

Mountain passes are higher at low latitudes for madicolous insect communities of the Neotropical region

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Funding information

Fundação de Amparo à Pesquisa do Estado de São Paulo, Grant/Award Number: 2018/11068-9 and 2020/01762-5

Editor: Sabine Rumpf

Abstract

Aim: To test whether spatial turnover patterns of mountain madicolous insect communities in the Southern Hemisphere support the ‘mountain passes are higher in the Tropic’ hypothesis (MPHT). To do this, we compared madicolous communities in the Amazon Mountains (equator) and the Atlantic Forest Mountains (23°S).

Location: Brazil.

Methods: We characterized madicolous insect communities in two elevational gradients between 90 to 3000 m a.s.l. separated by 23° of latitude, totalling 108 sampling sites. Since the MPHT predicts a more intense turnover along elevational gradients at lower latitudes than at higher latitudes, we evaluated beta diversity in the Amazon mountains, at the equator, and in the Atlantic Forest mountains, in the subtropical region. We quantified multiple-site abundance-based dissimilarity to assess whether beta diversity was different between both regions. We also performed constrained ordination (db-RDA) analyses to assess whether community dissimilarity (balanced variation in abundances) was uniquely or jointly explained by environmental, spatial and/or elevational predictors. Additionally, we independently assessed the relationship between community dissimilarity and altitudinal difference in each region and tested for differences in model parameters between regions.

Results: Although we found high species turnover in both regions, the community variation explained by environmental factors and altitude was higher in the Amazon than in the Atlantic Forest, as evidenced by db-RDA and altitudinal difference models. In general, communities were remarkably constrained by spatial predictors, which result from low dispersion capacity of most madicolous insects and low connectivity of madicolous systems. Consequently, the composition of madicolous insects notably diverged between regions, highlighting the complementarity and high conservation value of both systems.

Main Conclusions: Our results indicate that the MPHT explains, at the community level, the differences between low- and high-latitude mountain systems in community turnover along elevational gradients, even within a relatively short latitudinal distance in the Southern Hemisphere.

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KEYWORDS

altitude, Amazon, aquatic insects, Atlantic Rainforest, Tropical region, turnover

1 | INTRODUCTION

The idea that 'mountain passes are higher in the Tropics' (MPHT), raised by Janzen (1967), is considered one of the main outcomes of the Climate Variability Hypothesis (Dobzhansky, 1950; Stevens, 1989; Stevens, 1992). Janzen's hypothesis states that, because tropical species experience less climatic oscillations compared with temperate species, and because the temperature overlap between low- and high-elevation sites is minimal in tropical mountains, elevational gradients would result in more effective barriers for species dispersal in the tropics than in temperate zones (Ghalambor et al., 2006; Gill et al., 2016; Janzen, 1967; Polato et al., 2018). In other words, climatic variation along elevational gradients rather than mountain sizes would determine the ranges of mountain species, selecting for organisms with narrow thermal tolerances and limited dispersal ability in the tropics (Janzen, 1967). At the community level, this would translate into more marked community turnover along elevational gradients at lower latitudes than at higher latitudes.

More than 50 years after Janzen's publication, the MPHT hypothesis is still being widely tested and discussed, emphasizing its great importance for our knowledge on montane biodiversity (e.g. Gill et al., 2016; McCain, 2009; Polato et al., 2018; Shah et al., 2017). However, most of these studies, including Janzen's original publication, attempt to compare northern-temperate versus tropical regions, while there is little evidence of whether the same contrast can be observed between low-latitude and high-latitude communities in the Southern Hemisphere. Although Janzen has stated that the central idea of his hypothesis would apply to other regions, the climatic variation resulting from seasonality is generally less intense in the Southern Hemisphere, mainly due to the strong oceanic influence (Chown et al., 2004). Thus, selection for wider niches at higher latitudes should be weaker in the Southern Hemisphere, which would reduce the contrast between low-latitude and high-latitude community turnover along elevational gradients. Besides that, comparisons between regions often consider large latitudinal differences (frequently higher than 40°) (e.g. Gill et al., 2016; Janzen, 1967; Polato et al., 2018), and it is still unknown if smaller latitudinal extents would allow observing the same patterns.

