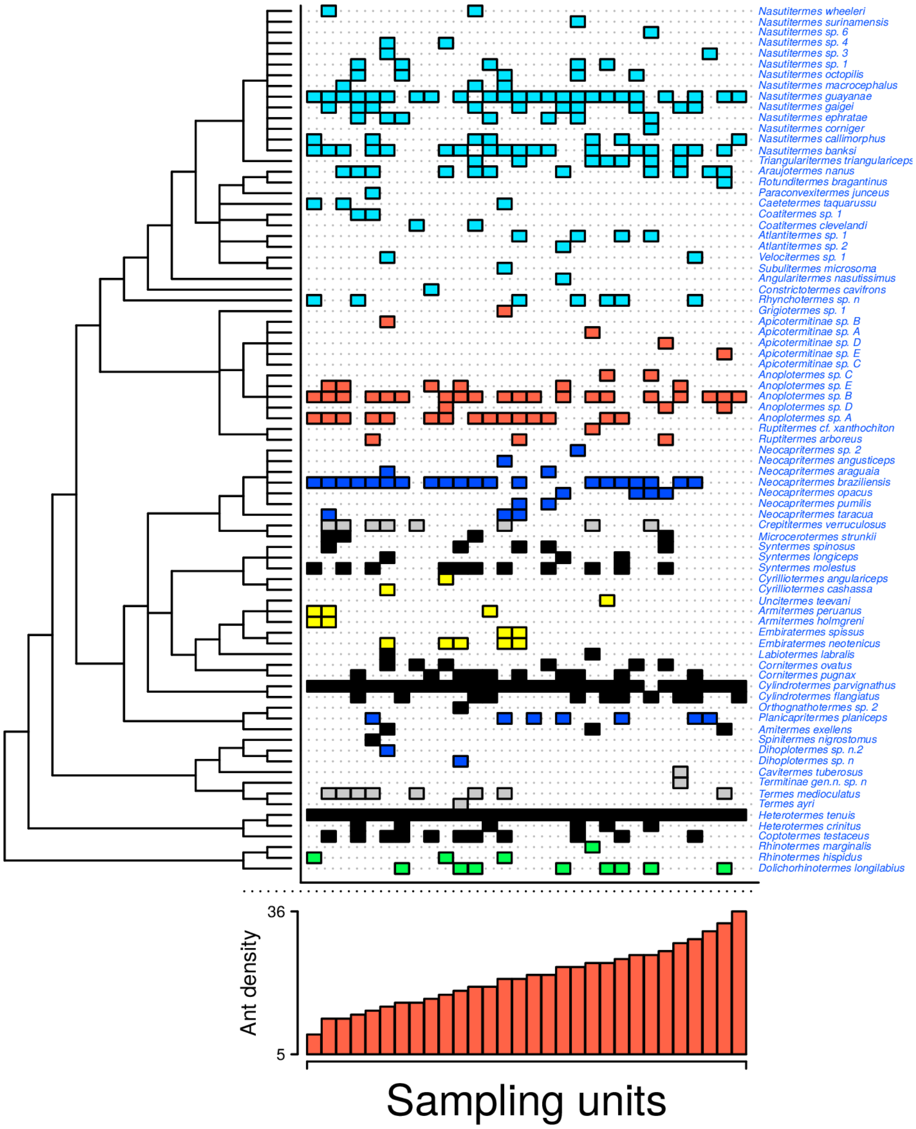

Figure 2.6 Diagram of termite species presence against ant predator density.

CHAPTER 3: CLIMATE, SOIL NUTRIENTS, AND ISOLATION BY DISTANCE CONTROL SPECIES RICHNESS AND COMPOSITION OF TERMITE ASSEMBLAGES IN THE AMAZONIAN RAINFOREST.

Abstract

Aim: To quantify the relative importance of climate, soil conditions, tree cover, and isolation by distance in controlling termite abundance, species richness, and species composition.

Location: Brazilian Amazonian rainforest

Methods: We sampled termites in 198 250 m x 2 m belt transects. Environmental data for each transect were obtained from local measurements and remote sensing. The spatial structure of termite assemblages at small and large spatial scales was represented by Moran Eigenvector Maps (MEMs) based on the geographical position of each transect. MEMs were included as covariates in regression models along with climate variables, and measures of soil chemistry and texture, and vegetation structure. From the regression models, we partitioned termite abundance, species richness, and species composition into spatial and environmental components.

Results: In contrast to most other published studies, termite abundance and species richness were negatively correlated with mean annual temperature and precipitation at large spatial scales ($-0.40 < r < -0.24$). Assemblage structure was also associated with soil calcium, and the geographic position of the transects. Between 30% and 37% of the variance in termite community structure could be attributed only to the geographic position of the transects. When large-scale spatial autocorrelation was statistically removed, termite community structure at small spatial scales was mostly associated with measures of soil texture and tree cover.

Main conclusions: At large spatial scales, the negative correlation between termite community structure, temperature, and precipitation could be explained by the distribution of soil calcium, which is highest in the northern Guiana Shield and in the Southern Brazilian Shield. Although isolation by distance may have strong effects on termite species composition, there is no evidence that major rivers are important barriers to termite dispersal, in contrast to many vertebrate groups in Amazonia.

Key-words: beta-diversity; Environmental filtering; Moran Eigenvector Maps; neutral theory; riverine barrier hypothesis; spatial autocorrelation.

Introduction

The spatial distribution of species is affected by geographical barriers to dispersal (Krasnov *et al.*, 2005; Bin *et al.*, 2009), and by the environment (Laliberté *et al.*, 2014). At large geographic scales, dispersal limitation is likely to affect the distribution of species with low dispersal capacity (Thompson & Townsend, 2006). In contrast, at small geographic scales species are less limited by dispersal, and show stronger associations with environmental conditions than with geographic isolation (Whittaker *et al.*, 2001). Despite the importance of both dispersal limitation and the environment on species distribution, and the importance of the geographic scale on these processes (Whittaker *et al.*, 2001), few studies in Amazonia have been able to separate their effects across multiple geographic scales.

In Amazonia, the distribution of vertebrates at large spatial scales has been associated with the presence of geographical barriers to dispersal, such as rivers (Ribas *et al.*, 2011; Pomara *et al.*, 2014; Boubli *et al.*, 2015). However, other taxa with higher dispersal capacity, such as small-seeded plants (Gascon *et al.*, 2000; Pomara *et al.*, 2014) and insects (Penz *et al.*, 2014), are unlikely to be limited by dispersal imposed by riverine boundaries. The distribution of major ant clades is spatially distinct within Amazonia, but do not reflect the influence of riverine barriers (Solomon *et al.*, 2008), which might suggest that other barriers to dispersal or environmental factors are more important than rivers.

Several studies of Amazonian plants (Tuomisto *et al.*, 2003; Costa, 2006; Kristiansen *et al.*, 2012) and animals (Menin *et al.*, 2007; Tarli *et al.*, 2014) have also found that the similarity in species composition between sites is correlated with differences in soil texture and chemistry. However, most of these studies are conducted at small spatial scales, and it is not known if results obtained at small spatial scales can be scaled up to explain the distribution of species at large scales. Recent studies found that the distribution of palm trees is strongly associated with soil texture at small spatial scales (Costa *et al.*, 2009), whereas soil chemistry is more important at large scales (Kristiansen *et al.*, 2012). At large spatial scales, soil chemistry can be the best predictor of species composition in Amazonia (Tuomisto *et al.*, 2003, 2014; Higgins *et al.*, 2011; Kristiansen *et al.*, 2012). However, dispersal limitation is also likely to affect species distribution (Eiserhardt *et al.*, 2011), and separating the effects of dispersal and environmental control in species composition, and attributing them to small or large scale processes, is difficult.

In this study, we investigated how changes in termite abundance, species richness, and species composition are associated with geographic distance and differences in climate, soil texture and chemistry, and tree cover between sites from small to large geographic scales. We hypothesized that local environmental conditions of soil texture, soil chemistry, and tree cover would be more strongly associated with changes in species composition at small geographic scales, whereas geographic distance and climate would be more strongly associated with changes in species composition at large scales.

Along with ants, termites are the most abundant animals in tropical forests (Fittkau & Klinge, 1973; Watt *et al.*, 1997), and show strong associations with climate

(Dawes-Gromadzki & Spain, 2003; Davies *et al.*, 2015), soil conditions, and vegetation (Davies *et al.*, 2003). Individual termite species also have specific nesting and feeding preferences, and soil-feeding termites are likely to show stronger associations with soil conditions than wood-feeding termites (Davies *et al.*, 2003). We hypothesized that soil-feeding termites would be more strongly associated with soil texture and chemistry than would wood-feeding termites.

Methods

Study area

The study area encompassed an extent of 271,563 km^2 of the Brazilian Amazonian rainforest (Fig. 1a), and included three climate types: Tropical Rainforest Climate (Af), Tropical Monson Climate (Am), and Tropical Savanna Climate (Aw; Peel *et al.*, 2007). The study area covers a gradient in annual precipitation from ~1,800 mm in the southern and the northern areas to ~2,000 mm in central areas. The vegetation in the field sites is predominantly characterized by dense evergreen forests, but also includes savannas, campinaranas (open forests), and small areas of lowland forests subject to periodical flooding (< 5% of total). Elevation ranged from 32 m to 145 m asl (mean = 83.88), and soil clay content ranged from < 0.5% to 87% (mean = 34%). Details on each sampling location can be found in the Appendix S1 in Supporting Information.

Sampling design and data collection

Termites were sampled between December 2008 and September 2014 in 199 250 m long transects grouped in 13 regular grids (Fig. 1a). Each grid had from five to 31 transects. Transects were separated by at least 1 km from one another, and followed an elevation isocline to minimize variation in edaphic conditions within each transect (Fig. 1a). Transects were established at least 10 m away from the nearest walking trail. One transect was flooded during sampling, but termites were not found on trees above the water level, so we removed the transect from analyses.

Along the central line of each transect, five equally-spaced 5 x 2 m sections were surveyed for termites. In 60 transects, five additional sections per transect were surveyed, and in 28 transects, seven additional sections were surveyed, for a total of 1,486 sections surveyed. In each section, three investigators searched for termites for 20 min, yielding 1 hour of sampling per transect, and a total of 1,486 hours of sampling for the entire study. Each section was thoroughly searched for termites in the soil, fallen logs, small branches, standing trees, and nests. Nests in trees above 2 m were not surveyed. Termite soldiers and workers were hand-collected and stored in 4 ml containers filled with 95% EtOH. Voucher specimens of all species are deposited in the Entomological Collection of the National Institute of Amazonian Research (INPA), Manaus, Brazil.

We assigned each termite species to one of three feeding guilds following Davies *et al.* (2003): wood feeders, soil feeders, or leaf-litter feeders. Termite community was analyzed as a whole, and separately for wood- and soil-feeding termites. Leaf-litter feeders comprised a small fraction of species, and were not analyzed separately from other groups.

At the transect level, we analyzed termite community structure with predictor variables of mean annual temperature, mean annual precipitation, altitude, tree cover, soil clay content, and soil nutrients of P, Ca^{2+}, K^{+}, and Mg^{2+}. Mean annual temperature and precipitation were obtained at the 0.5 arc min resolution (~1 km) from bioclim (Hijmans *et al.*, 2005). Other climatic variables are correlated with mean annual temperature and precipitation, and were not included in our analyses.

Altitude data for each transect were obtained in 90 m resolution rasters from The Global Land Survey Digital Elevation Model (GLSDEM; USGS, 2008), provided by The Global Land Cover Facility (GLCF), University of Maryland (www.landcover.org). In the study region, altitude data were generated primarily from images from the Shuttle Radar Topographic Mission (SRTM; NSF OpenTopography Facility, 2013). Altitude data obtained from remote sensing were strongly correlated with *in situ* measurements obtained from a GPS device placed along the central line of each transect ($r = 0.89$; $n = 90$). Because SRTM data were available for all our transects, only SRTM data were used in our models.

Percentage of tree cover was also obtained from GLCF at a 30 m resolution scale (Sexton *et al.*, 2013), and data quality was visually inspected by comparison with aerial pictures from our field sites available at http://ppbio.inpa.gov.br. Tree cover in each transect was calculated as the average tree cover in a radius of 90 m around the starting point of each transect.

Soil nutrients and soil texture were obtained for most transects (n = 147) from previous surveys (http://ppbio.inpa.gov.br). For soil measurements, five soil samples were collected at a depth of 5 cm at 50 m intervals along each transect, pooled, and analyzed for texture and soil chemistry. Before analysis, soil 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).

To include transects with missing soil data, we inputed missing soil data into transects by randomly selecting observed values from other transects. Although this procedure add noise to the data, and potentially reduce the power of the tests, it does not increase type I error rates.

Data analysis

Because the number of sections sampled in each transect ranged from five to 12, we rarefied the termite data on those transects in which more than five sections were sampled. For each termite species in each transect, we calculated the species abundance and probability of occurrence (presence) expected in a random draw of five sections per transect. We provide details on rarefaction calculations, and comparisons with a random removal of sections in Appendices S1 and S2 in Supporting Information.

Termite abundance and species richness per transect were calculated as the average abundance and average species richness that would be achieved by sampling five sections per transect. To quantify the turnover in termite species composition, we calculated the Bray-Curtis dissimilarity index between all pairs of transects, based on the matrix of average species abundances per transect. We performed a Principal Coordinates Analysis (PCoA) on the pairwise matrix of dissimilarities, and used the first two PCoA axes as response variables representing changes in termite species composition.

Spatial structure on termite community

Over large areas, ecological communities show strong spatial autocorrelation (Koenig, 1999); therefore areas close to each other should exhibit similar composition of species. Spatial autocorrelation in biological communities can result from neutral processes, such as random dispersal, and non-random processes, such as species responses to spatially structured environmental variables (Legendre & Gauthier, 2014). If all relevant environmental data are included, spatial statistical analyses can be used to disentangle the effects of environmental variables on species distribution from species spatial distribution not caused by the environment. Because we were interested in the spatial distribution of species caused both by environmental variables and historical dispersive/evolutionary processes, we included spatial predictors as explanatory variables in our models (Peres-Neto & Legendre, 2010).

To describe the spatial structure on the termite community, we constructed Moran Eigenvector Maps (MEMs) based on the geographical location of sampled transects. MEMs are orthogonal descriptions of spatial autocorrelation, and can be constructed based on the geographical distance separating transects (Griffith & Peres-Neto, 2006;

Dray *et al.*, 2012; Legendre & Gauthier, 2014). MEMs are usually constructed by creating an initial weighting matrix (*W*), which describes the connectivity between sampling units. An *eigen* analysis is then performed on the centered matrix *W* (Griffith & Peres-Neto, 2006), creating spatial vectors.

To represent the hierarchical nature of our sampling design, we created two matrices representing (1) the connectivity between pairs of transects within a grid and (2) the connectivity between pairs of transects in different grids. The two matrices were combined to create a single connectivity matrix *W,* which represented the connectivity between all pairs of transects. The within-grid connectivity was determined by the proximity between transects, so that all adjacent transects were connected to each other (Fig. 1b). The connectivity between grids was determined by a Gabriel graph (Legendre & Legendre, 2012). The combined matrix *W* describing the connectivity between all pairs of transects was used in an *eigen* analysis for MEMs construction (see detailed information on MEMs construction in Appendix S1).

The MEM analysis generated 197 vectors representing spatial autocorrelation which could be used individually as covariates in regression models. To reduce the number of spatial predictors in our models, we selected only those MEMs with significant spatial structure. We determined the significance of MEMs by comparing the observed Moran's *I* index of each MEM with expectations based on a Monte Carlo randomization (Dray *et al.*, 2006, 2012; Griffith & Peres-Neto, 2006). Additionally, we selected only those MEMs with high explanatory power for a given response variable by performing a forward selection of MEMs based on the adjusted R^2 values (Peres-Neto &

Legendre, 2010). Because different vectors can have distinct explanatory power for each measure of the termite community, forward selection was conducted independently for termite abundance, species richness, and the first two PCoA axes of termite species composition. Broad or fine scale MEMs were defined by having large or small associated eigenvalues (Dray *et al.*, 2006, 2012; Griffith & Peres-Neto, 2006).

We performed multiple linear regression analyses using termite abundance, species richness, and PCoA1 and PCoA2 as response variables. The selected MEMs were incorporated as covariates in regression models along with environmental variables. We used variance partitioning to separate : 1) variation in species distribution explained "purely" by the environment (F), 2) variation in species distribution explained "purely" by spatial autocorrelation, possibly caused by neutral processes (S), 3) variation in species distribution caused by spatially structured environmental variables that cannot be separated from dispersal or other neutral processes (E+S), and 4) unexplained or residual variation in species distribution (R). Spatial and Spatial+Environmental variance was further partitioned into variance explained by broad and fine scale spatial autocorrelation.

As an alternative to multiple regression on PCoA axes for termite species composition, we performed a Redundancy Analysis (RDA) on the Hellinger transformed termite abundance data, and a distance-based RDA Analysis (dbRDA) using the pairwise Bray-Curtis dissimilarities as response variable. The Hellinger transformation transforms Poisson or negative-binomial-like data into normal-like data, and is recommended when analyzing community data (Legendre & De Cáceres, 2013). The results from RDA and dbRDA were similar to those using the PCoA axes of species composition and are only shown as a supporting information (Appendix S2 & Appendix S3).

Altitude was correlated with mean annual temperature (r = 0.49) and mean annual precipitation (r = 0.56), and Mg was correlated with K (r = 0.56) and Ca (r = 0.50), therefore altitude and Mg were not included in regression models. The remaining variables were weakly correlated to each other (r < 0.4) and were used as independent predictor variables.

We conducted all analyses in the R program (R Development Core Team, 2013). Altitude and tree cover data were extracted from raster files using the raster package (Hijmans & Etten, 2013). We used the spdep package (Bivand, 2013) to create the connectivity matrix between grids using a Gabriel graph. RDA and variance partitioning analyses were performed by using R code modified from Dray *at al.* (2012), and functions from the vegan package (Oksanen *et al.*, 2008). Moran's *I* and bootstrap functions to perform significance tests on MEMs were created specifically for this study, and are available at http://files.figshare.com/1926471/AdditionalFunctions.R We provide the R script with all code necessary to replicate our study as a Supplement (Appendix S3) and a step-by-step document explaining all analyses conducted in R (Appendix S2). We made all termite data publicly available at http://files.figshare.com/1926478/TermiteProject.csv under Creative Commons – BY license. Links for downloading termite data and R functions are also provided in Appendix S2 and Appendix S3.

Results

We found a total of 271 termite species in 4,389 colonies. Termite abundance and species richness per transect was higher in the southern (N = 16.2 ± 4.4; S= 13.4 ± 3.5) and northern (N = 16.9 ± 4.8; S = 11.8 ± 3.1) parts of the Amazonian forest than in central Amazonia (N = 12.9 ± 4.6; S = 9.2 ± 2.8).

Twelve percent of the variation in termite abundance and 23% of the variation in species richness could be explained either by spatial variation at broad geographic scales (Fig. 2a-b) or by environmental variables with broad scale spatial autocorrelation (Fig. 2c-d). Although termite abundance and species richness were higher in areas with high Ca ($r = 0.28$ and $r = 0.25$), and lower in areas with high mean annual temperature ($r = -0.24$ and $r = -0.40$) and precipitation ($r = -0.27$ and $r = -0.28$), only clay content and tree cover were associated with an increase in termite abundance and species richness when spatial autocorrelation was controlled for (Table 1). Despite the significant association of these environmental variables with termite abundance and species richness (Table 1), 37 and 29% of the variation in termite abundance and species richness could be explained only by geographic distance, but not accounted for by the environment (Table 1). Environmental and spatial predictors combined explained 50 and 51% of the variation in termite abundance and species richness, respectively.

