

Geographic distance and vegetation structure rather than river barrier drive ant beta diversity across Central Amazonia

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Abstract

To understand better the effects of niche and neutral processes is important to disentangle the direct and indirect effects of each process, mainly if the environmental factors are geographically structured neglecting important indirect and synergic effects. We sampled ground-dwelling ant species on 126 plots distributed across eight sampling sites along a broad environmental gradient in Central Amazonia. Structural equation modelling was employed to quantify direct and indirect effects of geographic distance, the Amazon River's opposite margins, and environmental differences in temperature, precipitation and vegetation structure (Normalized Difference Vegetation Index) on ant beta diversity (Jaccard's dissimilarity). We found that geographic distance and NDVI differences had major direct effects on ant beta diversity. The major effect of temperature was indirect through NDVI, whereas precipitation had no detectable effect on beta diversity. The Amazon River had a weak influence on the ant composition dissimilarity. Our results challenge the major role often ascribed to riverine barriers in the diversification and distribution of Amazonian biota. Rather, ant compositional dissimilarity seems to be mainly driven by a combination of dispersal limitation and selection imposed by vegetation features and, indirectly, by temperature. We suggest that as NDVI differences decrease with geographic distance in the region, isolation by distance may have favoured phenotypic convergence between ant communities in the northern and southern borders of the Amazon Basin.

Introduction

Four higher-level processes can account for species compositional dissimilarity across sites: natural selection, ecological drift, dispersal and speciation (Vellend 2016). Selection arises due to (mis)matches between species requirements (i.e. their niche) and the environment. Accordingly, habitat conditions and resource availability can often explain assemblage species composition (Cottenie 2005). Species composition can also be driven by neutral or niche-independent processes, such as drift (random variation in births and deaths rates) and dispersal (species movement between sites) (Hubbell 2001; Cadotte 2006). For instance, geographic isolation associated with geographical barriers can prevent gene flow between populations, leading to speciation and contributing to assemblage dissimilarity (Oliveira et al. 2017; Boubli et al. 2015). However, niche and neutral processes are not mutually exclusive and the relative contributions of each process remain controversial (Matthews and Whittaker 2014). Importantly, most studies focus only on the direct effects of both processes, neglecting the structure of correlations between environmental and geographic factors and their indirect effects in generating patterns of diversity on larger scales.

Amazonia is the largest tropical forest remnant and a major cradle of biodiversity, being the source of much of the phylogenetic diversity spread over the Americas (Antonelli et al. 2018). Although the wide environmental variation of the region may explain part of the distribution of Amazonian biota (Ter Steege et al. 2006; Zuquim et al. 2014; Silva et al. 2019), large Amazonian rivers are thought to work as geographical barriers that preclude vertebrate dispersal (Cracraft 1985). For monkeys and understory birds, large rivers may foster allopatric speciation, resulting in compositional dissimilarity among

interfluves (Ribas et al. 2012; Boubli et al. 2015; Oliveira et al. 2017). Further, the Amazon River seemingly has a stronger role among the large rivers due to its massive size and possibly ancient formation (Oliveira et al. 2017; Ruokolainen et al. 2019; Fluck et al. 2020).

Despite recent developments, Amazonian biogeography is still strongly biased towards macroscopic organisms, particularly vertebrates (Ribas et al. 2012; Leite and Rogers 2013; Antonelli et al. 2018) and plants (Kristiansen et al. 2012; Zuquim et al. 2014; Tuomisto et al. 2019). This gap is important because most known species are small-bodied invertebrates, such as insects and arachnids, which may respond differently to selective or neutral process. These animals often reach very high population densities and can disperse for long distances both actively and passively (e.g. through the wind, over the water or attached to larger animals) (Kaspari et al. 2010; Yamane 2013; Hakala et al. 2019). Thus, environmental selection might be more important than ecological drift and dispersal limitation in driving their biogeographic patterns. Furthermore, recent studies suggest that large Amazonian rivers are not substantial dispersal barriers to several insect taxa (Dambros et al. 2017; Santorelli et al. 2018; Dambros et al. 2020;). Therefore, a major gap in Amazonian biogeography is whether the current understanding of larger animals and plant distribution patterns applies to most of its biodiversity, which is small-bodied.