In this study, we aim to assess whether the contrast in elevational gradients of community turnover predicted by the MPHT hypothesis can be observed between two Neotropical mountain ranges, one situated in the Atlantic Forest (23°S) and the other in the Amazon Forest (equator). Beta diversity analyses represent an important tool to test the MPHT hypothesis as communities at low-latitude mountains are expected to show a higher turnover of species along elevational gradients compared with those at higher latitudes. This can only be properly measured by disentangling the contribution of spatial turnover (i.e. species replacement) and nestedness patterns to overall

community dissimilarity (Baselga, 2010, 2013, 2017). The MPHT hypothesis predicts a latitudinal contrast in the width of species ranges, which should be observable in the rate at which species are replaced along the altitudinal gradient (spatial turnover). In contrast, nestedness patterns would imply that some species have wide altitudinal ranges while others have increasingly narrow ones. These nested patterns are also expected in altitudinal gradients and would impact beta diversity and broad-sense measures of dissimilarity (Baselga, 2010; Koleff et al., 2003). Thus, using a broad-sense index of dissimilarity affected by both patterns (i.e. species turnover and nestedness) would make it impossible to accurately test the MPHT hypothesis. Once we have measured the turnover component, multivariate analyses of beta diversity can be used to discriminate the role of different predictors on communities' composition, as it has been previously shown for other communities of aquatic invertebrates in mountainous ecosystems (e.g. Al-Shami et al., 2013; Callisto et al., 2021; Castro et al., 2019; González-Trujillo et al., 2020; Jiang et al., 2021; Wang et al., 2012).

In South America, wide mountain ranges are interspersed among vast territories of tropical forest, for example in the Atlantic Forest and in the Amazon. Both are among the most biodiverse forests in the world (Myers et al., 2000). However, the current taxonomic knowledge of these megadiverse tropical ecosystems is still scarce (the so-called Linnean shortfall, Lomolino, 2004; Whittaker et al., 2005). Indeed, about 86% of existing species are still unknown to science (Mora et al., 2011), and this gap of knowledge is mostly evident in tropical regions, where overlooked habitats can harbour a striking number of new species. An example of these is the madicolous habitat (also called hydropetric habitat, Thienemann, 1905), which can be described as a thin layer of water running over a substrate, most frequently rocky surfaces (Vaillant, 1955). These trickles of water can be originated by outcropping from rock slabs or formed at the splash zones marginal to streams or waterfalls. Despite its low complexity and small extension, madicolous ecosystems can harbour an outstanding diversity of insects, with many endemic and rare species most of them still waiting for formal description (Pivar et al., 2020; Shimabukuro & Trivinho-Strixino, 2018).

Madicolous ecosystems are frequently found in mountainous regions of tropical rain forests (Roque & Trivinho-Strixino, 2004; Shimabukuro et al., 2015; Silva et al., 2012; Trivinho-Strixino et al., 2012), what in addition to their reduced dimensions, make them idoneous systems to test hypotheses about the turnover of biological communities along elevational gradients. In the Atlantic Forest, richness patterns of the madicolous communities revealed a unimodal variation with altitude, with a larger number of species being found at intermediate elevations (Shimabukuro, 2021). However, species richness hides important aspects of diversity, such as differences in species identity or abundance among localities, which we address here to assess the MPHT hypothesis.

