



# Direct and indirect effects of geographic and environmental factors on ant beta diversity across Amazon basin

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## Abstract

Understanding the direct and indirect effects of niche and neutral processes in structuring species diversity is particularly challenging because environmental factors are often geographically structured. Here, we used Structural Equation Modeling to quantify direct and indirect effects of geographic distance, the Amazon River's opposite margins, and environmental differences in temperature, precipitation, and vegetation density (Normalized Difference Vegetation Index—NDVI) on ant beta diversity (Jaccard's dissimilarity) across Amazon basin. We used a comprehensive survey of ground-dwelling ant species from 126 plots distributed across eight sampling sites along a broad environmental gradient. We found that geographic distance and NDVI differences were the major direct predictors of ant composition dissimilarity. The major indirect effect was that of temperature through NDVI, whereas precipitation neither had direct or indirect detectable effects on beta diversity. Thus, ant compositional dissimilarity seems to be mainly driven by a combination of isolation by distance (through dispersal limitation) and selection imposed by vegetation density, and indirectly, by temperature. Our results suggest that neutral and niche processes have been similarly crucial in driving the current beta diversity patterns of Amazonian ground-dwelling ants.

**Keywords** Amazon River · Composition dissimilarity · Dispersal limitation · Invertebrates · Pitfall-traps

## Introduction

A key question in community ecology and biogeography is understanding the processes driving species distributions. Species distribution may result from (mis)matches

between their ecological requirements and the environment. Accordingly, habitat conditions and resource availability can often explain assemblage species composition (Cottenie 2005) albeit typically leaving much-unexplained variation (Soininen 2014). Assemblage composition can also be driven by neutral or niche-independent processes, such as dispersal ability (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 their relative contributions to beta diversity patterns remain controversial, especially because their importance can vary among taxa (Matthews and Whittaker 2014; Vellend 2016).

Environmental predictors are generally spatially structured, which results in important synergistic and indirect effects for the biota (Jiménez-Alfaro et al. 2016; Hurtado et al. 2019). For instance, climate directly affects vegetation density (Sun and Qin 2016), and both tend to diverge with increasing geographic distance across relatively large spatial

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extents. Therefore, geographic distance may directly affect species distribution, by dispersal limitation, and indirectly via correlation with environmental predictors, so that isolation by distance and by the environment may reinforce each other. Thus, accounting for the direct and indirect effects of geography and environment may help understand how different factors control species distributions.

One of the major drivers of species diversification in the Amazon are rivers (Wallace 1852; Cracraft 1985; Ribas et al. 2012; Boubli et al. 2015). Large Amazonian rivers are thought to work as geographical barriers that preclude vertebrate dispersal (Cracraft 1985). Large rivers may foster allopatric speciation for monkeys and understory birds, resulting in compositional dissimilarity among interfluves (Ribas et al. 2012; Boubli et al. 2015; Oliveira et al. 2017). On the other hand, environmental conditions seem to be more relevant than isolation caused by major rivers for some plant taxa (Dambros et al. 2020; Tuomisto et al. 2019). Currently, Amazonian biogeography is 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). Therefore, understanding if the current diversity distribution patterns apply to small-bodied invertebrates is critical to conservation planning and species distribution modeling of Amazonian biota.

Ants are highly diverse and abundant (Folgarait 1998; Baccaro et al. 2015) comprising more than 10% of the terrestrial animal biomass in tropical forests (Agosti et al. 2000). Rivers seem to be a more permeable barrier to ants than larger bodied animals (Dambros et al. 2020). Ants may cross rivers by dispersing both actively over the water and passively through the wind (Mlot et al. 2011; Yamane 2013; Hakala et al. 2019). Moreover, it is known that some environmental variables are essential in driving ant distribution at larger scales (Kaspari et al. 2000, 2004; Vasconcelos et al. 2010). For example, precipitation is correlated with ant species turnover (Vasconcelos et al. 2010), and vegetation density is strongly associated with both taxonomic and functional composition of ants (Wallis et al. 2017; Guilherme et al. 2019). Meanwhile, recent studies have revealed that isolation by distance is more important than environmental factors for invertebrate beta diversity, suggesting that dispersal limitation may have a more critical role in explaining ant species composition in Amazon forests (Dambros et al. 2017, 2020).