Termite species composition was distinct in northern, central, and southern parts of the Amazonian forest (Fig. 3a-b). Most of the broad scale variation in termite species composition could be explained either by geographic distance (Fig. 3a-b) or differences in environmental conditions between regions (Fig. 3c-d; shared $R^2 = 0.55$ and 0.39 for the first and second ordination axes of species composition, respectively). Termite species composition was associated with mean annual temperature ($r_{PcoA1} = -0.27$; $r_{PCoA2} = 0.48$), precipitation ($r_{PCoA1} = -0.68$; $r_{PCoA2} = 0.19$), clay content ($r_{PcoA1} = -0.29$; $r_{PcoA2} = -0.43$), Ca ($r_{PcoA1} = 0.43$), K ($r_{PcoA1} = 0.23$), and P ($r_{PcoA1} = 0.25$, $r_{PcoA2} = 0.30$). However, only mean annual temperature, clay content, and P were significantly associated with termite species composition when spatial variation was partialed out (Table 1). Geographic distance alone explained more variation in termite species composition than did environmental predictors alone (Table 1). Environmental and spatial predictors combined explained 92% and 69% of the variation in the first and second PCoA axes of termites species composition, respectively.

For soil- and wood-feeding termites, soil clay content was the most important environmental predictor of termite abundance, species richness, and species composition when spatial autocorrelation was controlled for (Table 1). However, the abundance and species richness of soil feeding termites was higher in areas of high soil clay content, whereas the species richness of wood feeding termites was lower in areas of high clay content in the soil. Soil feeding termites were also more abundant in areas with higher percentage of tree cover (Table 1), and soil feeding termites were more strongly associated with environmental variables and spatial predictors than were wood feeding termites (Table 1).

Discussion

In spite of a rich literature on the drivers of Amazonian diversity, most previous studies have been of vertebrates and plants, and most have been conducted in the more topographically complex areas of western Amazonia. In our study of termite assemblages in central, northern and southern Amazonia, climatic and soil variables were associated with several measures of community structure. However, differences in climatic conditions and soil variables were strongly correlated with the geographic distance between sites, making it difficult to separate direct effects of environment from effects of geographic isolation.

There are several examples of Amazonian plants and animals in which soil conditions have been implicated in controlling species occurrence (Menin *et al.*, 2007; Kristiansen *et al.*, 2012; Pomara *et al.*, 2014). However, many of these studies were conducted over a limited geographic area (but see Tuomisto *et al.*, 2003, 2014; Higgins *et al.*, 2011), and they may not scale up to explain species distribution over large areas of Amazonia. At small spatial scales, other studies have demonstrated associations of community structure with soil texture and chemistry (Costa, 2006; Menin *et al.*, 2007; Boelter *et al.*, 2014), and vegetation structure (Davies *et al.*, 2003; Boelter *et al.*, 2014). In this study, soil clay content and tree cover were the strongest predictors of small-scale variation in termite community structure (Table 1), but temperature, precipitation, soil calcium, and spatial autocorrelation were the strongest predictors over large scales (Fig. 2 & Fig. 3).

Large-scale climatic associations are often found for terrestrial taxa (Hawkins *et al.*, 2003; ter Steege *et al.*, 2010). However, the correlations for Amazonian termites are the reverse of the typical pattern: termite abundance and richness were higher in relatively colder and dryer areas of Amazonia. In open habitats such as savannas, surface temperatures of soil, leaves, and other exposed microhabitats can be very high (Kaspari, 1993), which suppress termite activity and abundance (Smith & Rust, 1994). Termite abundance is also lower in areas of high seasonal precipitation and areas that are periodically flooded (Dawes-Gromadzki & Spain, 2003). However, the negative association of termites with temperature and precipitation could also result from the effect of other variables correlated with climate. The relatively colder and drier areas with high termite abundance and species richness in our study coincide with the Guiana and Brazilian shields, ancient geological formations in the north and south where soil nutrient content can be higher than in central Amazonia (Quesada *et al.*, 2011). In our study, termite species composition varied with calcium concentration in the soil. Species richness and abundance were also positively correlated with soil calcium, especially for soil-feeding termites. Plants exhibit sharp discontinuities along edaphic gradients in western Amazonia. These discontinuities match soil types and cannot be predicted by changes in climate or by the presence of geographical barriers to dispersal (Higgins *et al.*, 2011). Although the number of sampling grids in our study was too small to capture abrupt discontinuities, it is likely that both climate and soil type affected the distribution of termite species because some measures of termite community structure were associated with temperature but not with soil nutrients (Table 2). Moreover, more than

29% of the variation in termite abundance, species richness, and species composition could be explained only by the geographic separation between areas, and not by soil type or climate. These results suggest that historical processes and dispersal limitation may also contribute to the distribution of species in the Amazonian forest.

In Amazonia, large rivers are important geographic barriers for vertebrate dispersal (Pomara *et al.*, 2014), and may have contributed to the diversification of Amazonian birds (Ribas *et al.*, 2011), frogs (Funk *et al.*, 2007; but see Boul *et al.*, 2007), and primates (Boubli *et al.*, 2015). In contrast, rivers are not associated with changes in species composition of plants (Higgins *et al.*, 2011; Kristiansen *et al.*, 2012; Pomara *et al.*, 2014), small mammals, and frogs (Gascon *et al.*, 2000). In our study, differences in termite species composition were strongly correlated with geogrpahic distance *per se*, but composition was not distinct across major rivers (Fig. 3). Indeed, we have often observed large termite swarms flying over major rivers (C. Dambros, *pers. obs.*), which might even facilitate dispersal in areas of densely covered forest. Collectively, our results and these other studies suggest that rivers may not be important barriers to dispersal for many plant and invertebrate taxa.

Although random dispersal might have shaped termite communities at broad geographic scales in Amazonia, we cannot rule out an important effect of past climate or geological events on contemporary termite distribution. Calcium rich areas in pre-Cambrian formations of the Guiana and Brazilian shields to the north and south could have played an important role in termite diversification and species assembly. The mixture of historical factors, climate, soil, and distance effects operating at large and small spatial scales have contributed to the complex patterns of species richness and composition in Amazonia.

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Supporting information

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

Appendix S1 Descriptions of sampling sites and methods.

Appendix S2 R script used for analyses.

Appendix S3 Annotated R script

Data accessibility

All termite data used in this study are available a compiled .csv file at figshare: http://files.figshare.com/1926478/TermiteProject.csv. Data are freely available for access, use, and distribution if appropriate credit is provided. Any modifications made must be indicated.

Biosketch

Cristian Dambros is interested in the effects of dispersal and species adaptations to the environment on macroecological patterns of species distribution. He has studied the macroecology of soil invertebrates, plants, and small mammals in tropical forests of Brazil. Visit www.uvm.edu/~cddambro for more details.

Tables

Table 3.1 Partial standardized coefficients for the association of termite community with environmental predictors after controlling for spatial structure on termite data and predictor variables
Variance was partitioned into individual environmental (R_{env}^2) and spatial (R_{space}^2) fractions. Explained variance was calculated as the adjusted R^2.

	All termites				Wood Feeders				Soil Feeders			
Environmental predictors	N	S	PCoA1	PCoA2	N	S	PCoA1	PCoA2	N	S	PCoA1	PCoA2
Mean ann. temperature	0.01	0.04	-0.18*	0.13†	0.08	-0.23**	0.02	-0.09	0.14†	0.06	0.11	-0.03
Mean ann. precipitation	0.08	-0.01	-0.08	0.08	-0.03	0.18*	-0.05	-0.28**	0.02	0.05	0.10	0.06
Tree cover	0.17*	0.16*	0.09	-0.08	0.04	-0.06	0.04	0.11*	0.29***	0.25**	0.01	0.10
Clay content	0.19*	0.18*	-0.17*	-0.34***	-0.13	-0.22**	-0.17*	0.18*	0.29***	0.27***	-0.18*	-0.27***
lnCa	0.12	0.06	0.08	-0.02	-0.09	<0.01	0.02	-0.18	0.13†	0.14*	-0.06	-0.10
lnK	-0.03	-0.04	0.02	-0.03	0.04	0.05	0.03	0.05	-0.12	0.01	-0.03	-0.05
lnP	0.07	0.05	0.05	0.15*	0.20*	0.23**	0.13†	-0.07	-0.03	-0.04	0.13†	-0.03
df	190	190	190	190	190	190	190	190	190	190	190	190
F	3.08**	1.95†	1.88†	6.33***	2.76**	2.89**	1.09	2.73*	4.99***	5.54***	2.50*	2.55*
R_{total}^2	0.50	0.54	0.92	0.69	0.46	0.38	0.82	0.45	0.63	0.56	0.87	0.68
$R_{env\text{-}space}^2$	0.03	0.01	0.00	0.08	0.03	0.04	0.00	0.02	0.06	0.07	0.01	0.02
$R_{space\text{-}env}^2$	0.37	0.33	0.37	0.30	0.36	0.22	0.40	0.22	0.41	0.31	0.32	0.50

$^{***}P < 0.001$ $^{**}P < 0.01$ $^{*}P < 0.05$ $^{\dagger}P < 0.1$.

Figure legends

Figure 1. Location of sampling grids (red circles) and transects (black circles) in the Brazilian Amazonian forest (dark gray; a), and representation of network corresponding to possible routes of dispersal for termites, which was used as a representation of spatial structure of termite data (b). Numbers in (a) represent the number of transects sampled in individual grids. Five 5 x 2 m sections were sampled in each transect. Black arrows in (b) represent network connectivity between transects within a grid. Green and dashed arrows represent the connectivity between transects located in distinct grids (metacommunity). Transects within a grid were connected to all neighbors in a radius of $\sqrt{2}$ km, which represents all neighboring transects, including the diagonal (Moore neighborhood). The probability of dispersal between transects within a grid, and the probability of dispersal from a given transect to other grids was set to $\frac{1}{N\,of\,neighbors+1}$. The connectivity between grids was determined by constructing a Gabriel graph as suggested by Dray *et al.* (2012) and Legendre and Gauthier (2014).

Figure 2. Termite abundance and species richness observed (a-b), predicted by environmental variables (c-d), and not explained by environmental variables (residual; e-f). Bar plots at the lower right corner of figures show the variance explained (R^2) by Moran Eigenvector Maps (MEMs), from broad scale to fine scale MEMs. All 197 MEMs

were grouped into 28 bins (smoothed MEMs; Dray *et al.* 2012). Filled bars represent groups of MEMs explaining more variance on termite data than expected using a Monte Carlo permutation test.

Figure 3. Scores of first and second ordination axes of a Principal Component Analysis (PCoA) representing termites species composition as observed (a-b), predicted by environmental variables (c-d), and not explained by environmental variables (residual; e-f). Bar plots at the lower right corner of figures show the variance explained (R^2) by Moran Eigenvector Maps (MEMs), from broad scale to fine scale MEMs. All 197 MEMs were grouped in 28 bins (smoothed MEMs; Dray et al. 2012). Filled bars represent groups of MEMs explaining more variance on termite data than expected using a Monte Carlo permutation test. The PCoA analysis was performed using the Bray-Curtis index of dissimilarity between all pairs of transects.

Figures

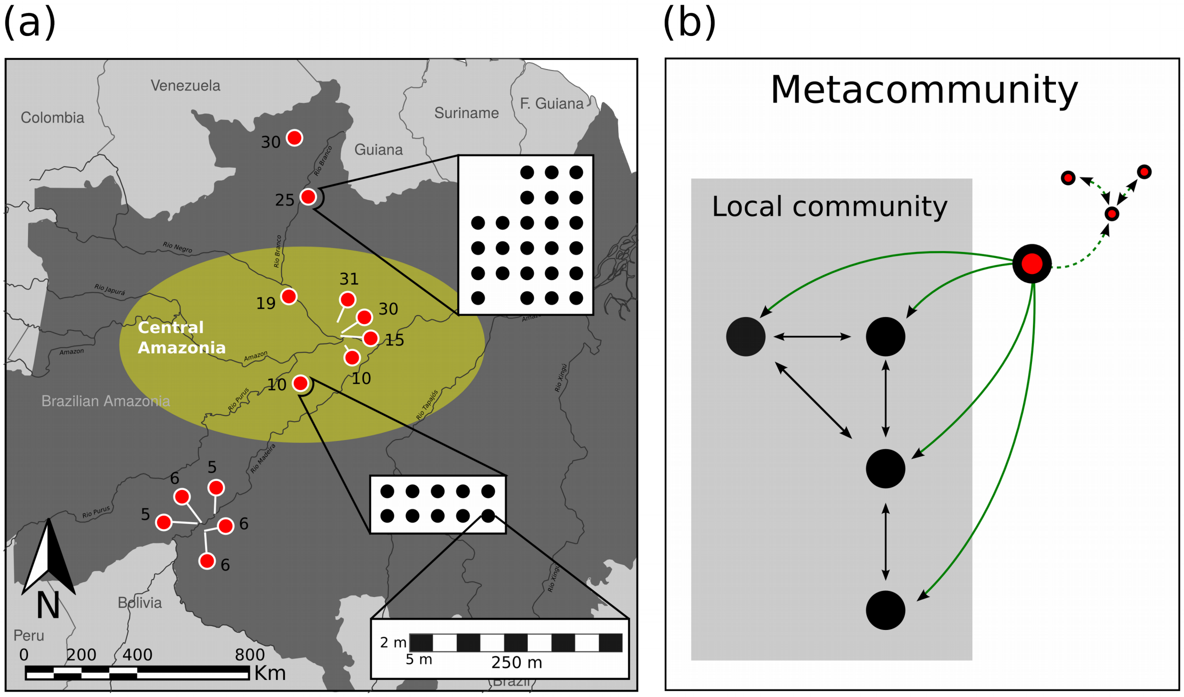

Figure 3.1 Location of sampling areas in the Brazilian Amazonian forest, and representation of network corresponding to possible routes of dispersal for termites

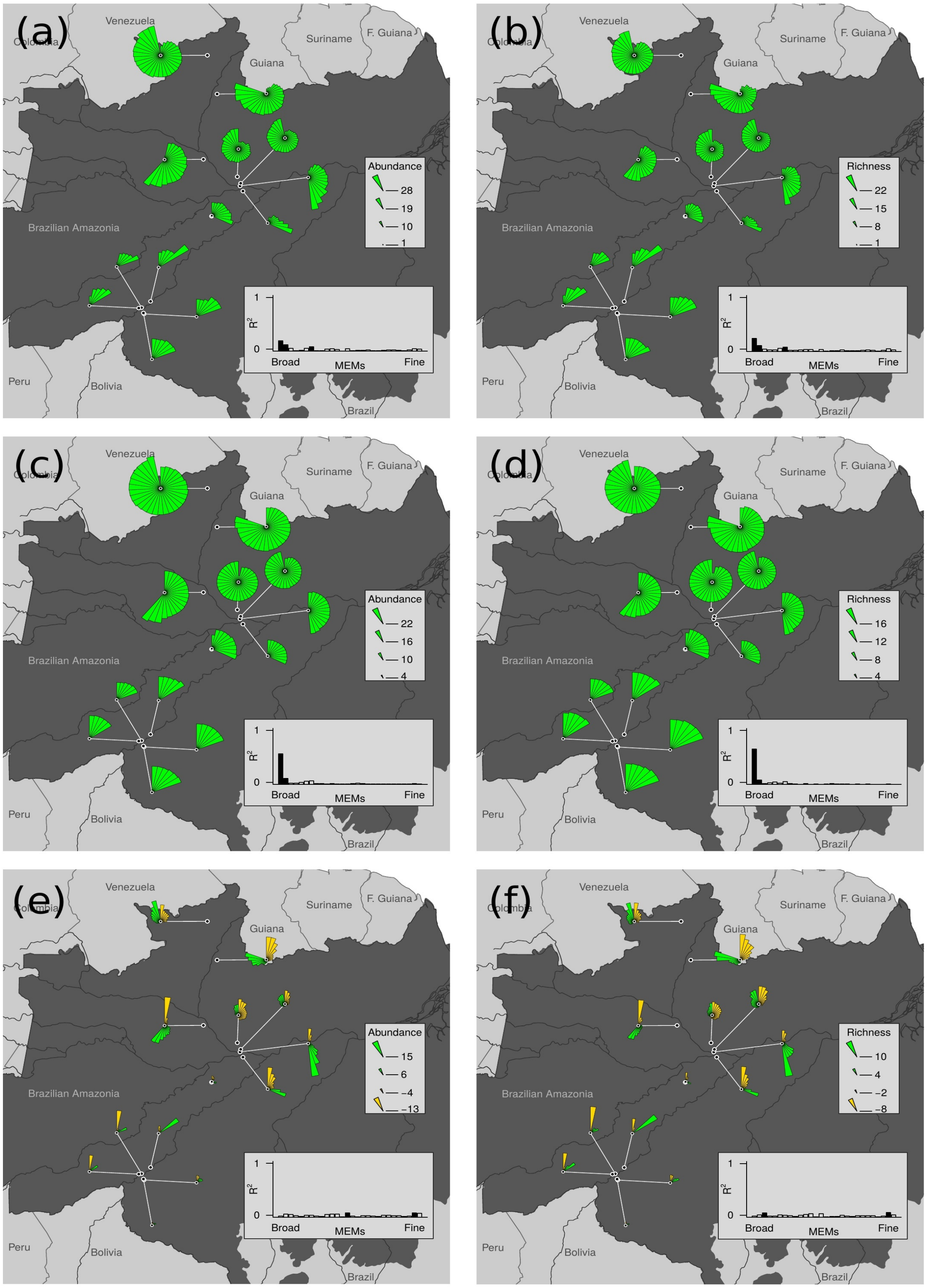

Figure 3.2 Termite abundance and species richness observed, predicted by environmental variables, and not explained by environmental variables

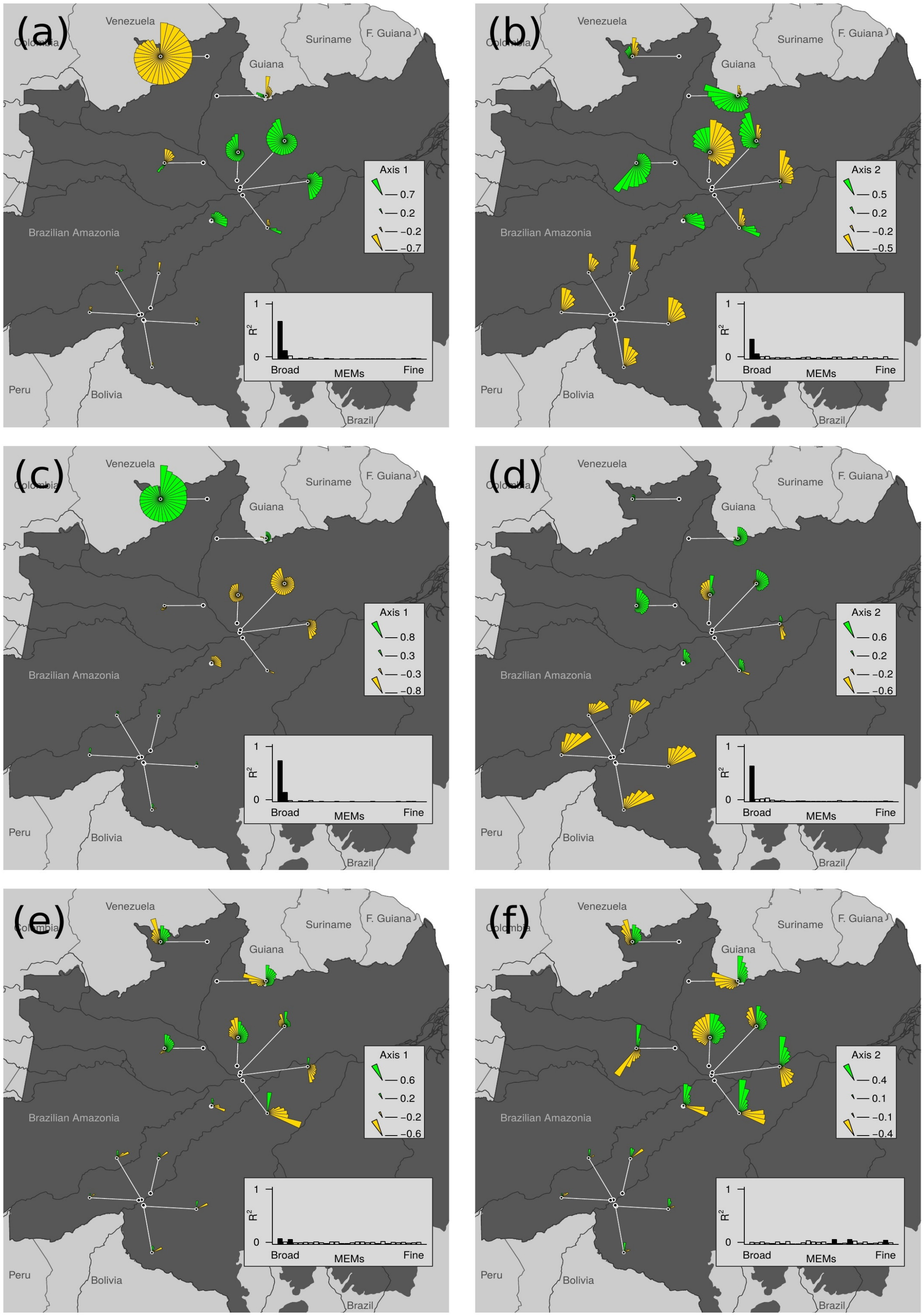

Figure 3.3 Scores of ordination axes of a Principal Component Analysis as observed, predicted by environmental variables, and not explained by environmental variables

CHAPTER 4: EFFECTS OF NEUTRALITY, GEOMETRIC CONSTRAINTS, CLIMATE, AND HABITAT QUALITY ON SPECIES RICHNESS AND COMPOSITION OF ATLANTIC FOREST SMALL-MAMMALS

Abstract

Aim: To compare the fit of models of climate, habitat quality, neutral processes, and geometric constraints to species richness and composition of small mammal assemblages.