Following Janzen's hypothesis, if climatic variability experienced by taxa increases with distance from the equator, the Atlantic Forest mountains, which are at the transition zone between the tropical and the southern temperate region, should present different dissimilarity patterns compared with the Amazon mountains, located at the equator. Thus, we predict that:

1. Local communities along an elevational gradient at lower latitude (i.e. in the Amazon) will be more different from each other and, thus, the region will show higher biotic heterogeneity (or higher multiple-site dissimilarity) derived from species turnover than communities along a similar elevational gradient at higher latitude (i.e. in the Atlantic Forest).
2. Community turnover along the elevational gradient in the Amazon will also be more associated to altitude and environmental variables than in the Atlantic Forest.
3. The relationship between community turnover and altitudinal difference will be tighter and steeper in the Amazon than in the Atlantic Forest.
4. Amazon and Atlantic Forest communities will present markedly distinct compositions.

2 | METHODS

2.1 | Study area and field survey

The study was carried out in two Neotropical biomes of high conservation interest, the Atlantic Forest and the Amazon. Sampling sites along mountain ranges were chosen to cover the full elevational range in each biome, from 0 to 2800 m.a.s.l. in the Atlantic Forest

and from 90 to 3000 m.a.s.l. in the Amazon (Figure 1). All sampling sites are located within protected reserves to minimize anthropogenic disturbance of the studied communities.

In the Atlantic Forest, the sampling sites were distributed in three slightly separated mountains to cover the full elevational range in the biome. The first, Corcovado Mountain (G1) ($23^{\circ}26'782''S/45^{\circ}11'567''W$), represents the lowest elevational gradient, with altitude ranging from 20 m.a.s.l. to 1100 m.a.s.l. The second, Pedra do Sino Mountain (G2) ($22^{\circ}27'707''S/43^{\circ}01'815''W$), represents the intermediate elevational gradient, with altitude ranging from 1200 to 2000 m.a.s.l. The third, Pedra da Mina Mountain (G3) ($22^{\circ}23'955''S/44^{\circ}50'991''W$), is the highest elevational gradient, ranging from 1700 to 2800 m.a.s.l. The region is defined as a humid subtropical zone, characterized by an oceanic climate, without dry season and with temperate to hot summer (Alvares et al., 2013). Additional information about the study area and sampling sites can be found in Shimabukuro, 2021.

In the Amazon, a single mountain range (G4), the Neblina Mountain, comprises the full elevational gradient in this biome, from 90 to 3000 m.a.s.l. This mountain belongs to the Guiana Highlands, one of the most ancient and pristine places in the world and with the highest elevations in South America, outside the Andean domain. The geological formation dates back from the Precambrian, about 2 billion years ago, putting this region in the spotlight for biogeographical studies in South America (Kok et al., 2018; Rull, 2019). Nonetheless, the geographic isolation and the overlapping with the indigenous territory, which involves complex authorization procedures, explain why few scientific investigations have been developed so far in the region (Hammond, 2005; Rull & Vegas-Vilarrúbia, 2008). The region is defined as a tropical zone without dry season (Alvares et al., 2013).