In the present study, we used Structural Equation Modeling to quantify the direct and indirect effects of geographic (geographic distance, margin of the Amazon River) and environmental factors (differences in temperature, precipitation and Normalized Difference Vegetation Index [NDVI], a measure of chlorophyll or vegetation density) on ground-dwelling ant beta diversity across a latitudinal gradient in

Amazon basin. Based on the literature, we built a path diagram to represent the causal relationships assumed to occur among predictor variables (Sun and Qin 2016; Lochbihler et al. 2017) and their direct and indirect effects upon ant composition dissimilarity (Lassau et al. 2005; Vasconcelos et al. 2010; Wepfer et al. 2016). We hypothesized a larger indirect effect of geographic distance on ant beta diversity due to its known correlation with climate and NDVI. Accordingly, given the high habitat heterogeneity across the studied area, ant beta diversity should be more strongly and directed shaped by environmental factors (i.e., differences in climate and NDVI) than by dispersal limitation (i.e., geographic distance and river margin).

## Materials 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 in the Brazilian Amazon Forest, covering the geographical extent of approximately 1050 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 mainly characterized as dense ombrophilous forest. However, it also includes other vegetation such as savannas and white-sand forests with a small area subject to flooding in the rainy season (IBGE 2012) (Table 1).

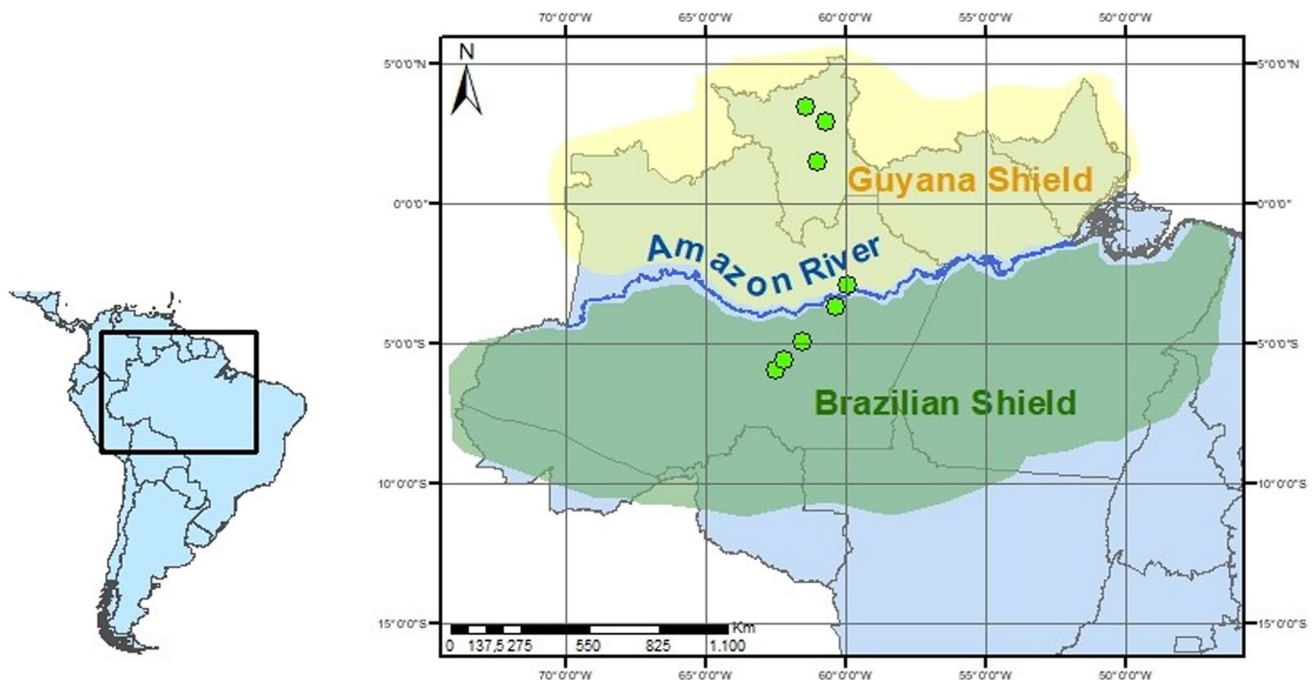
The sampled sites also cover a large variety of soil types (Quesada et al. 2011). Four sites are in the Guiana Shield, at the North of the Amazon River. This region has a greater predominance of Acrisols and Ferralsols. The other four sites are located at the South of the Amazon River, between the Purus and Madeira rivers. These sites have a predominance of Plinthosol 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 5 or 10 plots, totalizing 126 plots in the whole study area. Each grid has six parallel trails of 5 km located 1 km apart with