Location: The South American Atlantic Forest biome.

Methods: Using neutral models and mid-domain effect models, we simulated species spread in a spatially explicit array of grid cells representing the Atlantic Forest domain. We compared empirical patterns of species richness and composition with predictions of the neutral and mid-domain effect models. We also modeled individual species responses to climatic conditions and forest integrity, a measure of habitat quality.

Results: Habitat quality was the single best predictor of local species richness (α-diversity), but was a poor predictor of local species composition and of the decay in species similarity with distance (β-diversity). The neutral and mid-domain models generated very similar predictions, and were better predictors of species composition than of species richness. Climate variables were also strongly associated with overall species composition, but not with species richness.

Main conclusions: The species richness of small-mammal assemblages in the Atlantic Forest is best explained by variation in habitat quality. In contrast, the composition of small-mammal assemblages is best explained by models of limited dispersal (neutral and mid-domain) and effects of climate on local species composition. Collectively, these results suggest that regional patterns of species richness may be uncoupled from patterns of species composition. Both species richness and composition should be considered when evaluating the predictions of neutral and mid-domain effect models, and of correlations of community structure with climatic or habitat variables.

Key-words: α-diversity; β-diversity; cellular automata; dispersal limitation; distance-decay; Generalized Linear Model; habitat loss; mid-domain effect.

Introduction

At a variety of spatial scales, species richness and species composition are often correlated with measures of area (Storch *et al.*, 2012), contemporary climate (Hawkins *et al.*, 2003), habitat quality (Fahrig, 2003), and isolation by distance (Svenning & Skov, 2007). However, teasing apart the mechanisms underlying these correlations and attributing them to historical (Haffer, 1985; Carnaval & Moritz, 2008) versus contemporary factors (Hawkins *et al.*, 2003) is challenging.

Studies of habitat quality, climatic factors, and geometric constraints have usually focused on species richness (Fahrig, 2003; Hawkins *et al.*, 2003; Rangel & Diniz-Filho, 2005), whereas studies of dispersal and neutral processes have usually focused on species-abundance relationships (McGill *et al.*, 2006; Rosindell & Cornell, 2013), and distance-decay patterns (Smith & Lundholm, 2010; Diniz-Filho *et al.*, 2012). When these patterns are tested in isolation for single models, they may not be informative. For example, patterns of rank abundance distributions have poor discriminatory power for distinguishing niche and neutral processes (McGill *et al.*, 2006). Similarly, it may be difficult to distinguish effects of environmental filtering from effects of dispersal on distance-decay relationships (Smith & Lundholm, 2010).

Several studies in the Atlantic Forest biome of South America have explained the high species diversity in this forest by historical events associated with the limited species dispersal (Haffer, 1985; Carnaval & Moritz, 2008; de la Sancha *et al.*, 2014). Nevertheless, other processes such as species adaptation to contemporary climate (Carnaval and Moritz 2008; Carnaval *et al.* 2014), habitat availability (Chiarello *et al.* 1999; Tabarelli *et al.*, 2010), and the geometry of the Atlantic Forest (Prevedello *et al.* 2013) also contribute to the contemporary distribution of species.

In this study, we compiled data from 52 published studies on the species richness and composition of small mammals sampled across the Atlantic Forest biome of South America. We simultaneously compared the predictions of four models – contemporary climatic, habitat quality, neutral, and geometric constraints – on three patterns of species distribution: local species richness, species composition, and distance-decay relationships. We compared the relative performance of each of these models to each other, as well as to a null model that incorporated only sampling effects.

Methods

Study site

The Atlantic Forest extends from the northeast coast of Brazil to northern Argentina. This biome harbors several endemic and patchily distributed species (Costa *et al.*, 2000), which might suggest that dispersal limitation was an important determinant of species distributions. In agreement with models of random dispersal (Economo & Keitt, 2010) and species geometric constraints (Jetz & Rahbek, 2001), Costa *et al.* (2000) found that areas with higher small-mammal diversity are located in the central parts of the Atlantic Forest. Nevertheless, there is also evidence that small mammal composition in the Atlantic Forest is associated with climatic conditions (Carnaval *et al.*, 2014; de la Sancha *et al.*, 2014). Moreover, the Atlantic Forest is a highly perturbed region (Ribeiro *et al.*, 2009), and contemporary habitat quality could have a strong effect on local species richness and composition (Fahrig, 2003).

The data compiled for this study were collected across the entire area recognized as the Atlantic Forest biome (Fig. 1). This biome encompasses an extent of 102,012 km^2, of which only 7.9% is still intact. Habitat types in intact areas include rainforests, mixed (*Araucaria*) moist forests, semideciduous forests, dry forests, and upland grasslands. Rainforests tend to occur near the coast, whereas semideciduous and dry forests occur far from coast. Mixed forests are common in the south of the Atlantic Forest (Leite, 2002). The climate is moist tropical and subtropical, without a well-defined dry season, and with annual mean temperatures above 15ºC (Leite, 2002).

Data collection

We compiled a database of 52 studies from the primary literature in which small mammals were sampled in the Atlantic Forest (Table S1 in Supporting Information). We used the Google Scholar search tool with the keywords “small mammal”, “marsupial”, “rodent”, “community”, “composition”, “richness”, “diversity”, and “Atlantic Forest” (Table S1).

For inclusion in our database, we established a minimum sampling effort of at least 1000 trap-nights, 6 months of field work, and use of wire and/or Sherman live-traps installed on the ground or understory level of the forest. Studies area ranged from 5 to 185,000 ha ($\bar{x}$ = 16,295), with sampling effort from 600 to 64,000 hours of trapping ($\bar{x}$ = 9,178). The distance between sites ranged from 31 to 3,249 km ($\bar{x}$ = 1,026). The studies locations ranged from 32° 33’ S to 8° 15’ S and from 54° 58’ 12’’ W to 35° 4’ 48” W. The number of species recorded in each study ranged from 1 to 27 ($\bar{x}$ = 8.16). From each selected survey, we obtained local species composition. The species recorded from 75 surveyed locations were aggregated into 26 2×2° grid cells for analysis (Fig. 1). To account for possible sampling effects, we included the number of trapping hours in each grid cell as a covariate in our models (detailed description below).

In rasters of 2.5 arc minutes, we also compiled the 19 environmental variables available in Bioclim (http://www.worldclim.org/bioclim): annual mean temperature (1), mean diurnal temperature range (2), isothermality (3), temperature seasonality (4), maximum and minimum temperature of the warmest and coldest months (5 and 6), temperature annual range (7), mean temperature of the wettest, driest, warmest, and coldest quarters (8-11), annual precipitation (12), precipitation of the wettest and driest months (13 and 14), precipitation seasonality (15), and precipitation of the wettest, driest, warmest, and coldest quarters (16-19). We then averaged the measure of each environmental variable within each 2×2° grid cell. Because most of the climatic variables are correlated with one another, we summarized them with a Principal Component Analysis. The first principal component axis was used as a predictor variable in all models. We present the results using individual climatic variables in the supplemental material (Figs. S1-S5).

Habitat quality was quantified with information available from each study. We classified forest status of each study on a scale from 1 to 5 (1 = highly disturbed forest, including clearings, 2 = secondary forest, 3 = disturbed primary forest, 4 = conserved primary forest with patches of old secondary forest; 5 = conserved primary (old growth) forest). Areas of primary forest were characterized by an intact canopy with no evidence of previous clearing (Eiten, 1983); secondary forests were characterized by evidence of regeneration after clearing and land use (Eiten, 1983; Veloso *et al.*, 1991). We calculated the average habitat score for the studies that were located in each grid cell.

Analysis

The number of species encountered in each grid cell (S), and the pairwise similarity in species composition, as measured by the Jaccard similarity index, were used as response variables. The Jaccard similarity index between two grid cells takes into account the similarity in species identity and the number of shared species between the grid cells (Baselga, 2012). However, the Jaccard index is also affected by differences between sites in species number, and may be correlated with patterns of species richness as well as species composition. To investigate the changes in species identity between two grid cells independently from differences in species richness, we partitioned the Jaccard similarity index into components of turnover and nestedness (Baselga, 2012), and used the turnover component as a response variable.

Dispersal-based models

To estimate the influence of dispersal limitation on species richness (S) and composition (Jaccard and Jaccard turnover indices), we created a network of interconnected grid cells representing the Atlantic Forest (Fig. S6). This network was used to estimate the flux of species or individuals among grid cells in simulation models. Two models were used to recreate the species distribution under dispersal alone: the spreading dye model (Jetz & Rahbek, 2001), and the neutral model (Economo & Keitt, 2008).

In both models, the entire area comprising the Atlantic Forest was divided in 55 2×2° grid cells, including the 26 for which small mammal data were available (Fig. 1). In the spreading dye model, the number of grid cells occupied by each small mammal species was recorded. The occurrence of each species for the entire Atlantic Forest (n = 55) was estimated from the grid cells in which small-mammal data were available (n = 26). One of the 55 grid cells was randomly selected and the species occurrence was spread from the selected cell into neighboring cells until the original number of occupied grid cells was achieved. Each cell had up to eight neighbors (Moore neighborhood; Fig. S6), and the model was bounded by the domain of the 55 grid cells. This procedure was repeated 10,000 times for the 64 species.

The neutral model was started with a single ancestral species occupying all 55 grid cells. In each generation, new species were added in each cell by point speciation with probability v, which was constant across all cells (see Economo & Keitt 2010 for more details). The constant ν represents the probability of an individual speciating, but could also be interpreted as the probability of adding a new species by immigration and simultaneously losing a single individual of a resident species. Both interpretations impose a zero-sum game on the total number of individuals. To model the probability of dispersal, we allowed a cell to be colonized only from an occupied neighboring cell (Moore neighborhood, Fig. S6), with all grid cells having the same migration rate (m). The local community size (number of individuals) was set the same for all grid cells ($N = 100$). The model was run for multiple generations (usually more than 30,000), until the α-diversity within grid cells (Probability of Interespecific Encounter; Hurlbert, 1971) and β-diversity between grid cells (Morisita-Horn similarity) reached a steady-state.

The neutral model of Economo & Keitt (2008) is probabilistic and does not require the simulation of each individual in the metacommunity. This model allowed us to investigate thoroughly the parameter space of m and ν. However, because the Economo & Keitt (2008) model does not generate species identities in different sites (but only the probability of two individuals selected at random in a pair of sites being from the same species) it does not allow one to calculate statistics based on composition (such as the Jaccard similarity index).

Nevertheless, it is possible to calculate the Morisita-Horn similarity matrix between all possible pairs of sites based on the probability of ancestry of individuals. Using the Limited-memory Broyden-Fletcher-Goldfarb-Shanno Box-constrained (L-BFSG-B) optimization algorithm (Byrd *et al.*, 1995), we estimated *m* and ν to maximize the correlation between the Morisita-Horn index of the neutral model and the Jaccard index of the observed data. These indices are usually highly correlated (Krasnov *et al.*, 2005; Chao *et al.*, 2006). To confirm this approach, we used the optimized parameters (*m* and ν) to simulate a single community with a burn-in of 30,000 generations, and then ran the model with 1000 time steps for 10,000 different simulations. The mean of the 10,000 simulations was used to calculate the Jaccard similarity index. The correlation between the Morisita-Horn index of the probabilistic model and the Morisita-Horn index of the simulated model was 0.9998. We used the species richness, the Jaccard similarity index, and the turnover component from the Jaccard similarity index from this simulation model as the predicted values from the optimized neutral model.

Environmental models

To test the association of species diversity with the climatic and habitat quality variables, individual logistic regressions were fitted for each species against the climatic and habitat quality variables. We refer to these models hereafter as the climatic and habitat models.

The logistic model estimates the effect of a predictor variable on the species probability of occurrence. These probabilities can then be used to estimate the effect of the predictor variable on the overall species richness (S) and composition.

To calculate the expected species richness and Jaccard pairwise similarity index based on the climatic and habitat models, the distribution of each species was simulated in a spatially explicit model (Rahbek *et al*., 2007). For each species, we assigned randomly species occurrences (1s) in grid cells based on the probabilities of occurrence predicted by a climatic or habitat variable. This procedure was performed independently for each grid cell, and the observed species occurrences were not preserved. Note that this model does not require the species to have contiguous ranges as in the spreading dye model. The simulation was replicated 10,000 times to calculate the mean species richness in grid cells, and the Jaccard index and turnover between each pair of grid cells. For species richness, similar results were obtained by summing the probability of occurrence of all species in a grid cell, as predicted by an individual climatic or habitat quality variable in logistic regressions.

Additionally, we fit a linear regression of S, and a distance-based RDA that used the Jaccard index and the turnover component of the Jaccard index, against the raw environmental variables. The results of these tests were very similar to those using the individual logistic regressions and are presented in the supplemental material (Figs. S3-S5).

Model Comparisons

We compared the four simulation models (spreading dye model, neutral model, climatic model, and habitat model) by their Mean Square Error (MSE). The MSE was calculated as the sum of the squared bias and the model variance (Gotelli *et al.*, 2009):

$$\sum (bias)^2 = \sum_{i=1}^{c} (O_i - E_i)^2 \quad ,$$

$$\sum (VAR) = \frac{1}{(R-1)} \sum_{k=1}^{R} \sum_{i=1}^{c} (U_{ki} - E_i)^2 \quad \text{, and}$$

$$\sum (MSE) = \sum (bias)^2 + \sum (VAR) \quad ,$$

where **O** represents the vector of observed values for each grid cell i, **E** is a vector of the mean expected values in the simulation model for each grid cell i, U_{ki} represents the value obtained in the kth simulation for the cell i, and R is the number of simulations run for each model.

Additionally, we ran individual linear regression models for species richness, and distance-based RDA (dbRDA) analyses for the Jaccard index of species composition and the turnover component of the Jaccard index, using as explanatory variables the predicted values from the spreading dye, neutral, climatic, and habitat models. Because sampling effort varied across the study area, and had the potential to affect both species richness and composition, we included the logarithm of the number of trap hours as a single predictor variable into the regression and dbRDA models. We then used the residuals from these models as response variables representing species richness and composition. At regional and local spatial scales, species richness and sampling effort often have an asymptotic relationship, which was nearly linearized by log transforming the number of trap hours.

Distance-decay analyses

To compare the effects of geographical isolation and environmental distance on the Jaccard similarity in species composition and the turnover component of similarity, we calculated the geographical distance (matrix D), and environmental distance (matrices H and C for habitat and climatic variables, respectively) between all pairs of grid cells. We then performed simple and multiple generalized linear models (GLMs) with log links on distance matrices to estimate the relationship between the similarity in species composition and the geographical and environmental distances (Millar *et al.*, 2011).

Because the Jaccard similarity is a proportion (proportion of shared species), the error of this model was fit with a binomial distribution (Millar *et al.*, 2011). *P*-values for the GLMs were calculated by permuting the rows and columns of the Jaccard similarity matrix 999 times. In each permutation, GLM coefficients were recorded, generating a null distribution of coefficients. Because we expect a negative relationship between the similarity in species composition and geographic, climatic, and habitat distances, *P*-values were calculated as the number of times that GLM coefficients were lower than observed + 1 divided by the number of permutations + 1 (one-tailed test).

All analyses were conducted in R (R Development Core Team, 2013, v. 3.0.2). Most of the summary statistics calculations were implemented by the authors, and are available at http://www.uvm.edu/~cddambro. We used the package Vegan (Oksanen *et al.*, 2008) for the remaining analyses.

Results

Patterns of species richness

All the models had a poor fit to species richness (Table 1; Figs 2 and S3). The maximum r^2 was only 0.21 for the habitat model, which had the lowest mean square error, variance, and bias. Both the neutral model and the spreading dye models generated the familiar peak of species richness in the middle of the domain of the Atlantic Forest, whereas the empirical peak of species richness occurred in two disjunct coastal grid cells (Fig. 2).

Patterns of species composition

Species composition (measured as principal coordinates of the Jaccard similarity matrix in dbRDA analyses) was best fit by the neutral model ($r^2 = 0.27$), the spreading dye model ($r^2 = 0.27$), and the climate model ($r^2 = 0.22$), but was poorly fit by the habitat model ($r^2 = 0.10$; Table 1). Most of the variation (24 %) in species composition was represented in the first principal coordinates axis of dbRDA. Species composition in the first principal coordinates axis was well-fit by the neutral model ($r^2 = 0.77$), the spreading dye model ($r^2 = 0.75$), and the climate model ($r^2 = 0.63$), but was poorly fit by the habitat model ($r^2 = 0.04$).

The analysis of the turnover component of the Jaccard similarity index generated results that were similar to the analysis of overall species composition (Table 1). However, the explanatory power of the climate ($r^2 = 0.39$), spreading dye ($r^2 = 0.43$), and neutral ($r^2 = 0.43$) models was higher than for the analysis of overall species composition (Table 1).

The four models generated contrasting predictions for the distance-decay relationship of species similarity versus geographic distance. The spreading dye and neutral models predicted a steep distance-decay function, whereas the climate model predicted a linear decay and the habitat model predicted no decay with distance (Fig. 4). The predictions of all four models differed from the empirical best-fit GLM exponential curve.

The similarity in species composition between two grid cells was associated with the geographical distance and climatic dissimilarity between cells ($b_{GLM} = -0.29$ and $b_{GLM} = -0.12$, respectively; Table 2). However, only geographical distance was correlated with the similarity in species composition when all predictor variables were included into a single model ($b_{GLM} = -0.23$; Table 2). Habitat quality was not significantly associated with the similarity in species composition in simple or multiple GLM models ($b_{GLM} \leq |0.02|$; Table 2). Similar results were found when the turnover component in the Jaccard similarity index was separated from the nestedness component.