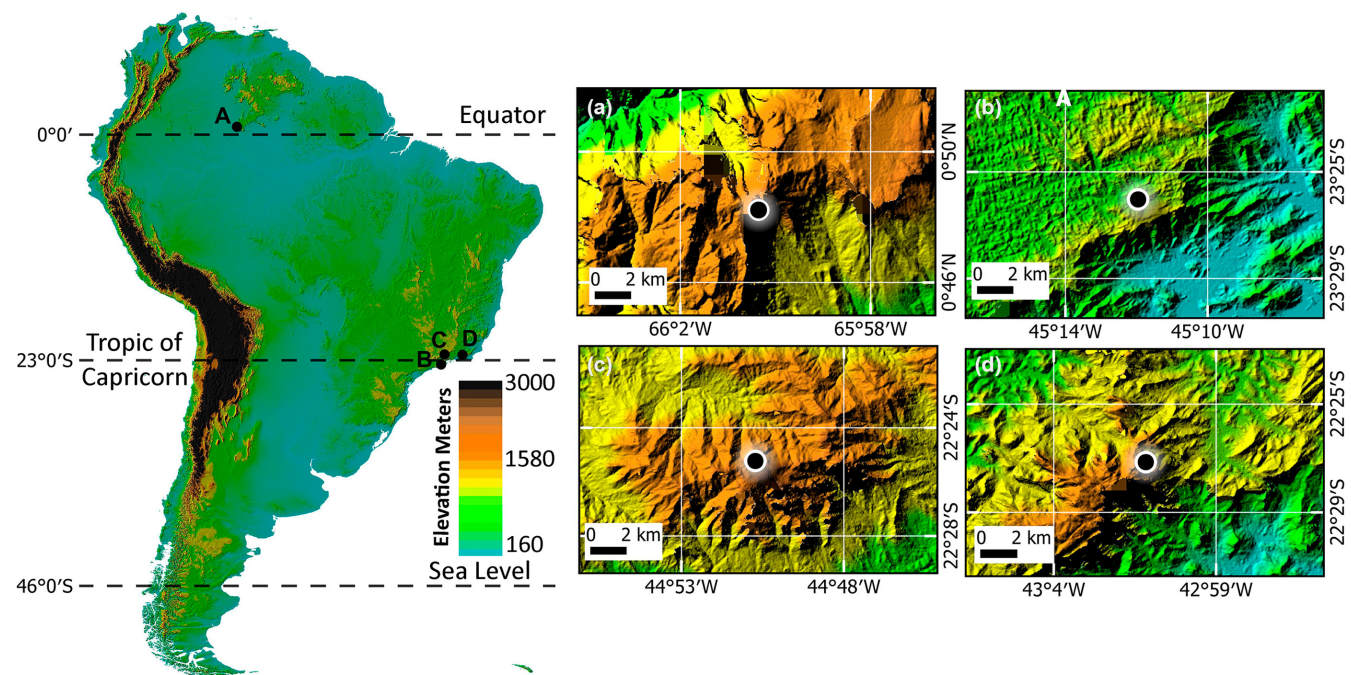


FIGURE 1 Location of the two studied elevational gradients in South America. (a) Amazon; (b–d) Atlantic Forest.

In the Atlantic Forest, we surveyed 73 sampling sites distributed in elevation intervals of 200–300 m in July–August 2013 and 2014. In the Amazon, we surveyed 36 sampling sites distributed in elevation intervals of 400 m, except at about 1200 m a.s.l., where we could not find madicolous habitats, in July–August 2019 (Figure 1). The number of sampling sites investigated at each elevation varied according to habitat's availability, ranging from two to nine (mean = 6.08 ± 2.64 [SD]) in the Atlantic Forest mountains and from three to eight (mean = 5.14 ± 1.57 [SD]) in the Amazon mountain. Sampling sites were distributed along stretches of about 30 m. The madicolous habitats analysed here were visually determined as those flowing over rocky substrates (Figure S1), with low depth (less than 1 cm), poor organic matter content, and without plants. At each sampling site, the communities of madicolous insects were sampled with two complementary methods to allow the detection of all development stages, and to facilitate identification at the species level. Adults were sampled with emergence traps (0.125 m² coverage area) installed above the madicolous habitats (Figure S1c). To increase the effectiveness of adult sampling, traps remained in the field for about 7 days (see Shimabukuro et al., 2015 for details on the trap mechanism). After trap removal, immatures were sampled with a hand net, 250 μ m-mesh, by washing the substrate in the area where the emergence traps had been installed. All individuals were sorted and identified in the laboratory to the lowest taxonomic resolution possible (genus, species or morphospecies), using stereomicroscope Zeiss Stemi 305 and optic microscopes Zeiss Axioskop 40 and Olympus BX40F-3, and specialized literature (Dominguez & Fernández, 2009; Hamada et al., 2014, 2018). Taxonomic resolution did not differ between localities, so that the proportion of identified genera/species was balanced in both regions. Individuals of all taxa were counted to estimate their abundance. All taxa were included in the analyses.