**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 of NDVI index	Average precipitation	Average temperature
Maracá	Longitude – 61.473 Latitude 3.396	Open ombrophilous forest, Semideciduous forest, Deciduous forest, Campinarana forest	0.44–0.62	1988 mm	26.74 °C
Cauamé	Longitude – 60.715 Latitude 2.883	Open savannah	0.05–0.18	1764 mm	27.98 °C
Virua	Longitude – 61.006 Latitude 1.441	Open ombrophilous 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 ombrophilous forest	0.57–0.66	2300 mm	26.47 °C
Manaquiri	Longitude – 60.308 Latitude – 3.673	Open ombrophilous forest	0.60–0.64	2218 mm	26.74 °C
Orquestra	Longitude – 61.555 Latitude – 4.994	Dense ombrophilous forest	0.56–0.60	2444 mm	26.91 °C
Capana	Longitude – 62.193 Latitude – 5.629	Dense ombrophilous forest	0.57–0.61	2184 mm	26.74 °C
Jari	Longitude – 62.504 Latitude – 5.953	Dense ombrophilous forest	0.59–0.61	2136 mm	26.57 °C

**Fig. 1** Map showing the location of collection points (green points) in the Brazilian Amazon Forest. The yellow color indicates the cover of the Guyana Shield in Brazilian territory and the green color shows

the cover of the Brazilian Shield on the map. The extension of the Amazon River along the study area is shown in the blue line

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). The plot's geographic position was measured with a GPS (Global Position System) using the reference

system 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. Voucher specimens were deposited at Instituto Nacional de Pesquisas da Amazônia—INPA's Invertebrate Collection.

## Environmental data

Climate information were retrieved from the bioclimatic variables of WorldClim version 2 (Fick and Hijmans 2017). We used average annual precipitation and temperature to represent major climatic gradients. Annual precipitation and temperature have important biological meanings, acting as predictors of available water and energy, respectively. Both are strongly correlated with other bioclimatic variables (Online Resource 1), 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 s (~ 1 km<sup>2</sup>).

Vegetation density was estimated using the NDVI (Petorelli et al. 2005; Wood et al. 2012; Wallis et al. 2017). NDVI is a remote-sensing measure of chlorophyll density and energy absorption (Myneni et al. 1995), which correlates with several factors that affect an ant's life, such as vegetation density, productivity and habitat structure (Kaspari et al. 2000; Bailey et al. 2004) and which may reflect habitat preferences of ant species to closed or open vegetation sites (Lassau 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 m<sup>2</sup>). One image was used to estimate NDVI for all plots of each sampling site, with the conditions that (1) the image had been obtained during the same month and year when the site had been actually sampled, and (2) had the smallest possible cloud coverage to avoid 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 ( $\beta_{jac}$ ) into its turnover ( $\beta_{jtu}$ ) and nestedness components ( $\beta_{jne}$ ) (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 a confirmatory analysis using Structural Equation Modeling (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).