Discussion

Patterns of species richness

At the biogeographic scale, species richness of many taxa is well-correlated with climate variables, especially temperature and precipitation (Hawkins *et al.*, 2003). At the regional scale of the Atlantic Forest, the best predictor of small-mammal species richness was a simple measure of habitat quality (Table 1; Fig. 2). Neutral or mid-domain effect models did not predict richness very well. Although our implementation of the neutral model was optimized to account for species composition, the fit did not improve when we optimized it for species richness ($r^2 = 0.11$ vs 0.09; results not shown). These results suggest that, in the absence of other factors, dispersal limitation and geometric constraints did not have a strong influence on species richness.

Our index of habitat quality in each grid cell quantifies fragmentation and forest loss, and our results are consistent with many other empirical and theoretical studies on these processes (Fahrig, 2003). Most species extinctions after perturbations occur directly from the loss of habitat area (Fahrig, 2003) and indirectly from changes in the microclimate of fragments (Saunders *et al.*, 1991). The reduction of population sizes by the fragmentation of patches also leads to stochastic extinctions, because small populations have a higher chance of declining to zero (May, 1973).

For entire communities of long-lived organisms, stochastic extinctions following perturbations can take hundreds or even thousands of years to significantly modify the composition and overall diversity (Diamond, 1972; Kuussaari *et al.*, 2009; Halley & Iwasa, 2011). Habitat loss usually has a stronger effect on species diversity (Fahrig, 2003), and the degradation of the Atlantic Forest probably has affected small mammal communities by the immediate loss of habitat area. Therefore, extinction debts (Tilman *et al.*, 1994) might still exist, which could lead additional species losses in the Atlantic Forest. Although forest fragmentation and habitat loss are important in the Atlantic Forest, the best-fitting model still explained only 21% of the variance in species richness (Table 1). Indeed, sampling effort alone (logarithm of number of trapping hours) explained more variation than did habitat quality ($r^2 = 0.40$), although the residual effect of habitat quality is still significant when the sampling effect is controlled for ($P = 0.02$).

Our implementation of the neutral model did not allow for variation in the species abundances across grid cells, so it could not incorporate the possibility of higher extinction rates in grid cells with low habitat quality. The inclusion of habitat quality as a proxy for species abundances in the neutral model could allow the estimation of the immediate (Dornelas, 2010) and long term (Halley & Iwasa, 2011) effects of habitat loss in small mammal communities. Similarly, in the spreading dye model, the probability of occupancy of a grid cell could be modeled as a function of habitat quality (Rahbek *et al.*, 2007).

Patterns of species composition

Surprisingly, habitat quality was not associated with the composition of small mammals in the Atlantic Forest. Usually, rare and specialized species are more affected by environmental perturbations than are common species, and such perturbations can lead to biotic homogenization by favoring a few dominant species in low-quality habitats (McKinney & Lockwood, 1999). However, in the Atlantic Forest, pairs of geographically distant grid cells supported distinct sets of species even when these cells were both comprised of low-quality habitats. Moreover, there was not a single dominant species occupying all low-quality habitats in the Atlantic Forest.

Dispersal limitation and diversification, as simulated in the neutral model, could cause disjunct patches with similar environments to evolve distinct sets of species. This type of model is potentially realistic for the Atlantic Forest small-mammals, which exhibit a high degree of endemism, with many rare and patchily distributed species (Costa *et al.*, 2000). However, our neutral and spreading dye models do not assume the presence of forest refugia or high diversification areas, which are commonly invoked to account for diversity in the Atlantic Forest (Haffer, 1985; Carnaval & Moritz, 2008; de la Sancha *et al.*, 2014).

Climatic conditions were also strongly correlated with the composition of species in grid cells. Along with dispersal limitation imposed by geographical distance, the climatic conditions of a grid cell could limit the immigration and establishment of species adapted to other climates. Recently, differences in climatic conditions between the northern and southern parts of the Atlantic Forest have been associated with changes in species composition for many taxa (Carnaval *et al.*, 2014). However, our results suggest that similar patterns could be generated by simple models of dispersal. Because areas far apart in the Atlantic Forest usually have distinct climates, it is difficult to determine whether these areas have distinct species due to their geographical separation or differences in climatic conditions (Legendre *et al.*, 2005; de la Sancha *et al.*, 2014).

As in many other studies, similarity in composition of Atlantic Forest small-mammals decayed with geographic distance between grid cells (Fig. 4; Table 2). These distance-decay relationships are often interpreted as evidence for community assembly via dispersal limitation, or of spatially structured environmental effects (Nekola & White, 1999). Although the distance-decay relationship for small-mammals can be fit by a GLM ($r^2 \sim 0.25$; Fig. 4), the shape of the curve does not match the quantitative predictions of the neutral or spreading dye models, which both generated a steeper decay profile. The climatic model predicted a much shallower distance-decay relationship, and the habitat model predicted no decay with distance (Fig. 4). As Tuomisto & Ruokolainen (2006) have emphasized, the distance-decay relationship is not measuring the same thing as species composition calculated by ordination methods. When species composition is measured with the PCoA ordination, the fit is considerably improved for both the neutral and spreading dye models ($r^2 = 0.74$, 0.73, respectively; Table 1), but is weaker for the climatic and habitat models ($r^2 = 0.62$, 0.11, respectively; Table 1).

Controversy of neutral and spreading dye modes

In our analyses, the neutral and spreading dye models generated predictions that were virtually identical for species richness and composition. This was not a surprise given that both models simulated the spreading of dispersal-limited species in a homogeneous bounded domain. Rangel & Diniz-Filho (2005) were the first to demonstrate that these models have qualitatively similar predictions for species richness. Our results indicate that these models also generate similar predictions for species composition. Despite the higher flexibility of the neutral model, in which species dispersal could range from highly limited to almost no limitation, the best fit of the neutral model for species composition was found with very limited dispersal, producing coherent species ranges as the mid-domain model.

In the last decade there has been a lot of debate about the validity and utility of neutral and mid-domain models in ecology (Colwell *et al.*, 2004; Currie & Kerr, 2008; Clark, 2012; Ricklefs, 2012). The main argument against neutral and mid-domain models is that other (non-neutral) processes can generate similar patterns of species distribution (Currie & Kerr, 2008; Rosindell *et al.*, 2012). When competing models generate similar predictions for a given metric, such as the neutral and spreading dye models, none of the models can be ruled out.

Despite the controversy, the neutral and mid-domain models continue to be popular because they are simple and parsimonious, and often have a strong predictive power, even when some assumptions are violated (Rosindell *et al.*, 2012). Moreover, these models can be easily extended for more realism (Rahbek *et al.*, 2007; Rosindell *et al.*, 2012).

Both the neutral and spreading dye models had similar predictions, and were better predictors of species composition than models based on individual species responses to climatic conditions and habitat quality. These results suggest that dispersal and geometrics constraints may contribute to variation in small mammal species composition across the Atlantic Forest. At smaller spatial scales, where dispersal limitation is not prominent, species adaptations to the environment are more likely to be important (Hurtt & Pacala, 1995). Because climate can limit species dispersal and establishment, it may be difficult to disentangle their separate effects.

In this study, local species richness (α-diversity) was best explained by a model of habitat quality, whereas regional species composition (β-diversity) was best explained by neutral or spreading dye models or by correlations with climatic variables. These results suggest that local and regional species diversity might result from different processes. Studies investigating only richness or composition are likely to conclude that either species dispersal or association with the environment is more important. In fact, both processes might act simultaneously with contrasting effects on richness and composition.

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Biosketch

Cristian Dambros is interested in the effects of dispersal and species adaptations to the environment on macroecological patterns of species distribution. He has studied the macroecology of soil invertebrates, plants, and small mammals in tropical forests of Brazil. Visit www.uvm.edu/~cddambro for more details.

Tables

Table 4.1 Fit of the climatic, habitat quality, spreading dye, and neutral models for species richness and composition.
Species composition was measured as the Jaccard similarity index and the turnover component of the Jaccard similarity index (Baselga 2012). BIASsq: Sum of squared bias; VAR: sum of model variance; MSE: sum of mean square errors (BIASsq + VAR). See main text for details on the BIASsq and VAR calculations. *P*-values were corrected for sampling effort by removing the effects of log transformed trapping hours on the response variables before analysis.

Response variable	Explanatory model	BIASsq	VAR	MSE	*P*	r^2
Richness	Climatic	1394.69	353.04	1747.73	0.47	0.01
	Habitat	1038.90	197.73	1236.63	0.019	0.21
	Spreading dye	1262.47	202.87	1465.34	0.624	0.09
	Neutral	1597.73	225.00	1822.73	0.459	0.09
Composition (turnover + nestedness)	Climatic	4.97	2.98	7.94	0.005	0.22
	Habitat	3.60	3.40	7.00	0.472	0.10
	Spreading dye	6.64	2.10	8.75	<0.001	0.27
	Neutral	5.91	4.06	9.97	<0.001	0.27
Composition (turnover)	Climatic	5.10	2.73	7.83	0.005	0.39
	Habitat	3.65	3.12	6.77	0.437	0.11
	Spreading dye	6.93	1.62	8.55	<0.001	0.43
	Neutral	6.23	3.83	10.06	<0.001	0.43

Table 4.2. Simple and multiple Generalized Linear Models (GLM) comparing the association of species similarity against geographical distance and environmental dissimilarity.

Geographical distance was the strongest predictor of the Jaccard similarity index both when analyzed in isolation or when combined with other variables. Similar results were found for the overall Jaccard similarity index and the turnover component of the Jaccard similarity index.

Response variable	Explanatory variable	b_{ind}	P_{ind}	b_{mult}	P_{mult}
Jaccard similarity (turnover + nestedness)	Geographic distance	-0.293	<0.001	-0.231	0.006
	Climatic dissimilarity	-0.119	<0.001	-0.033	0.158
	Habitat dissimilarity	-0.013	0.359	-0.015	0.355
Jaccard similarity (turnover)	Geographic distance	-0.319	<0.001	-0.207	0.01
	Climatic dissimilarity	-0.124	<0.001	-0.058	0.049
	Habitat dissimilarity	0.099	0.981	0.113	0.992

Figure legends

Fig. 1. Map of the Atlantic Forest (AF) showing the original sampling points (circles) and the 55 grid cells encompassing the entire AF. The diameter of each circle is proportional to the logarithm of sampled area.

Fig 2. Observed and predicted richness of the small mammal species in the Atlantic Forest. A: Observed, B-C: Predicted richness from logistic regression models of climate variables (B) and habitat quality (C), D-E: Predicted richness from the spreading dye model (D) and the neutral model (E). Open cells in (E) represent areas included in the models but where actual small-mammal data were not available. The spreading dye model and the neutral model predicted highest species richness in the center of the domain, but the two grid cells with the highest species richness were in two disjunct coastal grid cells. Habitat quality was the best predictor of species richness.

Fig 3. Observed and predicted composition of small mammal species in the Atlantic Forest. The composition was measured using the turnover component of the Jaccard similarity index (Baselga, 2012), and analyzed using a distance-based RDA model. Similar colors represent similar composition of species. A: Observed, B-C: Predicted composition from logistic regression models of climate variables (B) and habitat quality (C), D-E: Predicted composition from the spreading dye model (D) and the neutral model (E). Open cells in (E) represent areas included in the neutral model but where actual data were not available. The climatic, spreading dye, and neutral models performed equally well in explaining species composition in the Atlantic Forest.

Fig. 4. Decay in the similarity of species composition with geographical distance. The similarity in species composition was measured by the Jaccard similarity index between all pairs of grid cells (grey circles). The similarity was regressed against geographical distance, climatic and habitat quality distances using a Generalized Linear Model with binomial errors and a log link function. Habitat quality and climatic variables did not predict the exponential decay with geographical distance. The spreading dye model and the neutral model predicted a much steeper decay with distance than did the GLM.

Figures

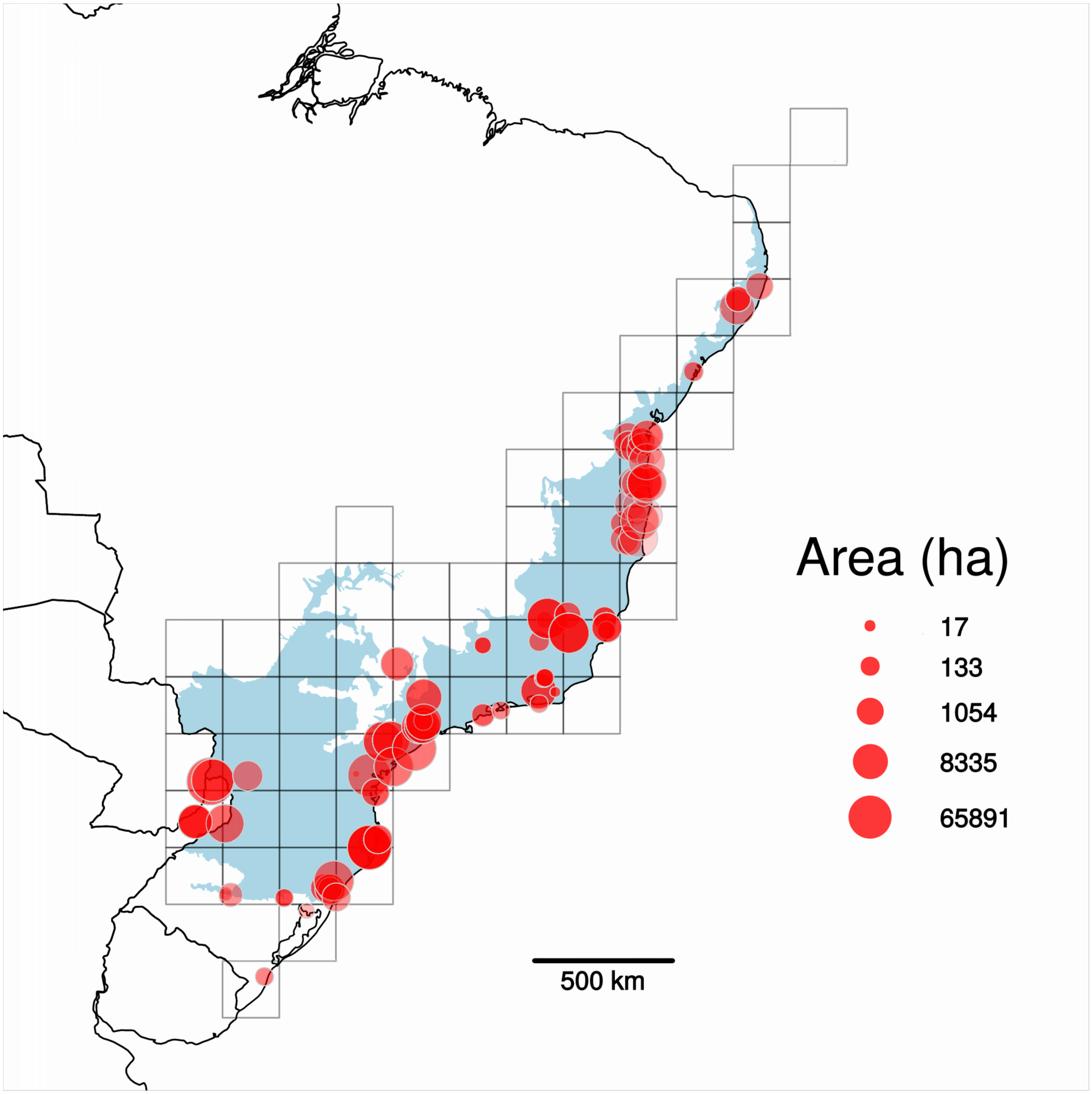

Figure 4.1 Map of the Atlantic Forest (AF) showing the original sampling points (circles) and the 55 grid cells encompassing the entire AF.

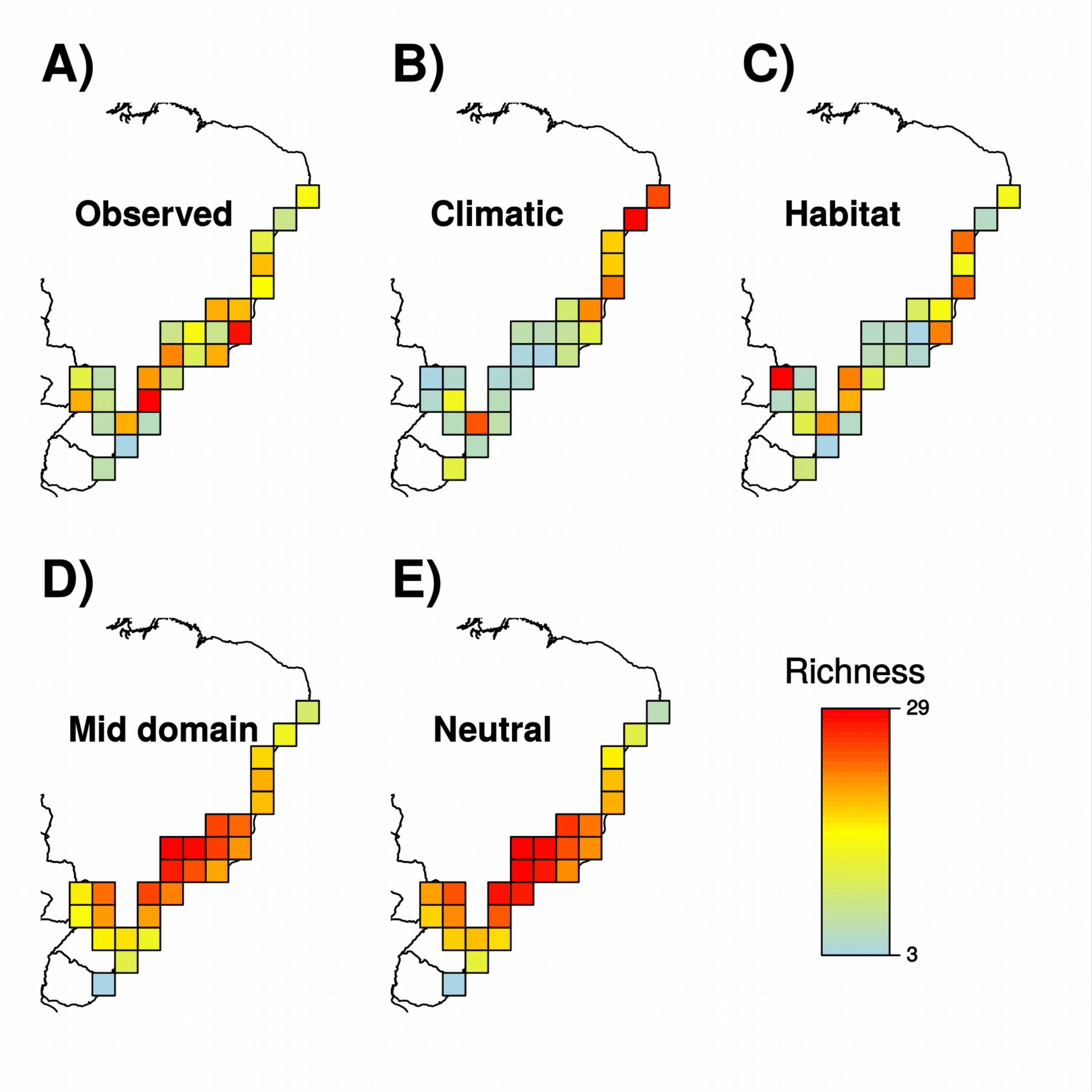

Figure 4.2 Observed and predicted richness of the small mammal species in the Atlantic Forest.