Water physicochemical parameters were also measured at each sampling site. Temperature, pH and dissolved oxygen were determined with an analytical kit (Alfakit®, Florianópolis, Brazil) and conductivity was measured with a portable conductometer CON300 (ION). Geographic coordinates and altitude of each sampling site were obtained in the field using a GPS (Garmin Etrex 10). Summary statistics of each abiotic variable are provided as maximum and minimum values in the Supplementary Material (Table S1). Additionally, we also conducted a Multivariate Analysis of Variance (MANOVA) to test for differences in physicochemical parameters between Amazon and Atlantic Forest sites (Table S2). The URL to the data that support these results can be accessed in the Appendix S1.

2.2 | Statistical analyses

2.2.1 | Assessment of multiple-site beta diversity

The variation in community composition (beta diversity) was assessed using the partitioning framework for abundance-based dissimilarity indices developed by Baselga (2013, 2017). Thus, abundance-based

dissimilarity was partitioned into two components: (i) balanced variation in abundance, when individuals of a species in one site are replaced by individuals of another species in the other site and (ii) abundance gradients, when individuals of a species are lost from site to site (Baselga, 2017). The use of such partitioning framework for abundance-based dissimilarity is essential to infer the processes that lead to assemblages' structure (Baselga, 2010, 2013, 2017).

To assess whether overall beta diversity was different between the Amazon and the Atlantic Forest, we used the partitioning framework for Bray-Curtis multiple-site dissimilarity index. Thus, we assessed the multiple-site abundance-based dissimilarity (β_{BC}), and its balanced variation (β_{BC-BAL}) and abundance gradient (β_{BC-GRA}) components (Baselga, 2017) in each region using the function 'beta.multi.abund' from betapart R package (Baselga et al., 2023; Baselga & Orme, 2012). Since the number of sampling sites differed between regions ($n=73$ in the Atlantic Forest, vs. $n=36$ in the Amazon), a resampling procedure (1000 random samples) was applied to compare multiple-site dissimilarity values obtained from random samples with the same number of sites in both regions. Moreover, to control for the elevational gradient, we implemented a stratified resampling method to ensure that such gradient was well represented in all resamples. To do so, we classified sampling sites into elevation categories (0–1000, 1000–2000 and 2000–3000 m a.s.l.) and randomly sampled four sites in each elevation category, with a total of 12 sites in each random sample. Multiple-site abundance-based dissimilarity was computed for each random sample. This procedure creates separate distributions of multiple-site dissimilarity for each region, thus allowing the empirical assessment of p-values for index (β_{BC} , β_{BC-BAL} and β_{BC-GRA}) comparison between regions. To assess the significance of one index being larger in one region than in the other, the probability of obtaining the opposite result by chance was empirically computed by comparing the estimated distributions of multiple-site dissimilarities.

2.2.2 | Abiotic correlates of community composition: Distance-based redundancy analysis (db-RDA)

First, we computed the pairwise abundance-based dissimilarity (Baselga, 2013) between all sampled sites within each region using the function 'beta.pair.abund' from betapart R package (Baselga et al., 2023; Baselga & Orme, 2012). Then, to assess the relationship between abiotic variables and community composition, we conducted a distance-based Redundancy Analysis (db-RDA, Legendre & Anderson, 1999) on the pairwise dissimilarity matrices of balanced variation in abundance (β_{bc-bal}), which is the abundance-based component that measures the substitution of individuals of one species by individuals of another species (analogous to the turnover component of incidence-based dissimilarity). The db-RDA was performed with the 'dbrda' function from vegan R package (Oksanen et al., 2019). Since altitude (the underlying factor to the MPHT hypothesis) is a proxy for other ecological

drivers that may change along the elevational gradient, we also included different sets of variables (environmental, spatial and altitudinal, see below) in the db-RDA analysis to have a more robust understanding of the factors driving the observed community dissimilarity. In db-RDA, a principal coordinates analysis is performed from the dissimilarity matrix. Then, the principal coordinates along with the explanatory variables are used to produce the redundancy analysis (Legendre & Anderson, 1999).