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

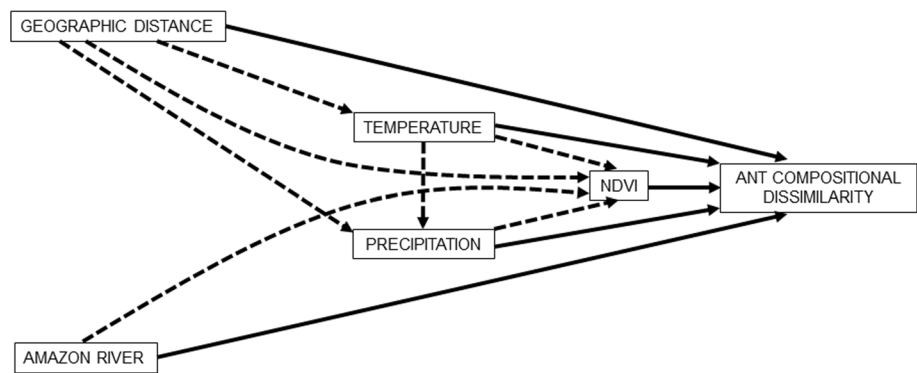
**Table 2** Linear models used to build the structural equation model of ant beta diversity

Models of hypothetical causal relationships in the path diagram												References
1	Ants	~	AR	+	GD	+	TD	+	PD	+	NDVI	Wepfer et al. (2016); Lassau et al. (2005)
2	NDVI	~	AR	+	GD	+	TD	+	PD			Sun and Qin (2016)
3	PD	~	TD	+	GD							Lochbihler et al. (2017)
4	TD	~	GD									Almeida et al. (2017)

All predictors were log-transformed (and summed to 1 as required to handle zeroes), except for the Amazon Riverbank

AR Amazon River, GD geographic distance, TD temperature difference, PD precipitation difference, NDVI NDVI difference

**Fig. 2** Path diagram of hypothesized direct and indirect effects ant beta diversity. Solid arrows indicate direct effects of one predictor on compositional dissimilarity, and dashed arrows indicate the direct effect of one predictor upon another predictor that may result in an indirect effect



and riverbank on dissimilarity through their putative effects on NDVI (Fig. 2). All predictors except riverbank were log-transformed (and summed to 1 as required to handle zeroes) to account for curvilinear relationships, and predictor effects were tested with permutation tests (999 permutations). MRM employs permutation tests to obtain  $P$  value due to non-independence among distances from the same site to other different sites. These tests do not require the assumption that the data are sampled from a specified probability distribution (Gotelli and Ellison 2004), although the residual distribution of compositional dissimilarity clearly approximates normality (Online Resource 1, Fig. S1).

To estimate the indirect effect of one predictor, we multiplied the coefficients along a given path in the path diagram. In contrast, a predictor's total effect (combined direct and indirect effects) was estimated by summing all coefficients along direct and indirect paths (Shipley 2016). To test the overall structural model fit, we used 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. Contrary to most tests, a non-significant  $P$  value ( $P > 0.05$ ) indicates a good model fit, indicating consistency between observed data and the hypothesized model (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 Burdett 2017), “adespatial” (Dray et al. 2021), “ade4” (Dray and Dufour 2007) and “betapart” (Baselga et al. 2020).

## Results

Over the 126 plots, we sampled 326 species/morphospecies of ants. The number of the ground-dwelling 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).