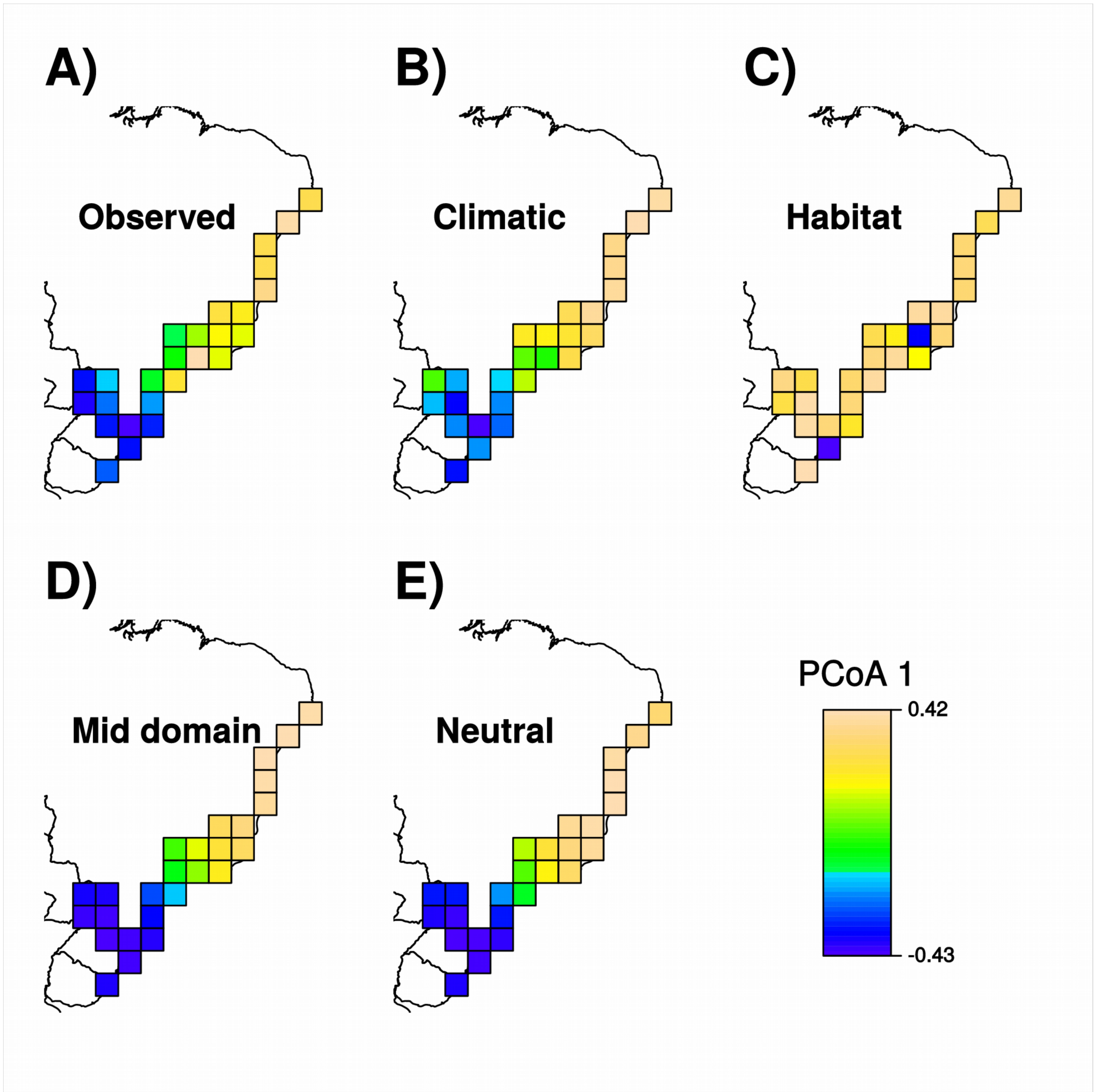

Figure 4.3 Observed and predicted composition of small mammal species in the Atlantic Forest.

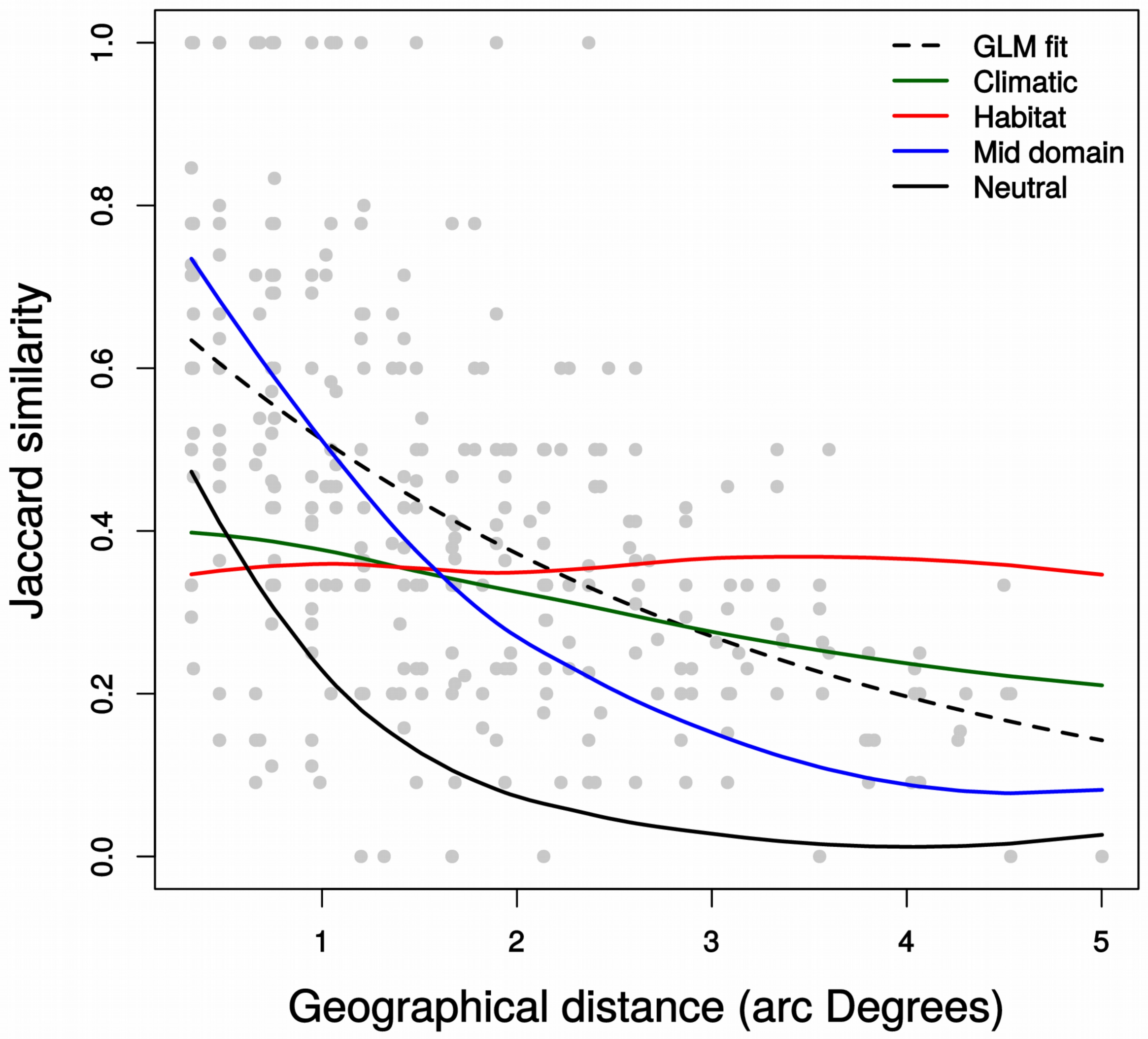

Figure 4.4 Decay in the similarity of species composition with geographical distance.

Figures (greyscale)

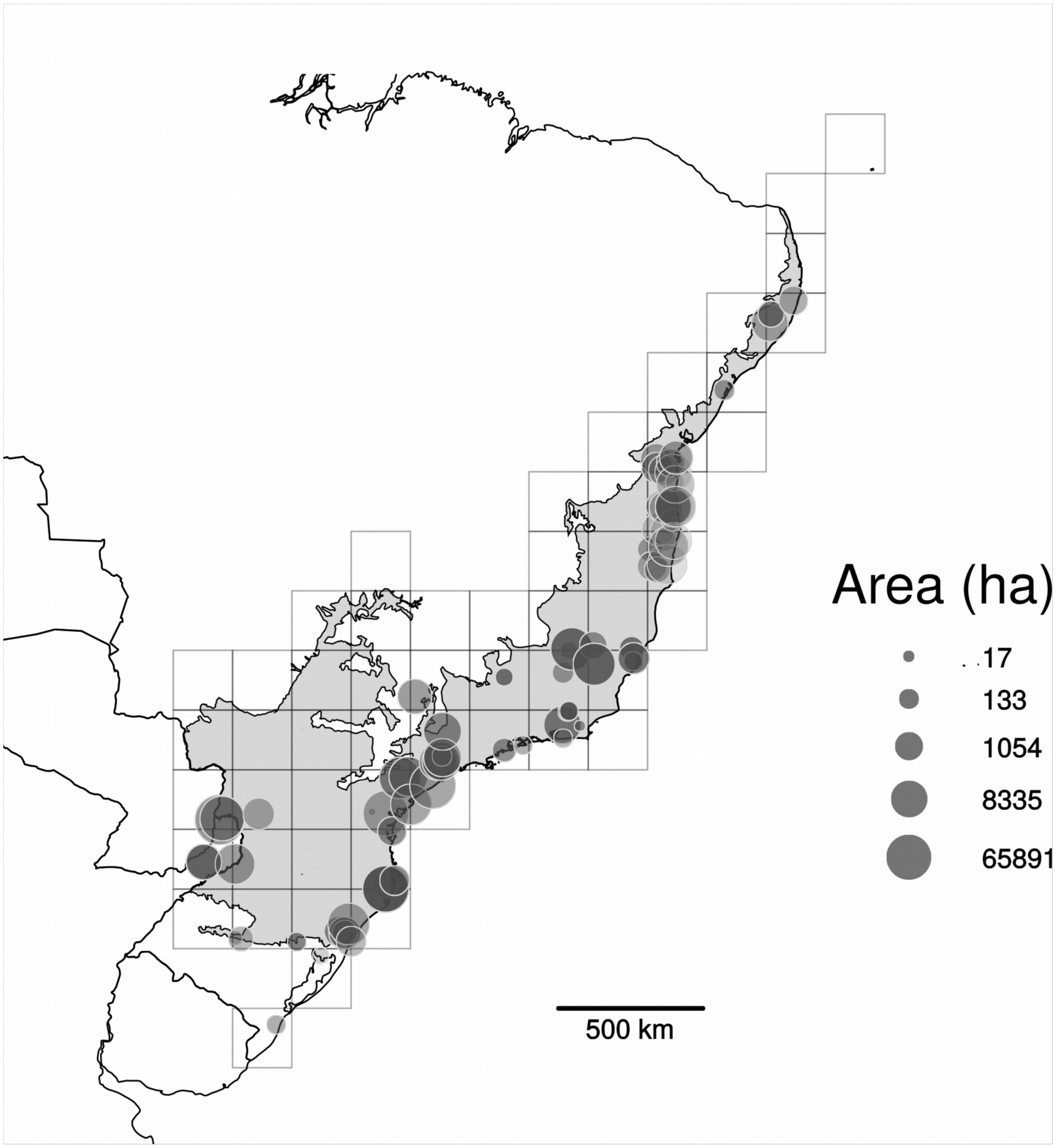

Figure 4.1 Map of the Atlantic Forest (AF) showing the original sampling points (circles) and the 55 grid cells encompassing the entire AF.

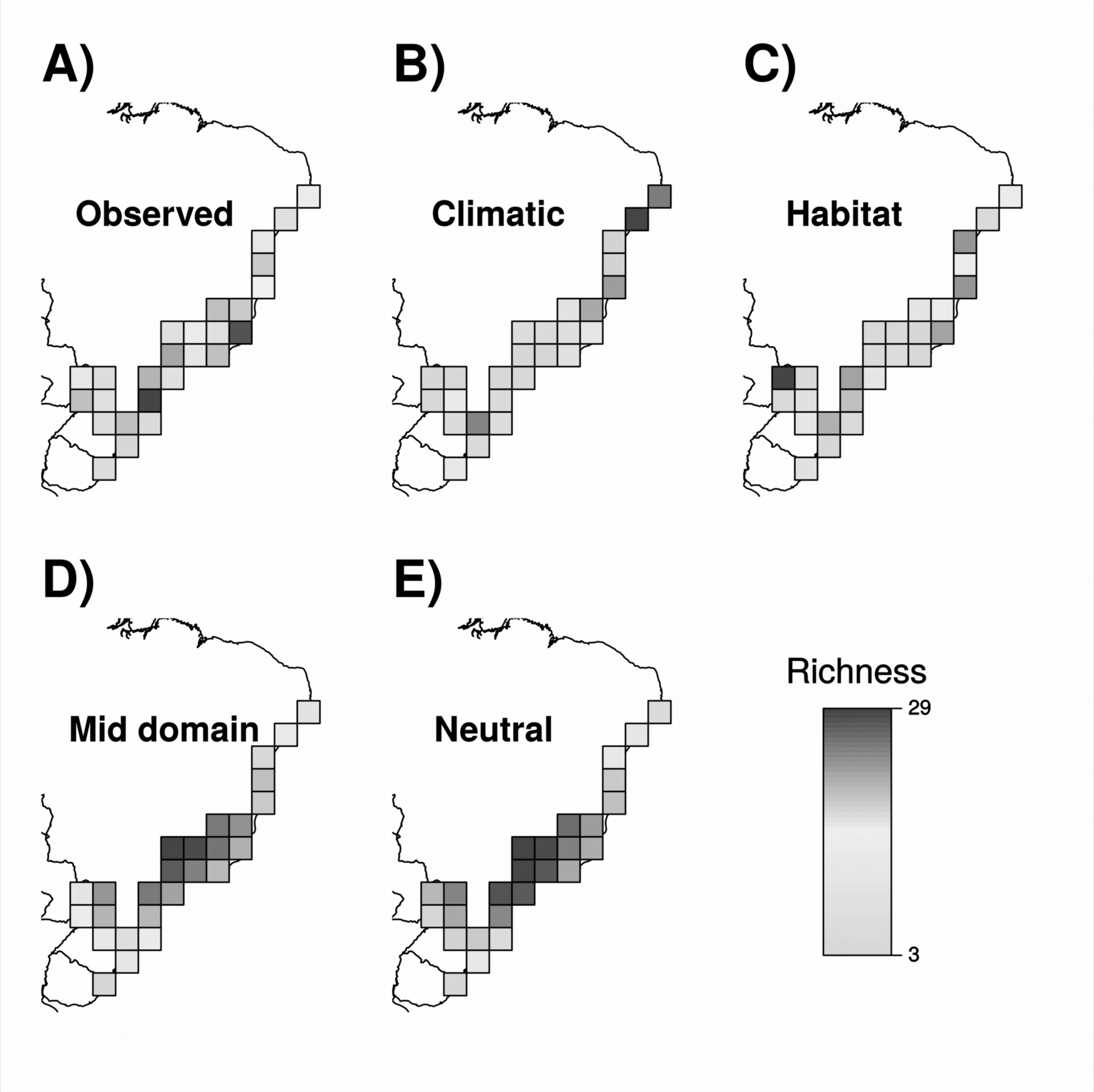

Figure 4.2 Observed and predicted richness of the small mammal species in the Atlantic Forest.

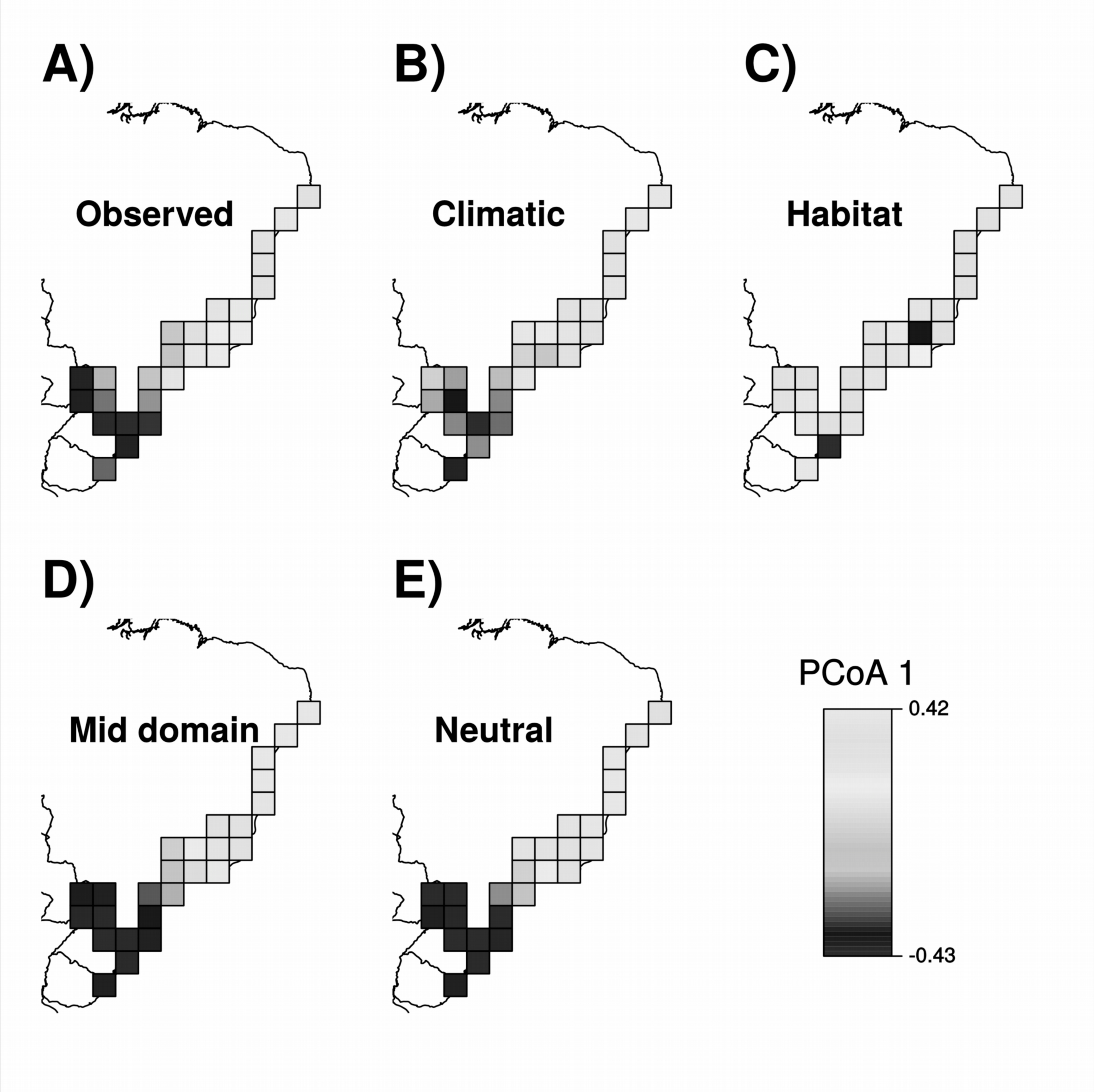

Figure 4.3 Observed and predicted composition of small mammal species in the Atlantic Forest.