Ants are a highly diverse, abundant and ecologically relevant group (Folgarait 1998; Baccaro et al. 2015). Ants comprise 25% of the terrestrial animal biomass in tropical forests (Agosti et al. 2000), performing many roles in the ecosystem such as seed dispersers (Ness et al. 2004), regulating other arthropod populations (Tarli et al. 2014; Dambros et al. 2016) and incorporation of organic material in the soil. Studies in Amazonia have shown that geographic distance can account for invertebrate beta diversity, including ants (Dambros et al. 2017, 2020), although climate and vegetation are also known to correlate with ant distribution in the region (Vasconcelos et al. 2010; Guilherme et al. 2019). However, environmental variables such as climate and vegetation are geographically structured, resulting in important indirect and synergistic effects (Jiménez-Alfaro et al. 2016; Hurtado et al. 2019). For instance, geography can affect climate that may affect communities both directly and indirectly, through vegetation. Also, if selective environmental pressures are geographically structured, isolation by distance and by the environment may reinforce each other, possibly facilitating speciation over entire communities (Wang and Bradburd 2014). Despite this, the important distinction between direct and indirect effects in ecological systems (Shipley 2016) has been largely neglected by biogeographic studies, which typically assume direct effects only, e.g. in standard variance partitioning analyses (Tuomisto et al. 2003; Vasconcelos et al. 2010; Fluck et al. 2020).

In the present study, we used structural equation modelling to disentangle and quantify direct and indirect effects of geography (geographic isolation, margin of the Amazon River) and environment (temperature, precipitation and Normalized Difference Vegetation Index, NDVI) on the beta diversity of ground-dwelling ants across a latitudinal gradient in Central Amazonia. We hypothesized that: (i) due to the large habitat heterogeneity across the studied spatial extent and potential for long-distance dispersal, ant beta diversity should be more directly shaped by environmental selection (i.e. differences in climate and NDVI) than by dispersal limitation (i.e. geographic distance and difference and river margin); and (ii) due to the

geographic structure of climate and the latter's effect on vegetation, we expected geographic distance to have mainly an indirect effect on ant beta diversity.

Material And Methods

Study sites

The ground-dwelling ants were collected in eight sampling sites maintained by the Brazilian Biodiversity Research Program; in Portuguese: Programa de Pesquisas em Biodiversidade, PPBio (Costa and Magnusson 2010). The sites are located in the Brazilian Amazon Forest, covering the geographical extent of approximately 1,050 km (between the first and last sampling point, in the North/South direction). The study area covers a precipitation gradient of ~ 1700 mm in the northern sites, to ~ 2400 mm in the central and southern sites. The vegetation type is mostly characterized as dense ombrophylous forest. It also includes other vegetation such as savannas and white-sand vegetation with a small area subject to flooding in the rainy season (Instituto Brasileiro de Geografia e Estatística - IBGE 2012) (Table 1).

Table 1

Sampling sites, geographic coordinates, vegetation types, range of NDVI, and precipitation and temperature averages at each sampling site.

Sites	Coordinates	Vegetation Types	Range NDVI Index	Average precipitation	Average temperature
Maracá	Longitude - 61.473 Latitude 3.396	Open ombrophylous forest, Semideciduous forest, Deciduous forest, Campinarana forest	0.44– 0.62	1988 mm	26.74 C°
Cauamé	Longitude - 60.715 Latitude 2.883	Open savana	0.05– 0.18	1764 mm	27.98 C°
Viruá	Longitude - 61.006 Latitude 1.441	Open ombrophylous forest, Campinarana forest Seasonal campinarana, Seasonal shrubby campinarana	0.25– 0.65	1897 mm	27.27 C°
Ducke	Longitude - 59.942 Latitude - 2.950	Dense ombrophylous forest	0.57– 0.66	2300 mm	26.47 C°
Manaquiri	Longitude - 60.308 Latitude -3.673	Open ombrophylous forest	0.60– 0.64	2218 mm	26.74 C°
Orquestra	Longitude - 61.555 Latitude - 4.994	Dense ombrophylous forest	0.56– 0.60	2444 mm	26.91 C°
Capana	Longitude - 62.193 Latitude - 5.629	Dense ombrophylous forest	0.57– 0.61	2184 mm	26.74 C°
Jari	Longitude - 62.504 Latitude - 5.953	Dense ombrophylous forest	0.59– 0.61	2136 mm	26.57 C°

The sampled sites also cover a large variety of soil types (Quesada et al. 2011). Four sites are in the Guiana Shield, at the north of the Amazon River. This region has a greater predominance of Acrisols and Ferralsols. The other four sites are located south of the Amazon River, in the interfluvium between the Purus and Madeira rivers. These sites have a predominance of Plinthosols soils, forming part of the Brazilian Shield (Quesada et al. 2011). The location of collection sites and the position of the Amazon River are shown in Fig. 1.