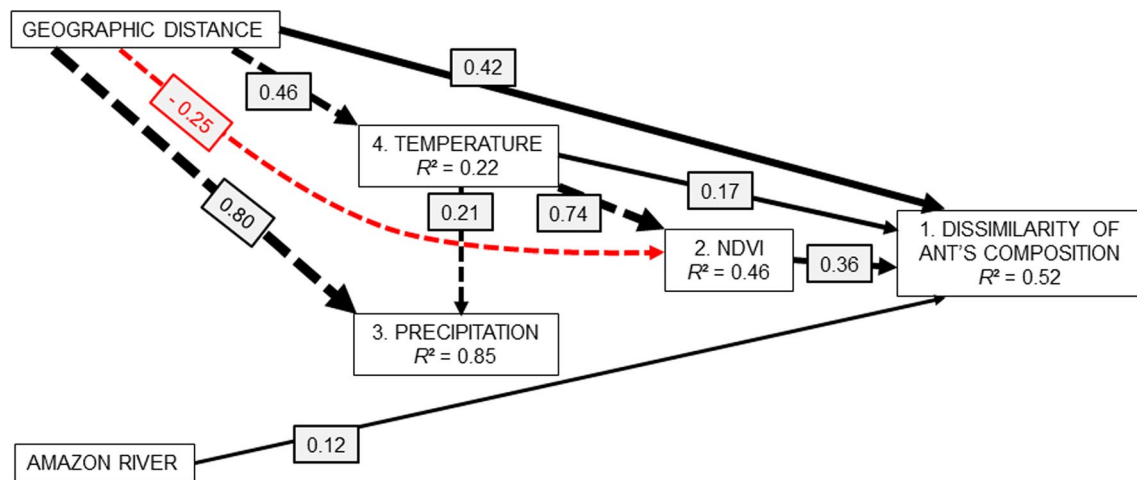
Our sampling plots encompassed natural open (“savanna-like”) areas, open forests and dense forests covering the large environmental heterogeneity typical of the Amazon basin. While the study area had relatively little variation in temperature (minimum = 26.35 °C; maximum = 28.04 °C; coefficient of variation = 1.63), variation in annual precipitation (minimum = 1737 mm; maximum = 2449 mm; coefficient of variation = 9.39) and NDVI (index minimum = 0.05; maximum = 0.66; coefficient of variation = 27.76) were greater.

The SEM showed that the hypothesized relationships between geography, environmental variables, and ant compositional dissimilarity provided a consistent data description (Fisher's  $C$  test = 2.30,  $P = 0.32$ ). The standardized coefficients indicated that geographic distance indirectly affected the ants mainly through NDVI and temperature, and its direct effect upon ant composition dissimilarity was slightly greater than that of NDVI and stronger than the other direct effects (Fig. 3). Temperature had an indirect effect on ant composition through NDVI, with NDVI showing a higher direct effect on ant beta diversity compared with climatic predictors (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 direct effects 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 a geographic barrier) and environmental selection (NDVI and temperature). Ant beta diversity was more strongly related to geographic distance and environmental variables than to a major geographic barrier (the Amazon River). This finding follows recent studies showing a limited role of large rivers in shaping Amazonian species distributions (Dambros et al. 2017,





**Fig. 3** SEM results showing the direct and indirect effects, on ant species dissimilarity across Amazon basin.  $R^2$  corresponds to models described in Table 2. Black and red arrows represent positive and

negative significant effects, respectively. Arrow width is proportional to the magnitude of standardized coefficients

2020; Santorelli et al. 2018; Fluck et al. 2020; Nazareno et al. 2021) and partially supports our hypothesis that selection along environmental gradients is the primary driver of biogeographic patterns for smaller-bodied animals such as ants. However, the results showed that geographic distance had a relatively robust and direct effect on ant dissimilarity, suggesting that neutral processes may be equally relevant to the ground-dwelling Amazonian ant species distribution.