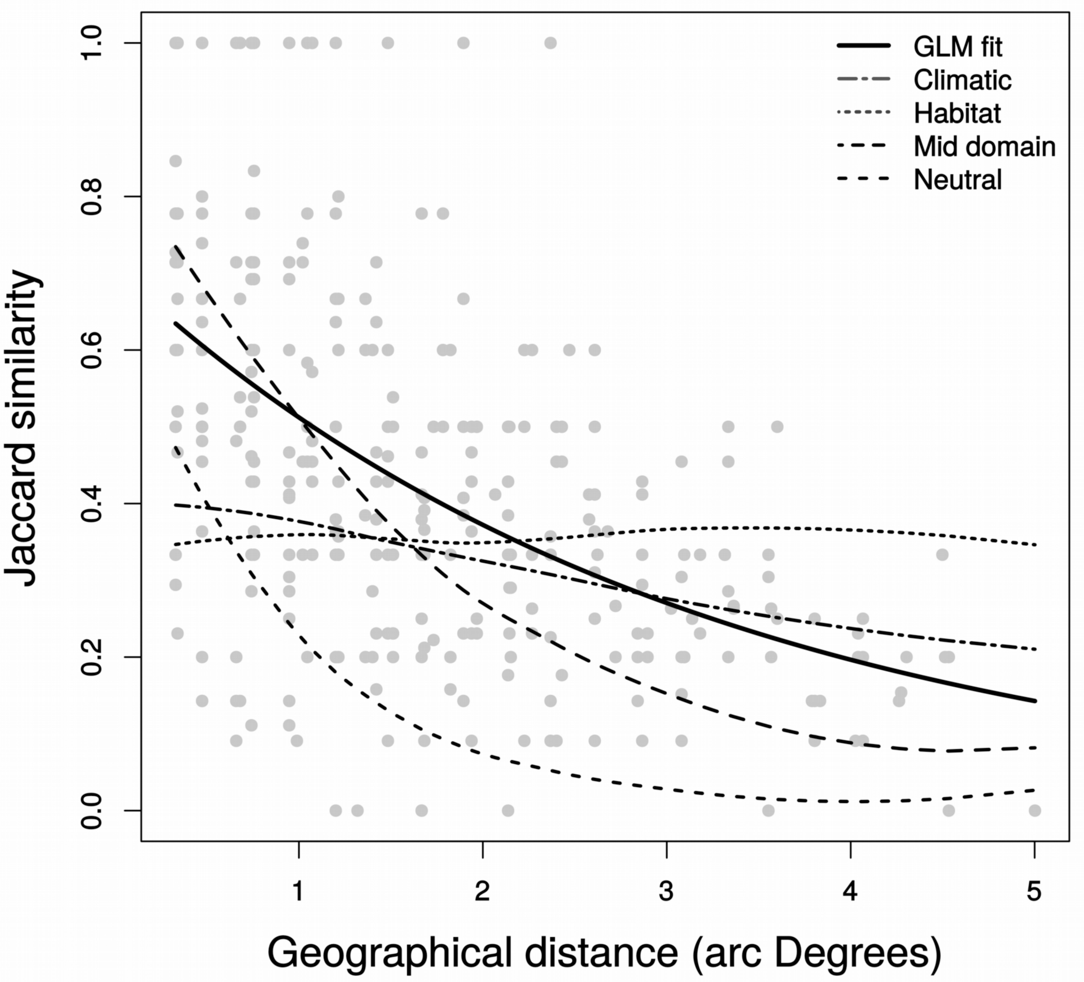

Figure 4.4 Decay in the similarity of species composition with geographical distance.

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APPENDIX A – Supplemental material for Chapter 1

Supplementary Tables

Table S1. Incidence of termite species collected in Ducke Reserve, Manaus, AM, Brazil. Counts are the occurrence of each species out of a possible maximum value of 300 (= 30 transects × 10 plots per transect).

Family	Subfamily	Species	Abundance
Rhinotermitidae	Coptotermitinae	*Coptotermes testaceus*	16
	Heterotermitinae	*Heterotermes crinitus*	8
		Heterotermes tenuis	86
	Rhinotermitinae	*Dolichorhinotermes longilabius*	10
		Rhinotermes hispidus	3
		Rhinotermes marginalis	1
Termitidae	Apicotermitinae	*Anoplotermes* sp.1	29
		Anoplotermes sp.2	27
		Anoplotermes sp.3	2
		Anoplotermes sp.4	3
		Anoplotermes sp.5	6
		Apicotermitinae sp.1	1
		Apicotermitinae sp.2	1
		Apicotermitinae sp.3	1
		Apicotermitinae sp.4	1
		Ruptitermes arboreus	3
		Ruptitermes cf. xanthochiton	1
	Nasutitermitinae	*Angularitermes nasutissimus*	1
		Araujotermes nanus	11
		Armitermes holmgreni	2
		Armitermes peruanus	3
		Armitermes teevani	1
		Atlantitermes sp.1	5
		Atlantitermes sp.2	1
		Caetetermes taquarussu	4
		Coatitermes cf. clevelandi	2
		Coatitermes sp.1	2
		Constrictotermes cavifrons	1
		Convexitermes junceus	1
		Cornitermes ovatus	11

	Cornitermes pugnax	14
	Cyrilliotermes angulariceps	1
	Cyrilliotermes cashassa	1
	Embiratermes neotenicus	6
	Embiratermes spissus	3
	Labiotermes labralis	2
	Nasutitermes banksi	25
	Nasutitermes callimorphus	9
	Nasutitermes corniger	1
	Nasutitermes ephratae	14
	Nasutitermes gaigei	12
	Nasutitermes guayanae	35
	Nasutitermes macrocephallus	3
	Nasutitermes octopilis	6
	Nasutitermes sp.1	11
	Nasutitermes sp.3	2
	Nasutitermes sp.4	2
	Nasutitermes sp.6	1
	Nasutitermes surinamensis	1
	Nasutitermes wheeleri	3
	Rhynchotermes sp.n.	7
	Rotunditermes bragantinus	1
	Subulitermes microsoma	1
	Syntermes longiceps	5
	Syntermes molestus	14
	Syntermes spinosus	5
	Triangularitermes triangulriceps	7
	Velocitermes sp.1	2
Termitinae	*Amitermes exellens*	3
	Cavitermes tuberosus	1
	Crepititermes verruculosus	8
	Cylindrotermes flangiatus	29
	Cylindrotermes parvignathus	130
	Dihoplotermes sp.n.	1
	Dihoplotermes sp.2	1
	Termitinae sp.n	1
	Microcerotermes strunckii	4
	Neocapritermes angusticeps	1
	Neocapritermes araguaia	3
	Neocapritermes braziliensis	40
	Neocapritermes opacus	4
	Neocapritermes pumilis	3
	Neocapritermes sp.1	1
	Neocapritermes taracua	4

	Orthognathotermes sp.n.	1
	Planicapritermes planiceps	9
	Spinitermes nigrostomus	1
	Termes ayri	1
	Termes medioculatus	8
	Total	692

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. For each sampling method, counts are the occurrence of each species out of a possible maximum value of 300 (= 30 transects × 10 plots per transect). Designation of predator status is from the *a priori* classification in Silva and Brandão (2010).

Guilds	Species	Bait	Pitfall	Winkler	Total	Predator
Arboreal generalist predators	*Pseudomyrmex sp. 01*		1		1	yes
	Pseudomyrmex sp. 02		1		1	yes
	Pseudomyrmex sp. 03		1		1	yes
Arboreal omnivores	*Allomerus octoarticulatus*		2		2	no
	Cephalotes sp. 03		4		4	no
	Cephalotes sp. 04		1		1	no
	Cephalotes sp. 05		1		1	no
	Crematogaster curvispinosa	1			1	no
	Crematogaster levior			1	1	no
	Crematogaster stollii		1		1	no
	Ectatomma tuberculatum	3			3	no
	Pachycondyla sp. 01	1			1	no
	Paraponera clavata		1		1	no
	Procryptocerus marginatus		1		1	no
	Xenomyrmex stollii			1	1	no
Arboreal omnivores, incidentally or seasonally foraging on the floor and litter	*Azteca sp. 01*	2	3	1	6	no
	Camponotus atriceps		3		3	no
	Camponotus crassus		1		1	no
	Camponotus novogranadensis	1	2	1	4	no
	Crematogaster sp. 01	1	1		2	no
	Crematogaster sp. 02		1		1	no
	Crematogaster sp. 03		1		1	no
	Crematogaster sp. 04		1		1	no
	Crematogaster sp. 05		1		1	no
	Dolichoderus sp. 01		1		1	no
	Dolichoderus sp. 02		1		1	no
	Dolichoderus sp. 03		1		1	no
	Dolichoderus sp. 05		2		2	no
Arboreal, incidentally or seasonally	*Camponotus sp. 02*		6		6	no
	Camponotus sp. 04	4	18		22	no
	Camponotus sp. 05	9	12		21	no

foraging on the floor and litter	*Camponotus sp. 08*		2		2	no
	Camponotus sp. 10		1		1	no
Army ant	*Eciton dulcius*		1		1	yes
	Eciton rapax		3		3	yes
	Labidus coecus		10		10	yes
	Labidus mars		1		1	yes
	Labidus praedator		20		20	yes
	Labidus spininodis		1		1	yes
	Neivamyrmex gibbatus		8		8	yes
	Neivamyrmex sp. 01		2		2	yes
	Neivamyrmex sp. 02		1		1	yes
	Neivamyrmex sp. 03		1		1	yes
	Neivamyrmex sp. 04		1		1	yes
	Nomamyrmex esenbeckii		4		4	yes
	Nomamyrmex hartigi		1		1	yes
Dacetini predators	*Basiceros balzani*		6	20	26	yes
	Basiceros iheringi			1	1	yes
	Basiceros pilulifera			1	1	yes
	Basiceros sp. 03		1		1	yes
	Strumigenys carinithorax		1		1	yes
	Strumigenys elongata			5	5	yes
	Strumigenys perparva		2	15	17	yes
	Strumigenys precava		1		1	yes
	Strumigenys smithii			1	1	yes
	Strumigenys sp. 01		24	79	103	yes
	Strumigenys sp. 02		8	8	16	yes
	Strumigenys sp. 03		3	4	7	yes
	Strumigenys sp. 04		1	2	3	yes
	Strumigenys sp. 05			1	1	yes
	Strumigenys sp. 07			2	2	yes
	Strumigenys trinidadensis		3		3	yes
	Strumigenys trudifera			3	3	yes
Generalists: generalized dolichoderinaes, formicinaes and myrmicinaes	*Blepharidatta brasiliensis*	5	37	32	74	no
	Brachymyrmex heeri	1	2		3	no
	Camponotus rapax	6	15	1	22	no
	Camponotus sp. 06		2		2	no
	Camponotus sp. 11			1	1	no
	Crematogaster brasiliensis	52	28	12	92	no
	Crematogaster erecta	2	2	1	5	no
	Crematogaster flavomicrops		1		1	no
	Crematogaster flavosensitiva	3	3	3	9	no
	Crematogaster limata	25	25	8	58	no
	Crematogaster sotobosque	3	29	31	63	no

Crematogaster tenuicula	143	144	72	359	no
Dolichoderus bispinosus		1		1	no
Gigantiops destructor	1	3		4	no
Lachnomyrmex amazonicus			1	1	no
Megalomyrmex sp. 02		4	1	5	no
Megalomyrmex sp. 04		1	2	3	no
Megalomyrmex sp. 05			1	1	no
Monomorium pharaonis	1	1		2	no
Nylanderia sp. 01	20	35	22	77	no
Nylanderia sp. 02	12	33	9	54	no
Nylanderia sp. 03	3	5		8	no
Ochetomyrmex semipolitus		16	5	21	no
Pheidole fracticeps	13	35	24	72	no
Pheidole meinerti	2	26	13	41	no
Pheidole sp. 01	4	30	1	35	no
Pheidole sp. 02	14	37	6	57	no
Pheidole sp. 04		4		4	no
Pheidole sp. 05		2		2	no
Pheidole sp. 06	19	31	3	53	no
Pheidole sp. 07		1		1	no
Pheidole sp. 08	9	23	1	33	no
Pheidole sp. 09	1	6	5	12	no
Pheidole sp. 11	1	15	27	43	no
Pheidole sp. 12		5		5	no
Pheidole sp. 13	3	18		21	no
Pheidole sp. 14	1	2		3	no
Pheidole sp. 15	2	29	1	32	no
Pheidole sp. 16		8		8	no
Pheidole sp. 17		5	1	6	no
Pheidole sp. 18	4			4	no
Pheidole sp. 19	3	14	5	22	no
Pheidole sp. 21	5	3		8	no
Pheidole sp. 22		6	7	13	no
Pheidole sp. 23	2	4		6	no
Pheidole sp. 25	3	7	2	12	no
Pheidole sp. 26	2	10		12	no
Pheidole sp. 27	3	3		6	no
Pheidole sp. 28		4	1	5	no
Pheidole sp. 29	7	4	3	14	no
Pheidole sp. 30		2		2	no
Pheidole sp. 31	3	10	3	16	no
Pheidole sp. 32	11	29	2	42	no
Pheidole sp. 33		4		4	no

	Pheidole sp. 34	3	1	2	6	no
	Pheidole sp. 35		12	3	15	no
	Pheidole sp. 36	2	10		12	no
	Pheidole sp. 37	8	4	1	13	no
	Pheidole sp. 38	2	9	1	12	no
	Pheidole sp. 39	2	13	3	18	no
	Pheidole sp. 40	1			1	no
	Pheidole sp. 41		1		1	no
	Pheidole sp. 42		19		19	no
	Pheidole sp. 43		2		2	no
	Pheidole sp. 44		6		6	no
	Pheidole sp. 45		6		6	no
	Pheidole sp. 46		3		3	no
	Pheidole sp. 47		3	6	9	no
	Pheidole sp. 48		1		1	no
	Pheidole sp. 49		2	2	4	no
	Pheidole sp. 50		7		7	no
	Pheidole sp. 51		5		5	no
	Pheidole sp. 52		2		2	no
	Pheidole sp. 53		1		1	no
	Pheidole sp. 54		6	1	7	no
	Pheidole sp. 55		17	1	18	no
	Pheidole sp. 56			1	1	no
	Pheidole sp. 58			1	1	no
	Solenopsis geminata		10	7	17	no
	Wasmannia auropunctata	14	47	40	101	no
	Wasmannia iheringi		1		1	no
	Wasmannia scrobifera		2		2	no
Hypogaeic generalist predators	*Hypoponera sp. 01*		2	7	9	yes
Hypogaeic generalist predators with vestigial eyes	*Hypoponera sp. 02*		2	1	3	yes
	Hypoponera sp. 03		1	2	3	yes
	Hypoponera sp. 04		7	6	13	yes
	Hypoponera sp. 05		1	2	3	yes
	Hypoponera sp. 06		1	19	20	yes
	Hypoponera sp. 07		1	1	2	yes
	Hypoponera sp. 08		1	1	2	yes
Large-sized epigaeic generalist	*Anochetus diegensis*		5	3	8	yes
	Anochetus emarginatus		1		1	yes
	Anochetus horridus		3	3	6	yes
	Ectatomma edentatum	5	32	6	43	yes
	Ectatomma lugens	2	44		46	yes

predators	*Gnamptogenys acuminata*		2		2	yes
	Gnamptogenys moelleri		2		2	yes
	Gnamptogenys sulcata		1		1	yes
	Gnamptogenys tortuolosa		8		8	yes
	Leptogenys sp. 01		1		1	yes
	Leptogenys sp. 02		4		4	yes
	Odontomachus brunneus		1		1	yes
	Odontomachus caelatus	3	4	1	8	yes
	Odontomachus haematodus	2	2		4	yes
	Odontomachus laticeps		2		2	yes
	Odontomachus meinerti		1		1	yes
	Odontomachus opaciventris		4	4	8	yes
	Odontomachus scalptus		1	1	2	yes
	Pachycondyla apicalis		2		2	yes
	Pachycondyla commutata		1		1	yes
	Pachycondyla constricta	2	23	7	32	yes
	Pachycondyla crassinoda	1	34		35	yes
	Pachycondyla harpax		17	2	19	yes
Leaf-cutters	*Atta sp. 01*	1	2		3	no
	Atta sp. 02		1		1	no
Litter-nesting fungus-growers	*Acromyrmex sp. 01*		2		2	no
	Apterostigma sp. 01		1		1	no
	Apterostigma sp. 02		5		5	no
	Apterostigma sp. 03		1	1	2	no
	Apterostigma sp. 04		1	2	3	no
	Cyphomyrmex cf. lectus			1	1	no
	Cyphomyrmex cf. peltatus		19	18	37	no
	Cyphomyrmex laevigatus		3	6	9	no
	Cyphomyrmex sp. 01		1		1	no
	Mycocepurus smithii		1		1	no
	Mycocepurus sp. 01		1		1	no
	Myrmicocrypta sp. 01		5	1	6	no
	Myrmicocrypta sp. 02			1	1	no
	Sericomyrmex sp. 01		9		9	no
	Sericomyrmex sp. 02		1		1	no
	Trachymyrmex bugnioni		1		1	no
	Trachymyrmex opulentus		7		7	no
	Trachymyrmex sp. 01		8		8	no
	Trachymyrmex sp. 02		7	2	9	no
	Trachymyrmex sp. 03		4		4	no
	Trachymyrmex sp. 04		4		4	no
	Trachymyrmex sp. 05	4	61	3	68	no
	Trachymyrmex sp. 06		1		1	no

	Trachymyrmex sp. 07		4		4	no
	Trachymyrmex sp. 08		2		2	no
	Trachymyrmex sp. 09		2		2	no
	Trachymyrmex sp. 10		2		2	no
	Trachymyrmex sp. 11		1		1	no
Medium-sized epigaeic generalist predators	*Gnamptogenys horni*	1	18	8	27	yes
	Gnamptogenys relicta			2	2	yes
	Hylomyrma immanis			1	1	yes
	Leptogenys wheeleri		2		2	yes
	Megalomyrmex balzani	2	3		5	yes
	Pachycondyla arhuaca		3		3	yes
	Pheidole cephalica	2	3	1	6	yes
Medium-sized hypogaeic generalist predators	*Rogeria alzatei*		1	3	4	yes
Small-sized hypogaeic generalist foragers	*Carebara sp. 01*		3	1	4	no
	Carebara sp. 03			5	5	no
	Carebara sp. 04			1	1	no
	Carebara urichi		7	5	12	no
	Discothyrea sp. 01			1	1	no
	Pheidole sp. 24	2	19		21	no
	Solenopsis sp. 01		21	11	32	no
	Solenopsis sp. 02	1	17	11	29	no
	Solenopsis sp. 03	4	12	9	25	no
	Solenopsis sp. 04		11	3	14	no
	Solenopsis sp. 05		16	35	51	no
	Solenopsis sp. 06	1	3	27	31	no
	Solenopsis sp. 07		7	5	12	no
	Solenopsis sp. 08	1			1	no
	Solenopsis sp. 09	1	2	2	5	no
	Solenopsis sp. 10			3	3	no
	Tapinoma sp. 01		1		1	no
Specialist predators living in the soil superficial layers	*Acanthostichus sp. 01*		2		2	yes
	Centromyrmex brachycola		1		1	yes
	Prionopelta punctulata		3	18	21	yes
Subterranean mealbug-dependent species	*Acropyga sp. 01*		7	1	8	no
	Acropyga sp. 02		1		1	no
	Total	478	1661	776	2915	

Table S3. Slope coefficients for multiple regressions of termite community structure against predictor variables. PCA1 and PCA2 summarize several correlated variables that could potentially affect termite community composition and diversity. PCA1 is mostly correlated to correlated to soil sand content (r = -0.76), Altitude (r = 0.91), Na (r = 0.82), Al (r = 0.92), Fe (r = 0.80), N (r = 0.77), and Conductivity (r = 0.87). PCA2 is mostly correlated to P (r = 0.66), K (r = 0.68), Ca (r = 0.80), and Mg (r = 0.84). All variables were standardized prior to analyses. R^2 values for abundance and richness were calculated using Cox and Snell's (1968) method.