Experimental design and ant sampling

We used the RAPELD sampling design to sample ants (Magnusson et al. 2013). Each collection site gives access to permanent plots where several organisms and environmental variables have been surveyed (Costa and Magnusson 2010). The sampling sites are structured by a grid-shaped system with 30 plots, and modules with five or ten plots, totaling 126 plots in the whole study area. Each grid has six parallel trails of 5 km located 1 km apart with five permanent plots distributed at least 1 km apart along each trail. Each module has one or two trails following the same sampling design of the grids. The plot is 250-m long and 1-m wide, following the altitudinal contours to minimize within-plot environmental variation (Magnusson et al. 2013). Plot geographic position was measured with a GPS (Global Position System) using the reference system datum WGS84. Geographic coordinates were obtained at the central part of the plots.

Ants were collected between September 2006 and June 2012, and all collections were carried out in the respective dry season. Ants were sampled with pitfall traps (plastic cups 8 cm long by 9.5 cm in diameter), placed at 25 m intervals, totalling ten traps per plot. Overall 1260 pitfalls were deployed. Pitfalls were buried until their edge remained at the same level as the ground and filled with 1/3 of 70% alcohol and a few detergent drops. After 48 h the traps were collected. All ants were sorted and stored in 90% alcohol (Souza et al. 2016). Ants were identified up to genus level using taxonomic keys (Baccaro et al. 2015), morphotyped, and when possible, identified to species level using available taxonomic keys or by specialists and by comparison with specimens deposited in zoological collections (<https://ppbio.inpa.gov.br>). Voucher specimens were deposited at INPA's Invertebrate Collection.

Environmental data

To evaluate how the environment may influence ant species compositional dissimilarity between plots, we extracted information on climate and vegetation. Climate information was collected from the bioclimatic variables of WorldClim version 2 (Fick and Hijmans 2017). We used average annual precipitation and temperature to represent major climatic gradients, as they have clear biological meanings as availability of energy and water, respectively, strongly correlate with other bioclimatic variables (Appendix Supplementary), and have been shown to affect ant species composition (Vasconcelos et al. 2010; Ramos et al. 2018). The data were downloaded at a spatial resolution of 30 seconds (~ 1km²).

Vegetation structure was estimated using the Normalized Difference Vegetation Index (NDVI). NDVI is a measure that summarizes many factors that affect an ant's life, such as primary productivity and habitat

complexity (Kaspari et al. 2000; Bailey et al. 2004; Pettorelli et al. 2005). To obtain NDVI data, images from the Landsat 4–5 Thematic Mapper (TM) satellite were extracted from the United States Geological Survey-USGS website. The images obtained had pixels with a spatial resolution of 30 m (~ 900 m²) and were related to each location’s collection period (month/year). Images with less cloud coverage were selected within each collection (month/year) in each location to avoid cloud coverage interference in obtaining the NDVI values, NDVI values were extracted from each pixel where the plots were present.

Data analysis

We first applied the multi-site Jaccard dissimilarity index to species presence-absence data to measure overall ant beta diversity among plots. Since beta diversity has different components, we decomposed the overall beta diversity (β_{jac}) into its turnover (β_{jtu}) and nestedness components (β_{jne}) (Baselga 2010). As the overall beta diversity almost totally consisted of turnover ($\beta_{jtu} = 0.986$; $\beta_{jne} = 0.003$) we used the undecomposed, pairwise Jaccard dissimilarities to represent between-plot beta diversity in the analysis.

The predictors of beta diversity were three environmental Euclidean distances (difference in average annual precipitation, difference in average annual temperature, and difference in NDVI), geographic distance, and riverbank (whether plots were at the same or opposite riverbanks, coded as a dummy variable), all computed for each pair of plots. Then, to investigate expected causal relationships among these variables, we applied Structural Equation Modelling (SEM) (Shipley 2016). SEM consists of building a set of linear models (Table 2) representing the hypothesized relationships in a path diagram (Fig. 2), which in the current case were estimated with multiple regressions on distance matrices (MRM) (Lichstein 2007).

Table 2

Linear models used to build the Structural Equation Model on ants beta diversity. A.R.: Amazon River, G.D.: Geographic distance, T.D.: Temperature Difference, P.D.: Precipitation Difference and NDVI: NDVI Difference.