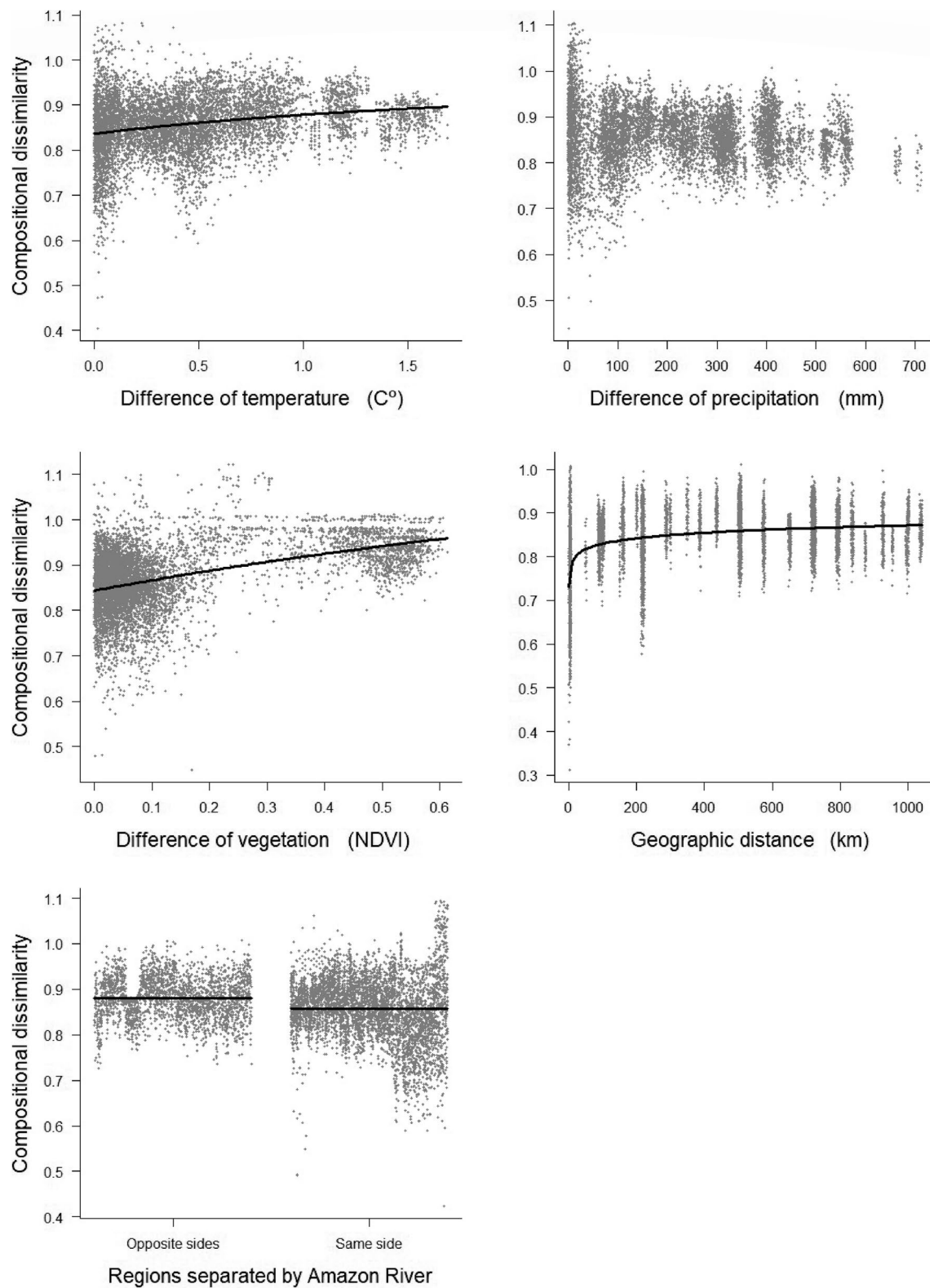
We hypothesized that climate would affect directly and strongly ant species dissimilarity. Temperature affects ant thermoregulation, shaping thermal niches (Cerdá et al. 1998; Cerdá and Retana 2000; Kaspari et al. 2019) and is related to species richness globally (Dunn et al. 2009). Indeed, we found that temperature directly affected compositional dissimilarity, corroborating that even the low variation in mean annual temperature among the Amazon forests sampled may affect the physiology of ectothermic animals such as 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 ( $b$  direct =  $0.36$ ) (Fig. 3). Relationships between temperature and vegetation productivity (which is correlated with NDVI) are known to affect ant species richness (Kaspari et al. 2000, 2004). For instance, temperature limits primary productivity, and productivity limits the abundance of consumer taxa, cascading to higher trophic levels (Kaspari et al. 2000). Indeed, the total effect of temperature had the same magnitude as the strongest direct effect, attributed to geographic distance (i.e., the sum of direct and indirect effects,  $b$  total =  $0.36 + 0.17 = 0.43$ ).