We followed a variation partitioning approach to assess the unique and shared contribution of different types of predictors in explaining the differences in community composition in the Amazon and the Atlantic Forest communities. Thus, predictors were classified into three sets and independent db-RDA analyses were computed for each set: 1. Environmental, including temperature, pH, conductivity and dissolved oxygen; 2. Spatial, including the quadratic polynomial for geographic coordinates (x , y , x^2 , $2xy$, y^2); 3. Altitude, which also included the quadratic function (alt^2). The quadratic functions were used to better describe the relationship between variables and the observed community dissimilarities because relationships may present a unimodal behaviour. Relevant variables within each set of predictors were selected using the function 'ordiR2step' from the vegan R package (Oksanen et al., 2019), which performs a forward model selection based on adjusted- R^2 and p -value. The variables selected by the 'ordiR2step' were included in the final models. Once the final model for each set of predictors was defined, we used the 'varpart' function from the vegan R package (Oksanen et al., 2019) to assess their unique and relative contribution.

2.2.3 | Relationship between community turnover and altitudinal differences

To assess the relationship between community turnover (β_{bc-bal}) and altitudinal difference, we fitted negative exponential models with community dissimilarity as dependent variable and altitudinal difference as predictor separately for the Amazon and the Atlantic Forest. These models were fitted using the 'decay.model' function in betapart R package, which implements the methods introduced in Gómez-Rodríguez and Baselga (2018) and Martínez-Santalla et al. (2022). Thereafter, we assessed whether any difference in model parameters (intercept and slope) between the Amazon and Atlantic Forest was significant using the function 'zdep' in betapart, which implements the methods introduced in Martín-Devasa et al. (2022).

2.2.4 | Differences between Amazon and Atlantic Forest communities

We used non-metric multidimensional scaling (NMDS), with the 'metaMDS' function from vegan (Oksanen et al., 2019), to visually represent the dissimilarity in community composition based on

the pairwise measure of balanced variation in abundance (β_{bc-bal} , Baselga, 2013) for both regions. To test if communities from Amazon and Atlantic Forest were significantly different, we complemented the NMDS with an ANOSIM analysis (Clarke, 1993) with 9999 permutations.

3 | RESULTS

A total of 12,462 individuals (about 70% immature stages), belonging to 356 taxa of madiculous insects, were identified in both mountain ranges. The most abundant orders were Diptera, Trichoptera, Coleoptera and Ephemeroptera, both in terms of species richness (47%, 17%, 14% and 12%, respectively) and abundance (72%, 14%, 6% and 4%, respectively). Less abundant orders were Odonata, Plecoptera, Hemiptera and Lepidoptera.

The multiple-site Bray-Curtis dissimilarity (i.e. overall abundance-based dissimilarity) was high and not significantly different between regions (average $\beta_{bc} = 0.94$ and 0.96 in the Amazon vs. the Atlantic Forest, $p = .075$). The partitioning of overall abundance-based dissimilarity showed that such high dissimilarity was largely driven by the balanced variation in abundance (average $\beta_{bc-bal} = 0.87$ and 0.90 in the Amazon vs. the Atlantic Forest, $p = .163$), while the contribution of abundance gradients was notably low (average $\beta_{bc-gra} = 0.07$ and 0.06 in the Amazon vs. the Atlantic Forest, $p = .310$).

The db-RDA analyses showed contrasting results between both mountain ranges (Figure 2), with a larger explained variation in the Amazon mountain ($R^2 = 0.59$; Adj- $R^2 = 0.50$; $p = .001$) than in the Atlantic Forest mountains ($R^2 = 0.37$; Adj- $R^2 = 0.29$; $p = .001$). In the most parsimonious models, the selected predictors were largely the same in both regions. Altitude, altitude², O₂, conductivity, pH, and the quadratic polynomial for geographical coordinates (y , x , y^2 , xy and x^2) were included in the Amazon while altitude², O₂, conductivity, temperature, and the quadratic polynomial for geographical coordinates, except for x^2 , were included in the Atlantic Forest models. Notably, community composition showed a linear relationship with altitude in the Amazon, while it was quadratic in the Atlantic Forest. In the Amazon region, the specific relationship between community composition and the selected spatial variables (x , y , y^2 , xy and x^2) are presented in Figure S2.