Models of causal hypothetical relationships in path diagram										References	
Ants	~	A.R.	+	G.D.	+	T.D.	+	P.D.	+	NDVI	Wepfer et al. 2016; Lassau et al. 2005
NDVI	~	A.R.	+	G.D.	+	T.D.	+	P.D.			Sun and Qin 2016
P.D.	~	T.D.	+	G.D.							Lochbihler et al. 2017
T.D.	~	G.D.									Almeida et al. 2017
Notes: All predictors were log-transformed, except Amazon River bank											

Based on the literature, we built the path diagram including hypothesized direct effects of both environment (temperature, precipitation, and NDVI) and geography (distance and riverbank) on ant dissimilarity and indirect effects of geography on dissimilarity through the environment (Fig. 2). We also included indirect effects of climate (temperature and precipitation) and riverbank on dissimilarity through

their putative effects on vegetation (NDVI) (Fig. 2). All predictors except riverbank were log-transformed to account for curvilinear relationships, and predictor effects were tested with permutation tests (999 permutations). Overall structural model fit was tested using Fisher's *C* statistic, under the null hypothesis that the data were consistent with the hypothetical relationships, i.e. there was weak support to non-expected relationships in the path diagram ($P > 0.05$) (Lefcheck 2016).

All statistical analyses were performed in the R environment for statistical computing (R Core team 2020; version 4.0.1) with support of packages "vegan" (Oksanen et al. 2020), "ecodist" (Goslee and Urban 2007), "visreg" (Breheny and Burchett 2020), "adespatial" (Dray et al. 2021), "ade4" (Dray et al. 2020), "betapart" (Baselga et al. 2020) and "piecewiseSEM" (Lefcheck et al. 2020).

Results

Over the 126 plots, we sampled 326 species/morphospecies of ants. The number of ant species per plot varied from 2 to 56 species. The most frequent species was *Pachycondyla crassinoda* (Latreille, 1802) occurring in 73% (92) plots of the sampling sites. On the other extreme, more than 1/3 of the species were sampled once (73 species) or twice (40 species).

Our sampling plots encompassed open ("savanna-like") areas, open forests and dense forests covering the large environmental heterogeneity typical of the Central Amazon. While the study area has little variation in the range of temperature (minimum = 26.35 C°; maximum = 28.04 C°), variation in annual precipitation (minimum = 1737 mm; maximum = 2449 mm) and NDVI (index minimum = 0.05; maximum = 0.66) are much higher.

The SEM showed that the hypothesized relationship between geographic distance and barrier, environmental variables, and ant compositional dissimilarity provided a consistent description of the data (Fisher's *C* test = 2.30, $P = 0.32$). The standardized coefficients indicated that geographic distance indirectly affected the ants through vegetation and temperature, and its direct effect upon ant composition dissimilarity was slightly greater than that of NDVI and stronger than other direct effects (Fig. 3). Temperature had an indirect effect on ant composition through NDVI, with NDVI showing the strongest direct effect among environmental predictors on ant beta diversity (Fig. 3). The Amazon River had a relatively weak influence on ant distribution and precipitation did not affect ant species dissimilarity directly or indirectly (Fig. 3). The overall model explained 52% of the variation of ant composition dissimilarity across our 126 plots (Fig. 4).

Discussion

Our results highlight how the beta diversity of ground-dwelling ants is structured across the Amazon Basin through dispersal limitation (geographic distance and Amazon River) and environmental selection (NDVI and temperature). Remarkably, ant beta diversity was more strongly related to geographic distance and environmental variables than to a major, putative geographic barrier (the Amazon River). This finding is in accordance with the most recent evidence on the limited role of large rivers on Amazonian species

distributions (Dambros et al. 2017; Oliveira et al. 2017; Fluck et al. 2020; Dambros et al. 2020), and partially supports our hypothesis that selection along environmental gradients is the major driver of biogeographic patterns in smaller-bodied, shorter-lived animals such as ants. However, the results showed that geographic distance has a relatively strong, independent direct effect on ant species dissimilarity, suggesting that neutral processes equally relevant to the distribution and diversification of Amazonian ants.

We hypothesized that climate would affect directly and strongly ant species dissimilarity. Temperature affects ant thermoregulation, shaping thermal niches (Cerdá et al. 1998; Cerdá and Retana 2000; Kaspari et al. 2019) and also is related to species richness at larger scales (Dunn et al. 2009). Indeed, we found that temperature had a direct effect on compositional dissimilarity, corroborating that even the low variation in temperature of the Amazon may affect the physiology of soil arthropods (Pequeno et al. 2020). Nevertheless, temperature's greatest effect was indirect, through NDVI (b indirect = $0.74 \times 0.36 = 0.27$ vs. b direct = 0.17), which had the strongest direct effect among environmental variables (Fig. 3). Relationships between temperature and primary productivity (which is incorporated in NDVI) are known to affect ant distribution (Kaspari et al. 2000; Kaspari et al. 2004). For instance, temperature limits primary productivity, and productivity limits the abundance of consumer taxa, cascading to higher trophic levels (Kaspari et al. 2004). Our results extend this idea by showing that the combination of temperature and NDVI are also important factors influencing ant beta diversity. Indeed, the total effect of temperature had the same magnitude as the strongest direct effect, attributed to geographic distance (i.e. sum of direct and indirect effects, b total = $0.74 \times 0.36 + 0.17 = 0.43$).