NDVI was the environmental variable most directly related to differences in ant beta diversity. The vegetation

density gradient, estimated by NDVI, is related both to physical characteristics of the habitat (Wood et al. 2012) and resource availability (Pettorelli et al. 2005). Open areas are less humid and have less available resources, and therefore, may harbor more thermophiles (Cerdá et al. 1998) and/or species with different diets (Schofield et al. 2016). In addition, it is known that vegetation density can filter species based on their morphology (Kaspari and Weiser 1999; Gibb and Parr 2013; Schofield et al. 2016), since that morphology is also associated with feeding and foraging habitat (Guilherme et al. 2019). Our results corroborate that species ecological preferences are related to variation in vegetation density, with different communities occurring in a particular band of the vegetation gradient.

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. Locally, 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; Holanda et al. 2021). Regionally, the ant species composition changed along a longitudinal precipitation gradient (ranging from ~1600 to ~3100 mm) in the Amazon, with marked differences in precipitation between periodic flooded vs. unflooded forests (Vasconcelos et al. 2010). Our results suggest that the relative importance of rainfall may be smaller for ant assemblages in unflooded forests (122 out of 126 plots are in unflooded forests) and distributed along a less variable precipitation gradient, such as the study area investigated here.

The effect of geographic distance on species dissimilarity is consistent with the dispersal limitation hypothesis.



**Fig. 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

Although we predicted a mostly indirect outcome via environmental predictors, the relatively strong direct effect reported here is in accordance with recent data for some invertebrates, including termites and ants (Dambros et al. 2017, 2020). The curvilinear relationship shows that the major compositional difference occurs along the first 200 km, with compositional dissimilarity 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 disperse 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, others species may have the ability to fly over long distances (independent founding) (Keller and Passera 1989). Geographic distance may also account for unmeasured, spatially structured environmental variables (Landeiro and Magnusson 2011). In both cases, finding a suitable habitat for colony foundation is essential for successful ant dispersal (Helms 2018; Hakala et al. 2019). Thus, the environmental conditions close to the colony founded previously may influence the structured pattern of ant distribution.

The negative relationship between NDVI and geographic distance implies that farther sites have similar vegetation. This pattern is in accordance with our sampling design, given that open and white-sand forests are more concentrated in the extremes of our sampling gradient. Indeed, Guilherme et al. (2019) noted in the same region that there is an association between the average morphology of ant communities and vegetation density. Thus, our results corroborate that the negative coupling between geographic distance and NDVI differences across Amazon basin has favored phenotypic convergence between the region's Northernmost and Southernmost ant faunas.

The riverine barrier hypothesis is one of the major hypotheses in Amazonian biogeography (Wallace 1852; Cracraft 1985; Ribas et al. 2012; Boubli et al. 2015; Oliveira et al. 2017). 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 less likely to be effective obstacles to most ant species. The relatively little effect of the Amazon river on ant beta diversity is in line with recent studies based on species distribution data (Dambros et al. 2017, 2020; Santorelli et al. 2018; Silva et al. 2019; Fluck et al. 2020). Some ant species have been recorded dispersing through

rafting in deadwood or through wind currents (Yamane 2013) and, as recently shown for plants (Nazareno et al. 2021), maybe using rivers as corridors for long-distance dispersal. However, cryptic species can underestimate the role of riverine barriers if morphologically indistinguishable species occupy opposite river banks (Fernandes et al. 2013; Maximiano et al. 2020). Given that the number of cryptic species among invertebrates is usually high (Ross et al. 2010; Rosser et al. 2019; Sánchez-Restrepo et al. 2020), more studies focused on the evolutionary process (e.g., Ribas et al. 2012; Boubli et al. 2015; Alfaro et al. 2015) may help to understand better the role of rivers on Amazonian ant species distribution and diversification.

Overall, our results suggest that ant species dissimilarity across Amazon basin 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 geographical distance and vegetation density to predict ant species dissimilarity. However, the extent to which dispersal and selection have contributed not only to contemporary distribution patterns but also to ant speciation remains an open question.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00442-021-05083-7>.

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**Author contribution statement** DRG, PACLP, FBB, and EF conceived the idea. FBB, JLPS, and CRSN collected the data. DRG, FBB and PACLP analyzed the data and DRG wrote the article with substantial collaboration from all the authors.

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**Data availability** The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

**Code availability** The custom code used in analysis during the current study is available from the corresponding author on reasonable request.



## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical 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 the Brazilian Government].

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