Response variable	Intercept	Predator density	PCA1	PCA2	χ^2	*F*	R^2
Abundance	3.623***	-0.025***	-0.025†	0.001	20.275		0.491***
Richness	3.067***	-0.024***	-0.039*	-0.011	11.613		0.321**
PIE	0.975***	-0.003*	-0.013**	0		4.28	0.253*
NMDS1	0.063	-0.003	-0.056***	0.066***		30.208	0.751***
NMDS2	0.169†	-0.009†	-0.004	0.003		1.49	0.048
SES$_{\text{PIE}}$	0.989	-0.075†	-0.326**	0.021		3.503	0.206*
SES$_{\text{Richness}}$	0.479	-0.049	-0.157	-0.074		1.204	0.021

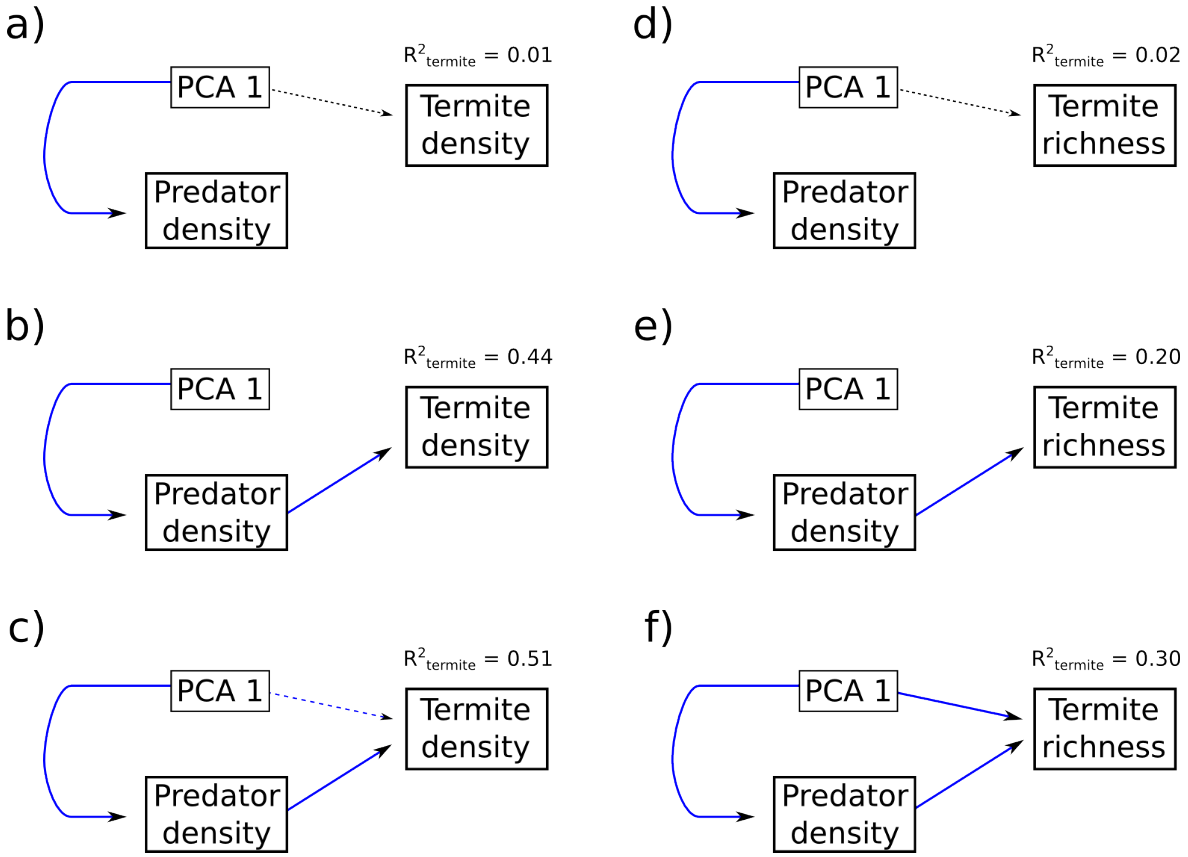
***P < 0.001 **P < 0.01 *P < 0.05 †P < 0.1.

References

Silva RR, Brandão CR (2010). Mophological patterns and community organization in leaf-litter ants assemblages. *Ecological Monographs*, 80: 107-124.

Supplementary Figures

Figure S1. Structural equation models (SEMs) with regressions between the environmental variables, the density of ant predators and the termite density (a-c) and richness (d-f). a;d. direct effects of the environmental variables on predator and termite density and richness. b;e. direct effect of the environmental variables on predator density and direct effect of predator density on termite density and richness. c;f. direct effect of the environmental variables on the predator density and on termite density and richness, and direct effect of predator density on termite density and richness. The solid, dashed, and dotted lines represent significant, marginally significant, and non-significant correlations at the 0.05 level, respectively. All the variables were standardized before the analysis. PCA1 summarize several correlated variables that could potentially affect termite community composition and diversity. PCA1 is mostly correlated to soil sand content (r = -0.76), Altitude (r = 0.91), Na (r = 0.82), Al (r = 0.92), Fe (r = 0.80), N (r = 0.77), and Conductivity (r = 0.87).


a)
$R^2_{termite}$ = 0.01
PCA 1
Termite density
Predator density
b)
$R^2_{termite}$ = 0.44
PCA 1
Termite density
Predator density
c)
$R^2_{termite}$ = 0.51
PCA 1
Termite density
Predator density
d)
$R^2_{termite}$ = 0.02
PCA 1
Termite richness
Predator density
e)
$R^2_{termite}$ = 0.20
PCA 1
Termite richness
Predator density
f)
$R^2_{termite}$ = 0.30
PCA 1
Termite richness
Predator density

APPENDIX B – Supplemental material for Chapter 2

Supplemental material for Chapter 2 is provided as online material only. The R script and annotated R script files are submitted along with this document, and available in the following links:

Supplemental material S1 – Annotated R script:

http://files.figshare.com/1926487/Termite.PCSDucke.pdf

APPENDIX C – Supplemental material for Chapter 3

APPENDIX S1 – DETAILED DESCRIPTION OF SAMPLING GRIDS, AND ADDITIONAL INFORMATION ON DATA ANALYSIS

Text S1 - Detailed description of rarefaction procedure applied to individual transects with more than five sections.

To calculate the abundance of each species expected by sampling five sections in those transects with more than five sections, we divided the species abundances by the number of sections sampled in a given transect. This measurement represents the density of termites from a particular species in the transect. For example, a species with abundance of 10 colonies in a transect with 10 sections has a density of 1 colony per section. To obtain the abundance expected in five sections, we multiplied the species density in a given transect by five. The expected abundance for all species within a transect was measured as the sum of the expected abundances for individual species.

To calculate the probability of a species to occur in a given transect by sampling only five sections, or the expected presence of a particular species in a given transect, we derived the following formula:

$$P(Occurrence|N, N_i, n) = 1 - \frac{(N-n)!}{N!} \frac{(N-N_i)!}{(N-N_i-n)!},$$

where N represents the number of sections surveyed, N_i represents the number of sections where species i was present, and n represents the number of sections to be subsampled (in our case n=5 for all transects).

The code to run this calculation in R is

```
1-(factorial(N-n)/factorial(N))*(factorial(N-
Ni)/factorial(N-Ni-n))
```

Note that this formula calculates the number of species that would be sampled in 5 sections at once from a larger pool without replacement. This calculation is different from sequentially sampling one section, replacing it, and repeating the procedure until five sections were obtained. In the later case, the calculation would be simply

$$P(Occurrence|N, N_i, n) = 1 - \left(1 - \frac{N_i}{N}\right)^n$$

The estimated species richness per transect was calculated as the sum of the probability of occurrence for all species sampled in each transect, or

$$E[S] = \sum_{i=1}^{S} \left[1 - \frac{(N-n)!}{N!} \frac{(N-N_i)!}{(N-N_i-n)!}\right]$$

Note that the results obtained by the formulas would provide the same results as randomly selecting five sections in each transects, and recording the species abundances, species richness, and presence and absence for each species. To demonstrate this, we randomly selected only five sections in all transects (rarefaction), and used measures, such as termite abundance, obtained in five sections for analyses. The random selection of sections was repeated 999 times for each transect, and the mean abundance, mean species richness, and mean abundance per species was recorded. Note that for transects where only five sections were sampled, the resulting recorded values were identical to the observed values because there is only one possible combination of five sections that could be selected in a randomization.

Text S2 - Detailed description of Moran Eigenvector Maps construction, and associated weighting matrix, *w.*

In our study, two sampling designs were used. In each of 12 sites within the Amazonian forest, we sampled from five to 32 transects spaced regularly in intervals of 1 km. The transects were organized within regular grids, whereas the sites had an irregular distribution. We determined that transects within a grid should be much more connected than transects in distinct grids. The idea in our procedure was to represent a local community within a grid, and a metacommunity among grids in a hierarchy. We established that 1) transects close to each other within a grid would be connected; and 2) that the connectivity between two transects within a grid would be equal to the connectivity of a transect with all transects outside the grid summed.

The connectivity matrix between pairs of transects within a grid was created by connecting each transect to all its adjacent transects in a radius of $\sqrt{2}\,Km$ (Moore neighborhood; 1 if connected, zero otherwise; Fig. 1b in manuscript). We then multiplied the within grid connectivity matrix by $1/(1 + n_i)$, where n_i represents the number of neighbors to which a given cell is connected to. We added 1 in the denominator because each transect was later connected to other transects outside the grid (Fig. 1b). The connectivity between grids was determined by a Gabriel graph (Legendre and Legendre 2012) and was used to determine the connectivity between pairs of transects in distinct grids (1 if connected, zero otherwise). The matrix of connectivity between transects in distinct grids was then multiplied element-wise by $1/[(1 + n_i)g_j]$, where g_j represents the number of transects sampled in the grid where a given transect is located. Finally, we summed both matrices to obtain *w*.

Moran Eigenvector Maps construction and selection

To create the MEMs, we run an *eigen* analyses on the final connectivity matrix *w*. The *eigen* analysis generated 197 vectors representing spatial autocorrelation from broad to fine spatial scales, which were determined from their associated *eigenvalues* (large and small *eigenvalues* represent broad and fine spatial autocorrelation, respectively; Dray *et al.* 2012).

To reduce the number of vectors to be included in our models, we performed two further steps. First, we assessed the spatial autocorrelation of MEMs by calculating Moran's *I,* and selected only MEMs significantly correlated with the geographical distance separating transects (Dray *et al*. 2012). Second, we created a regression or RDA model, when appropriate, using only MEMs as predictor variables of termite abundance, species richness, and species composition. We then run a forward stepwise selection of MEMs based on the adjusted R^2 of the model (Dray *et al.* 2012; Legendre and Gauthier 2014). This procedure was conducted independently for each response variable, and the final number of MEMs depended on the explanatory power of each MEM for a particular variable.

The selected MEMs were then divided into two groups: Broad and fine scale predictors. Finally, we applied a variance partitioning approach to separate the portion of variance in the response variable explained by 1) spatial autocorrelation in species distribution that could be a result of limited dispersal in fine scales; 2) spatial autocorrelation in species distribution that could be a result of limited dispersal in broad scales; 3) species association with environmental variables spatially structured in fine scales; 4) species association with environmental variables spatially structured in broad scales; 5) species association with non spatially structured variables; and 6) residual variation.

Supplemental material for Chapter 3 is partially provided as online material only. The R script and annotated R script files are submitted along with this document, and available in the following links:

Appendix S2 – R script used for analyses:

http://files.figshare.com/1926485/termite.amazonia6.R

Appendix S3 – Annotated R script:

http://files.figshare.com/1926482/termite.amazonia.Sample_abundRDA.pdf

APPENDIX D – Supplemental material for Chapter 4

Table S1. Studies surveyed and respective sampling location where small-mammal data were sampled.

Author and Year	State	Location	Latitude	Longitude	Sampling effort (hours)
Moura, 2003	BA	Projeto de Assentamento Zumbi dos Palmares	-19.9667	-40.5833	1000
Moura, 2003	BA	Fazenda Taquara	-22.5333	-42.2833	1000
Moura, 2003	BA	RPPN Estação Veracruz	-20	-42.65	1000
Moura, 2003	BA	Parque Nacional do Descobrimento	-23.5333	-46.9333	1000
Moura, 2003	BA	Fazenda Rio Capitão	-20.75	-42.85	1000
Moura, 2003	BA	RPPN Serra do Teimoso	-29.6667	-53.7167	1000
Moura, 2003	BA	Fazenda Monte Cristo	-19.8333	-41.8333	1000
Moura, 2003	BA	Fazenda Palmeiras	-27.7167	-48.5333	1000
Cademartori et al., 2008	RS	Lar Nazaré	-25.4833	-53.1167	1165
Lima et al., 2010	RS	Morro do Elefante	-21.55	-47.85	2240
Moura, 2003	BA	Fazenda Pedra Formosa	-23.7333	-47.0667	1000
Moura, 2003	BA	Fazenda Caititu	-22.5	-42.8667	1000
Moura, 2003	BA	Mata da Cara Branca – Veracel Celulose	-23.7167	-46.9667	1000
Pedó et al., 2010	RS	Fazenda Três Estrelas	-22.7167	-46.9167	2927
Moura, 2003	BA	RPPN Ecoparque de Una	-24.2333	-48.0667	1000
Moura, 2003	BA	Fazenda Orion – Serra das Lontras	-25.1667	-47.9833	1000
Moura, 2003	BA	Parque Nacional do Pau Brasil	-24.2833	-48.35	1000
Antunes et al., 2010	SC	Unidade de Conservação Ambiental Desterro	-29.1667	-50.0833	5760
Cerqueira et al., 1993	RJ	Restinga de Barra de Maricá (Mata de Restinga)	-20.4667	-41.8	58800
Finokiet et al., 2007	RS	Campo de Instrução de	-22.0333	-42.65	6360

		Santa Maria			
Machado et al.,	RS	Boca do Monte	-22.0333	-42.6833	4860
Cáceres e Monteiro-Filho, 2003	PR	COPEL Bigorrilho	-11.25	-37.4167	1800
Quadros et al., 2000	PR	Parque Estadual do Rio Guarani	-15.1667	-39.1167	2628
Moura, 2003	BA	Fazenda Alcoprado	-23.6	-46.9167	1000
Moura, 2003	BA	Fazenda Princesa do Pajaú	-13.5167	-39.0333	1000
Bittencourt & Rocha, 2003	RJ	Vila Dois Rios	-13.7	-39.2167	7474
Asfora & Pontes, 2009	PE	Reserva Ecológica Gurjaú	-13.5667	-39.7	1360
Asfora & Pontes, 2009	AL	Serra Grande Mill	-14.0167	-39.1333	1360
Sponchiado et al., 2011	RS	Estação Ecológica do Taim	-13.95	-39.45	1296
Bergallo et al., 1998	SP	Parque Estadual da Ilha do Cardoso	-13.85	-39.6667	5040
Dalmagro & Vieira, 2005	RS	Parque Nacional dos Aparados da Serra	-14.4167	-39.05	5178
Moura, 2003	BA	Estação Ecológica Nova Esperança	-14.3333	-39.0833	1000
Moura, 2003	BA	Fazenda São Roque	-15.15	-39.05	1000
Moura, 2003	BA	Fazenda Vista Bela	-15.1833	-39.3833	1000
Bergallo, 1994	SP	Estação Ecológica de Juréia-Itatins	-15.15	-39.5167	4307
Cáceres, 2004	PR	Piraquara	-15.6167	-39.15	1600
Pires et al., 2002	RJ	Reserva Biológica Poço das Antas (Ilha dos Barbados)	-15.9667	-39.3667	1618
Fonseca & Robinson, 1990	MG	Fazenda Esmeralda	-15.9167	-39.6333	19040
Barros-Battesti et al., 2000	SP	Itapevi	-16.3167	-39.1167	2888
Paglia et al., 1995	MG	Centro de Estudos de Florestas Naturais (Mata do Paraíso)	-16.2833	-39.4167	1920
Talamoni & Dias, 1999	SP	Estação Ecológica de Jatai	-16.5833	-39.9	2400
Stevens & Husband, 1998	SE	Estancia	-17.1	-39.3333	3072
Abel et al., 2000	SP	Morro Grande/Sabesp	-17.2833	-39.6667	1680
Moura, 2003	BA	Fazenda Subaúma	-17.1667	-39.8333	1000
Moura, 2003	BA	Fazenda São João	-16.5	-39.3	1000

Crespo, 1982	ARG	Parque Nacional Iguazú	-25.6333	-54.35	1000
Melo et al., 2010	RS	Parque Estadual do Turvo	-29.4667	-50.2167	6120
Passamani & Ribeiro, 2009	ES	Santa Teresa	-29.4667	-50.2167	3575
Fonseca & Robinson, 1990	MG	Fazenda Montes Claros	-23.35	-44.8333	19040
Umestu & Pardini, 2007	SP	Reserva Florestal do Morro Grande (Caucaia do Alto)	-20.3667	-40.4833	1008
Kasper et al., 2007	RS	Vale do Taquari	-20.8833	-44.8333	600
Graipel et al.,	SC	Reserva Volta Velha	-30.2333	-51.0333	19200
Casella, J.,	PR	Parque Nacional do Iguaçu	-29.7667	-51.8333	2500
Graipel et al., 2006	SC	Parque Municipal da Lagoa do Peri	-29.4167	-50.4	12132
Bonvicino et al., 2002	SP	Pedreira	-19.95	-42.55	1830
Gentile & Fernandez, 1999	RJ	Pamparrão	-27.1	-54.9667	12250
Pinheiro & Geise, 2008	SP	Parque Estadual da Serra do Mar	-27.8667	-48.8333	1680
Marques et al., 2011	RS	Floresta Nacional de São Francisco de Paula	-28	-48.8333	11596
Vieira & Monteiro-Filho, 2003	SP	Parque Estadual Intervales (Saibadela)	-19.95	-40.5333	15227
D'Andrea et al., 2007	RJ	Pamparrão. Porteira Verde e Bela Joana	-20.2667	-40.4667	5700
Pedó et al., 2010	RS	CPCN Pró-Mata	-24.5333	-47.25	2327
Vieira et al., 2009	RJ	Rio Macacu	-22.95	-42.85	1200
Pardini & Umetsu, 2006	SP	Reserva Florestal do Morro Grande	-26.0667	-48.6167	6048
Vieira & Monteiro-Filho, 2003	SP	Parque Estadual Intervales (Barra Grande)	-27.1667	-53.9167	3547
Asfora & Pontes, 2009	PE	Reserva Privada Frei Caneca	-25.4667	-48.8333	1360
Paresque et al., 2004	ES	Estação Biológica de Santa Lúcia	-23.1833	-44.2	3300
Paresque et al., 2004	ES	Reserva Biológica de Duas Bocas	-8.25	-35.0833	3352
Rocha et al., 2011	MG	Santo Antônio do Amparo	-8.7	-35.8333	10080

Pardini, 2004	BA	Reserva Biológica de Una	-9	-35.8667	36288
Stallings et al., 1991	MG	Parque Estadual do Rio Doce	-29.75	-50	64300
Pinto et al., 2009	ES	Viana	-29.6333	-53.9	2160
Cirignoli et al.,	ARG	Reserva Privada de Usos Múltiples Valle del Cuña Pirú	-32.55	-52.5167	5310
Bonvicino et al., 2002	MG/ES	Parque Nacional do Caparaó	-25.6833	-54.4333	3231
Cherem et al., 2011	SC	Parque Estadual da Serra do Tabuleiro	-25.4167	-49.3	42438

Figure S1. Observed and predicted richness of the small-mammal species in the Atlantic Forest. A: Observed; B-T: Predicted by the BioClim variables using individual logistic regressions. See main text for detailed description of BioClim variables.