NDVI integrates vegetation structure, plant species composition and productivity in a single measure, and any of these features could contribute directly to ant species turnover. For instance, habitat complexity is known to structure ant communities by filtering species based on their morphology (Kaspari and Weiser 1999; Wiescher et al. 2012; Gibb and Parr 2013; Guilherme et al. 2019; Nooten et al. 2019). Therefore, dissimilarity in species composition can reflect differences in ant morphological composition, consistent with relationships between mean community traits and habitat complexity shown for ants in the same region (Guilherme et al. 2019). Given that our sampling sites covered different vegetation types (e.g. from open savannas to dense forests), NDVI may also reflect a change in plant species composition or plant-based structure provision (litter structure), which may affect some ground-dwelling ant species (Donoso et al. 2010). An interesting venue for research is to understand how these different facets of vegetation are related to NDVI measures, and which variable is more related with ant species turnover.

Contrary to our hypothesis, precipitation had no direct or indirect effect after accounting for other predictors. This result is surprising given the expected role of precipitation at local and regional scales. It is possible that precipitation interacts with topography and, thus, affects ant species composition mainly in lowlands, due to disturbance caused by water percolation (Oliveira et al. 2009; Baccaro et al. 2013), or unpredictable flooding (Mertl et al. 2009). Vasconcelos et al. (2010) noted a change in ant species composition along a longitudinal (rather than latitudinal) precipitation gradient (ranging from ~ 1600 to ~ 3100 mm) in the Amazon, with marked changes in precipitation between periodic flooded vs. unflooded

forests. In fact, flooding may have strong effect on ant taxonomic and functional diversity (Majer and Delabie 1994; Pringle et al. 2019). It is possible that the relatively narrow precipitation gradient (ranging between 1737 and 2449 mm), associated with the relatively few plots subject to flooding investigated here, may have lowered the relative importance of precipitation.

The independent effect of geographic distance on species dissimilarity is consistent with dispersal limitation. Although we predicted a mostly indirect effect via environmental predictors, the relatively strong direct effect reported here is in accordance with recent data on some invertebrates, including termites and ants (Dambros et al. 2017, 2020). The curvilinear relationship shows that the major difference in dissimilarity occurs along the first 200 kilometres, remaining approximately constant afterward. Although studies about the dispersal distance of ants are scant (Helms 2018) this pattern is expected from the average dispersal kernel of organisms, e.g. a fat-tailed distribution, where many individuals are dispersing over short distances and few individuals dispersing over long distances (Hubbell 2001). This dispersal kernel pattern may also be related to the colony founding process, where some species are more restricted to nearby locations (dependent founding or nest-budding). In contrast, other species may have the ability to fly over long distances (independent founding) (Keller and Passera 1989) or be carried over, e.g. by rafting through major rivers (see below). In both cases, finding a good habitat for a new colony foundation is an essential part of successful ant dispersal (Helms 2018; Hakala et al. 2019). It is possible that selection may negatively affect long distance dispersal through the correlation between geographic distance and temperature difference, albeit it was weak (Fig. 3). In contrast, the correlation between geographic distance and NDVI difference was negative, so that farther sites had more similar vegetation (Fig. 3), which could actually facilitate long distance dispersal.

The correlation between geographic and environmental distances may couple genetic isolation along these gradients, thus reinforcing population divergence and speciation over time (Wang and Bradburd 2014). Yet, our analysis revealed that the strongest effect of geographic distance on environmental distance related to temperature, which only had a weak direct effect on compositional dissimilarity (Fig. 3). However, the negative relationship between NDVI difference and geographic distance implies that farther sites should select similar phenotypes by having similar vegetation. Therefore, there may have been phenotypic convergence between the Amazon Basin's northern and southern borders over time, which is consistent with the trait-vegetation relationships observed for ants across the region (Guilherme et al. 2019).