The ordination of communities based on the balanced variation in abundance was notably driven by spatial predictors in both regions (Figures 2a,b and 3a,b). The shared contribution between spatial and altitudinal predictors was relatively high and remarkably larger in the Amazon (Adj- $R^2 = 0.20$) than in the Atlantic Forest (Adj- $R^2 = 0.09$). Similarly, the contribution of environmental factors was larger in the Amazon than in the Atlantic Forest (Figure 3a,b), although such community variation was not uniquely explained by environmental predictors, but structured along spatial (Adj- $R^2 = 0.21$) or altitudinal (Adj- $R^2 = 0.09$) gradients. In the Atlantic Forest, the unique contribution of environmental factors (Adj- $R^2 = 0.07$) was similar to the one of spatial

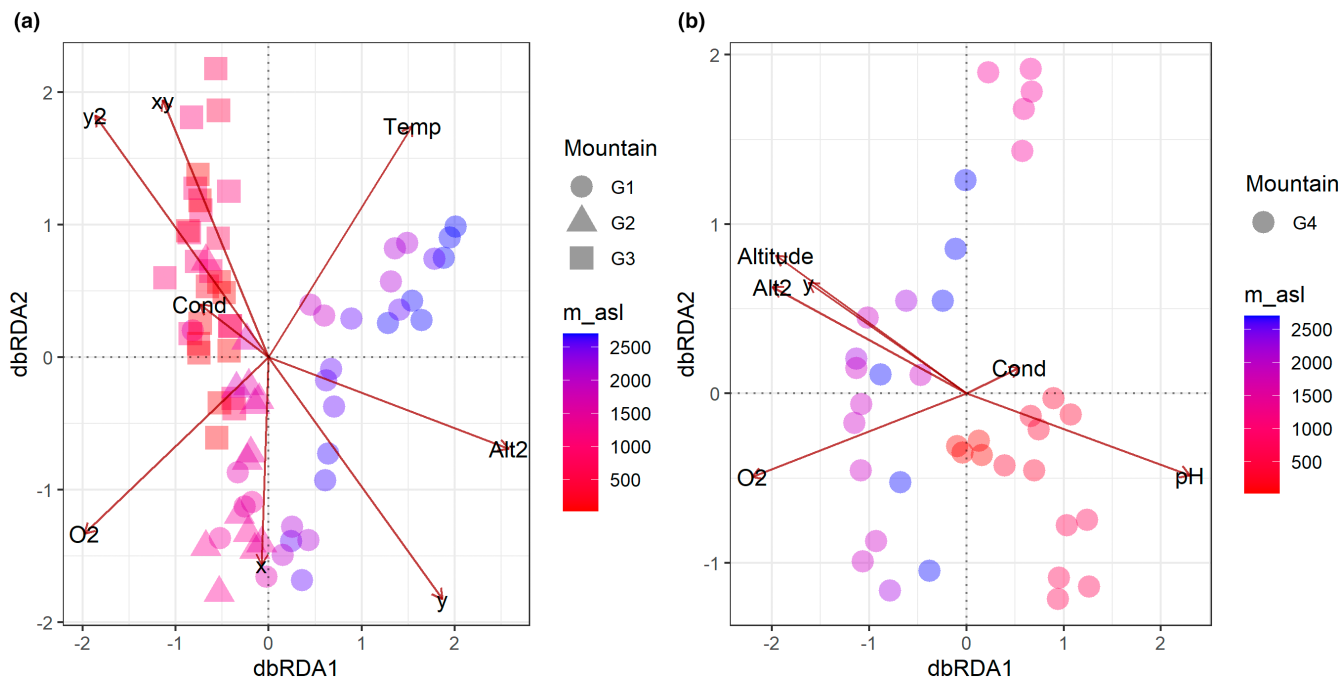
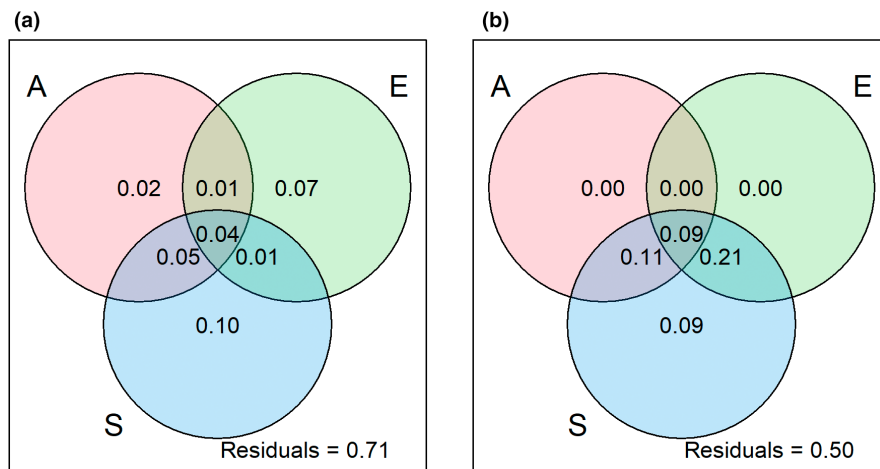