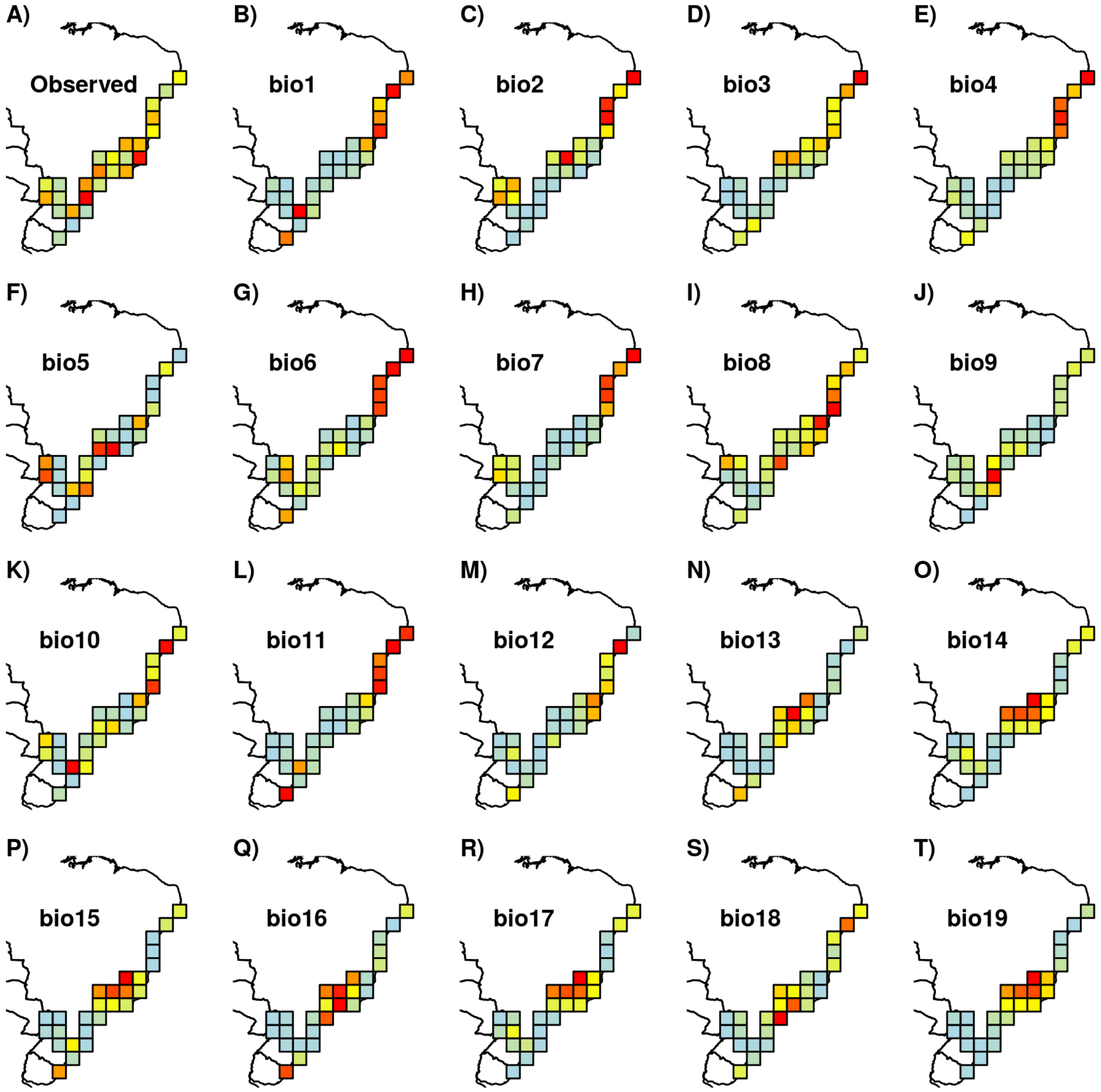


Figure S2. Observed and predicted composition of the small mammal species in the Atlantic Forest. The composition was summarized by the first ordination axis of a Principal Coordinates Analysis using the tunrover component from the Jaccard similarity index. A: Observed; B-T: Predicted by the BioClim variables using individual logistic regressions. See main text for detailed description of BioClim variables.

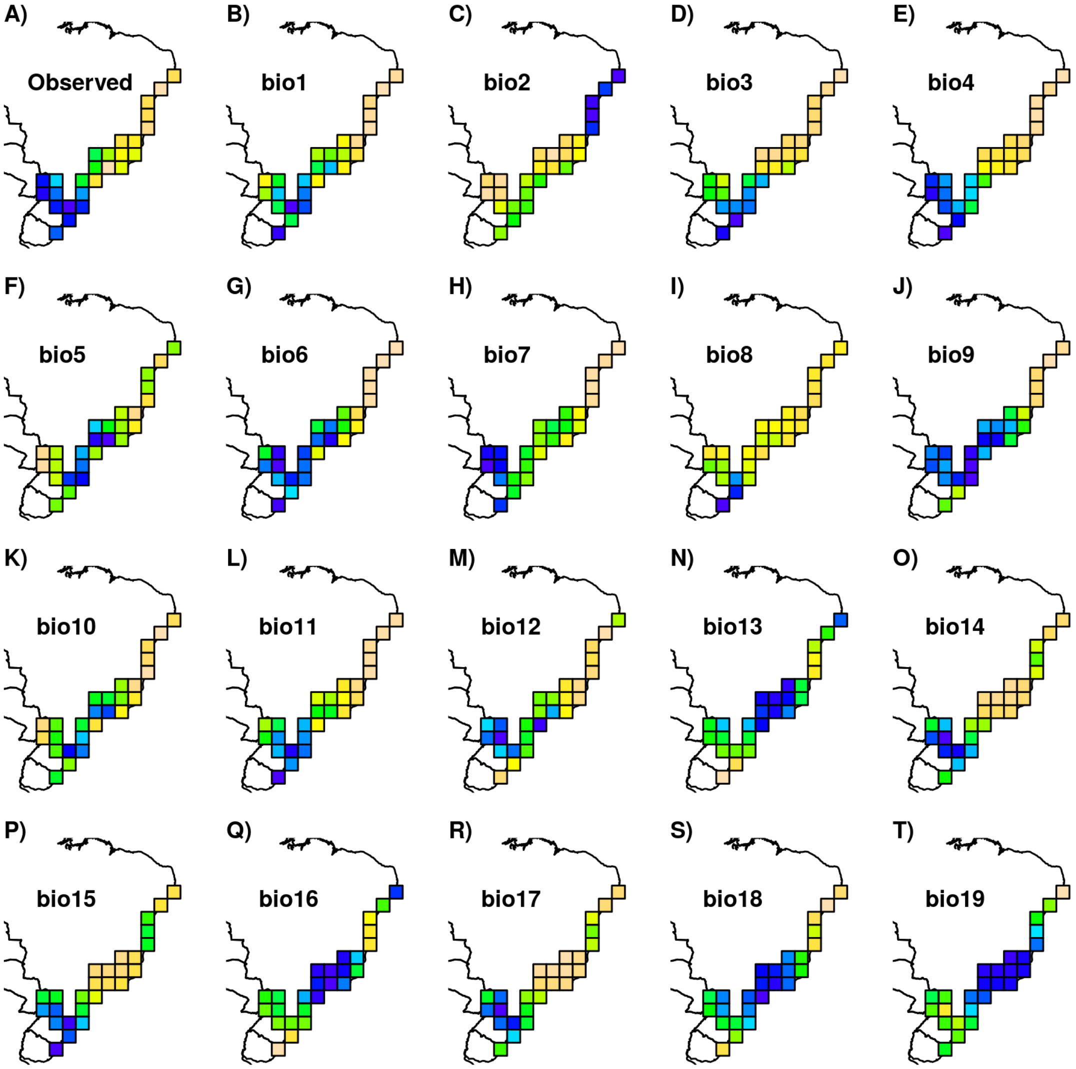


Figure S3. Fit of linear regression of species richness against the predictor variables (black line), and predictions for species richness based on logistic regressions fit for individual species against the predictor variables (red dots). See main text for detailed description of variables.

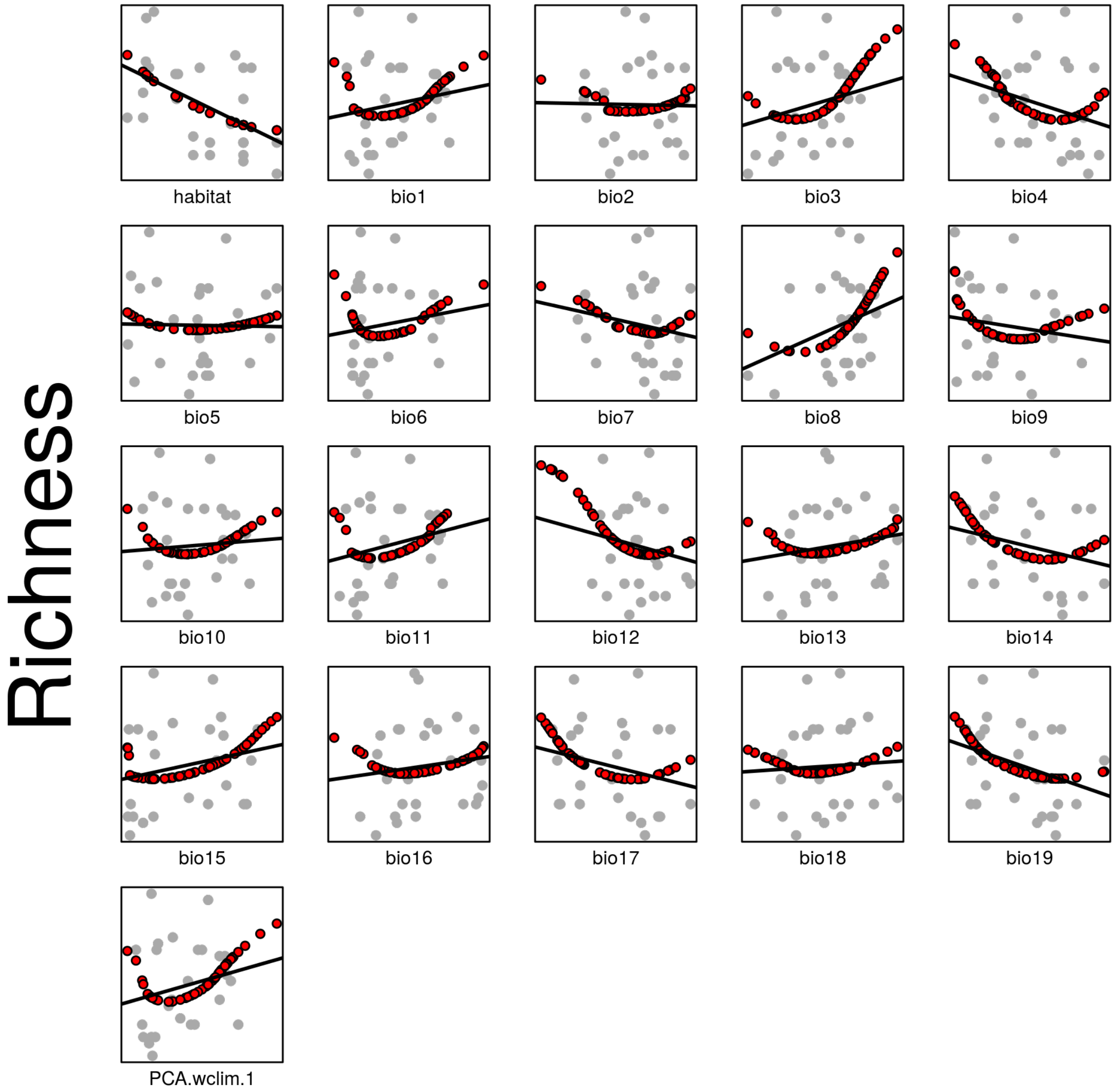


Figure S4. Fit of linear regression of PCoA1 against the predictor variables (black line), and predictions for PCoA1 based on logistic regressions fit for individual species against the predictor variables (blue dots). See main text for detailed description of variables.

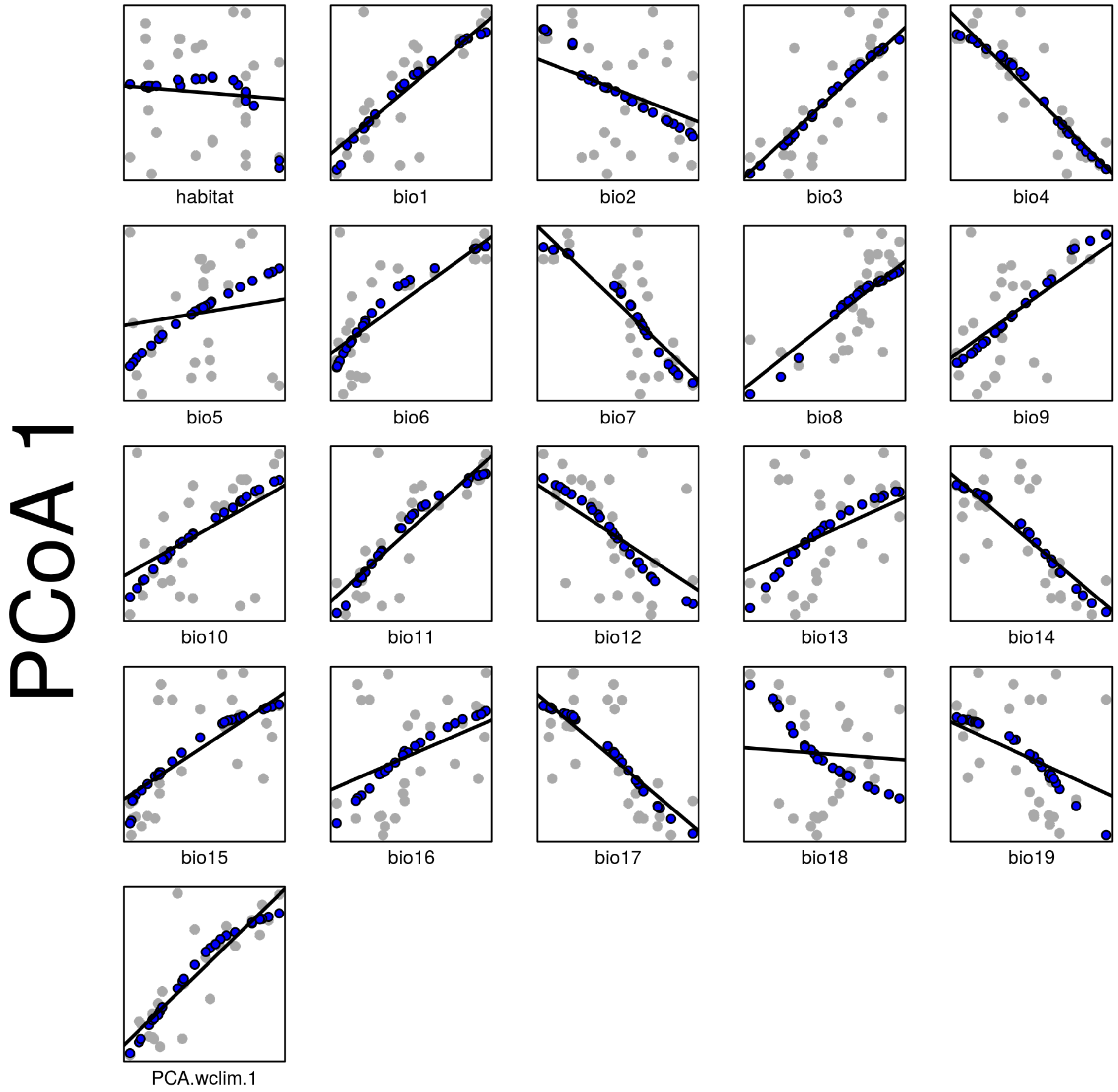


Figure S5. Fit of linear regression of PCoA2 against the predictor variables (black line), and predictions for PCoA2 based on logistic regressions fit for individual species against the predictor variables (blue dots). See main text for detailed description of variables.

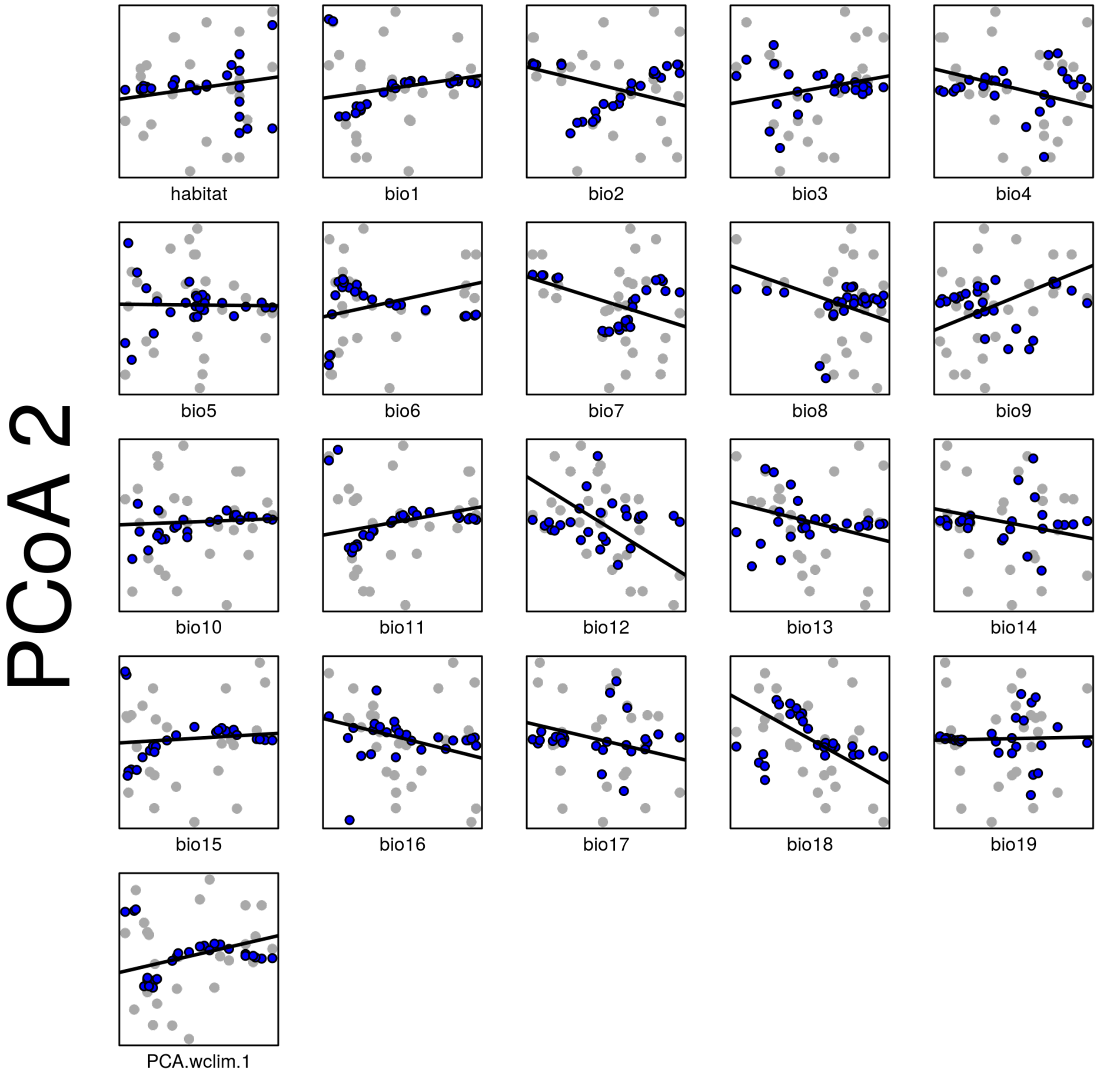


Figure S6. Network used for the spreading dye model and the neutral model simulation.