The riverine barrier hypothesis has been an influential idea in Amazonian biogeography, with several studies investigating Amazonian rivers' effect on species distribution and diversification (Wallace 1854; Cracraft 1985; Ribas et al. 2012; Boubli et al. 2015; Oliveira et al. 2017). However, based on species distribution patterns, there is increasing evidence that the river barrier effect may have been overestimated and that other factors may be more important to many taxa, especially smaller-bodied arthropods (Dambros et al. 2017; Santorelli et al. 2018; Silva et al. 2019; Fluck et al. 2020; Dambros et al. 2020). More studies focused on the evolutionary process (Ribas et al. 2012; Boubli et al. 2015; Alfaro et al. 2015; Ruokolainen et al. 2019) are needed to properly address this hypothesis, as the number of

cryptic species among invertebrates is usually high (Ross et al. 2010; Rosser et al. 2019; Sánchez-Restrepo et al. 2020). Cryptic species can underestimate the role of riverine barriers, but only if morphologically indistinguishable species occupy opposite river banks (Fernandes et al. 2013). The Amazon River is the most ancient between current large Amazonian rivers (Ruokolainen et al. 2019) and, therefore, the most likely to have produced allopatric speciation. As the Amazon River had a weak effect upon ant beta diversity, other tributaries are unlikely to be effective obstacles to most ant species. Furthermore, some ant species have been recorded dispersing through rafting in dead wood or through wind currents (Yamane 2013). Therefore, large Amazonian rivers may function as corridors for long-distance dispersal rather than dispersal barriers, although other factors may hamper long-distance dispersal success (e.g. colony foundation).

This study suggests that ant species dissimilarity across Central Amazonia is driven by a balanced combination of dispersal limitation and environmental selection. By explicitly measuring direct and indirect effects, we were able to show that climate (temperature and precipitation) and one major riverine barrier had secondary roles relative to spatial distance and vegetation structure. The extent to which dispersal and selection has contributed not only to contemporary distribution patterns but also to ant speciation remains an open question. Our results suggest that the negative coupling between geographic distance and vegetation differences across central Amazonia have favoured phenotypic convergence between northernmost and southernmost ant faunas in the region.

Declarations

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ETHICS APPROVAL – Ethics approval was not required for this study according to local legislation [law 11.794/08.10.2008 from Conselho Nacional de Controle de Experimentação Animal of Brazilian Government].

CONSENT TO PARTICIPATE – All patients included in this study gave written informed consent to participate in this research.

CONSENT TO PUBLISH – All patients provided written informed consent to publish the data contained within this article.

AVAILABILITY OF DATA AND MATERIALS – The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

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Figures

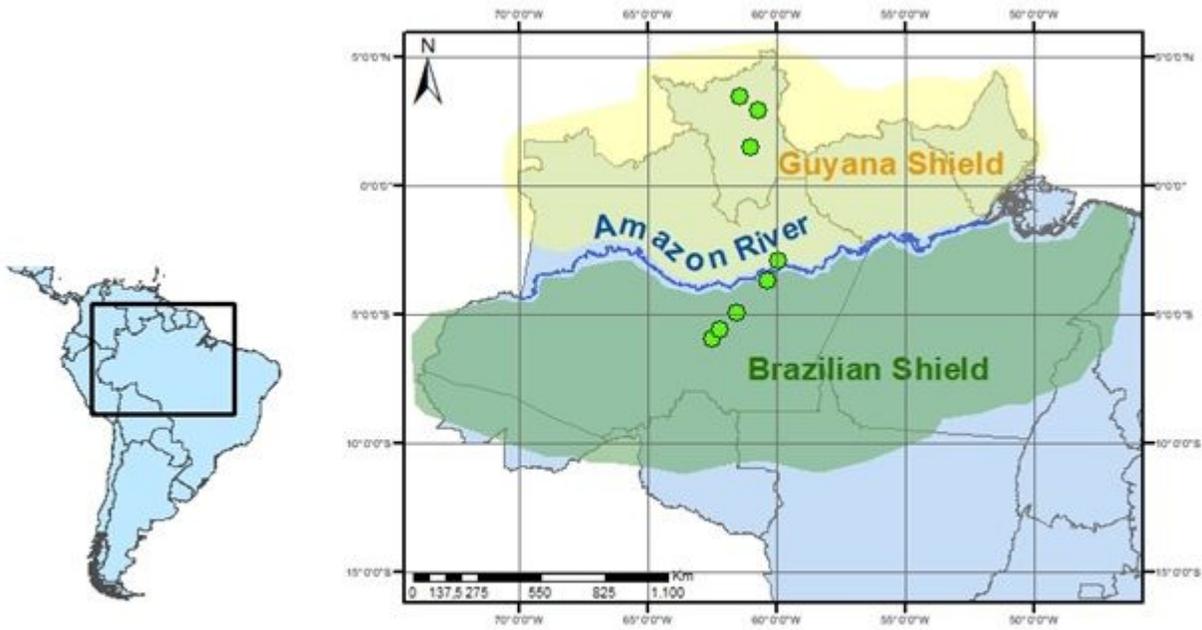


Figure 1

Map showing the location of collection points (green points) in the Brazilian Amazon Forest. The yellow colour shows the cover of Guyana Shield in Brazilian territory and green colour shows the cover of Brazilian Shield on map. The extension of the Amazon River along of study area it showed in blue transect.

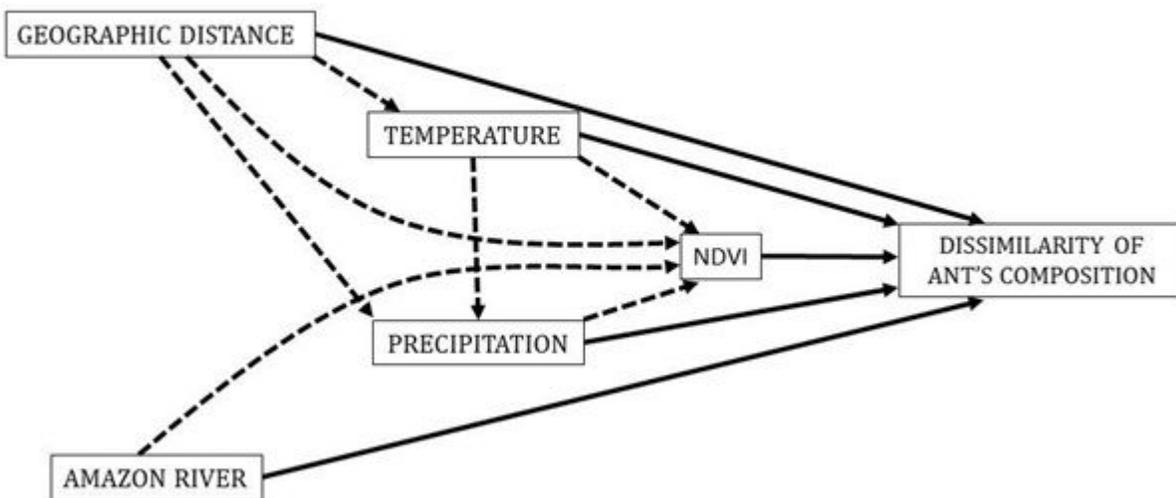


Figure 2

Path diagram including the hypothesized direct and indirect effects of the variables. Dashed and solid arrows indicate the indirect and direct effects respectively.

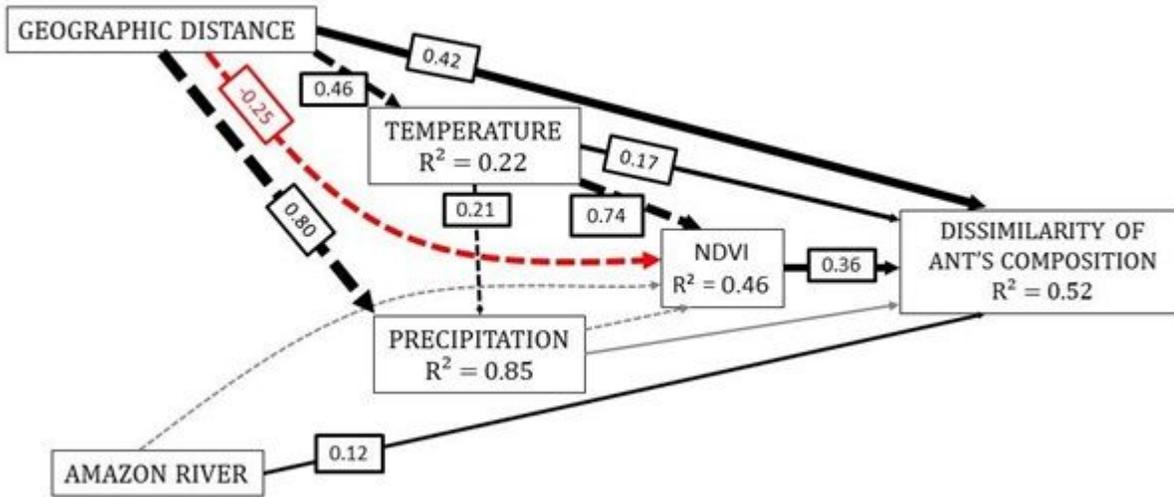


Figure 3

SEM results showing the direct and indirect effects of geography and environment on ant species dissimilarity across Central Amazonia. The R² correspond to models described in Table 1. Black and red arrows represent positive and negative significant effects, respectively. Grey arrows represent non-significant effects. Width is proportional to the magnitude of standardized coefficients.

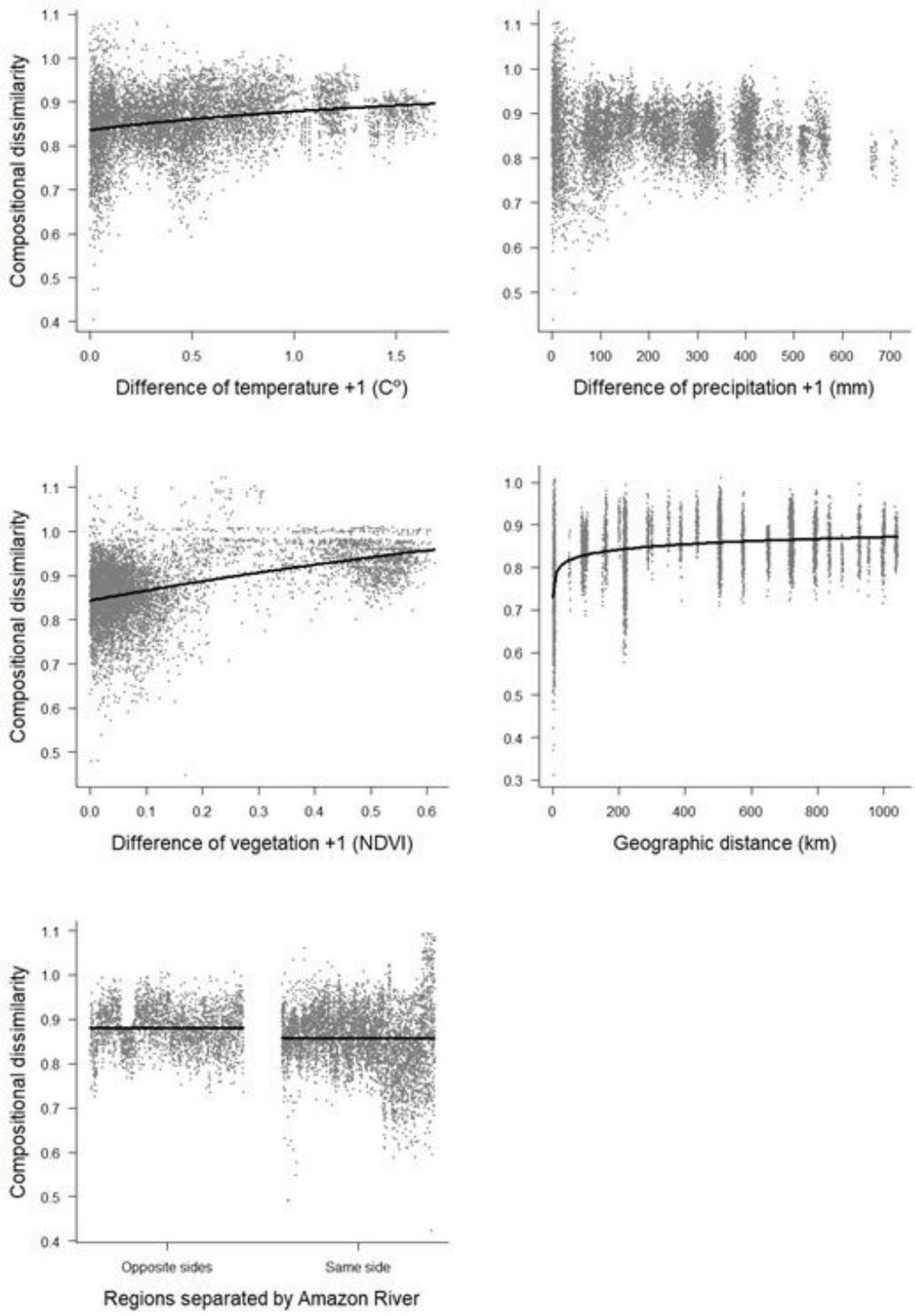


Figure 4

Partial regressions of ant compositional dissimilarity against direct predictors. The black line shows significant model fits. Each point is a comparison between a pair of plots. Vertical axes are partial residuals, so that plots show the expected effect of a variable when the other variables in the model are statistically held constant.

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