FIGURE 2 Distance-based redundancy analysis (db-RDA) showing the constrained ordination of madicolous communities based on balanced variation in abundance (β_{bc-bal}) in relation to environmental predictors (temperature, pH, conductivity and dissolved oxygen), altitudinal predictors (altitude and the quadratic function of altitude), and the spatial predictors (quadratic polynomial for geographic coordinates). (a) Atlantic Forest. (b) Amazon. Alt2, quadratic function of altitude; Cond, conductivity; O₂, dissolved oxygen; Temp, temperature; x, longitude; y, latitude. Variables not shown for the Amazon are presented as independent db-RDA for each predictor category (environment, spatial, altitude) (Figure S2a–c, in the Supplementary Material).

FIGURE 3 Variation partitioning showing the proportion of variation in community composition uniquely and jointly explained by environmental (E), spatial (S) and altitudinal (A) predictors. Community dissimilarity was measured as balanced variation in abundance (β_{bc-bal}). (a) Atlantic Forest. (b) Amazon.



predictors ($\text{Adj-R}^2=0.10$), and the unique contribution of altitude was small ($\text{Adj-R}^2=0.02$) (Figures 3b and 2a). We obtained similar results when considering the same set of variables in the db-RDA (Figure S3a–d).

The relationship between community dissimilarity (β_{bc-bal}) and altitudinal difference was significant in both regions (Figure 4), but the model explained more variation in the Amazon (pseudo- $r^2=0.31$, $p<.001$) than in the Atlantic Forest (pseudo- $r^2=0.12$, $p<.001$). Moreover, the rate at which community dissimilarity increases with altitudinal difference was significantly higher in the Amazon than in the Atlantic Forest ($b=0.0013$ vs. 0.0007 ; $z_{dep}=2.57$, $p=.010$). In

turn, the intercept was significantly lower in the Amazon than in the Atlantic Forest ($a=0.51$ vs. 0.73 ; $z_{dep}=-4.33$, $p<.001$).

The NMDS ordination evidenced that Atlantic and Amazon communities are markedly distinct (Figure 5), a fact that was statistically confirmed by an ANOSIM analysis ($R=0.561$; $p=.0001$).

4 | DISCUSSION

Turnover patterns of madicolous communities along elevational gradients support the ‘mountain passes are higher in the Tropic’

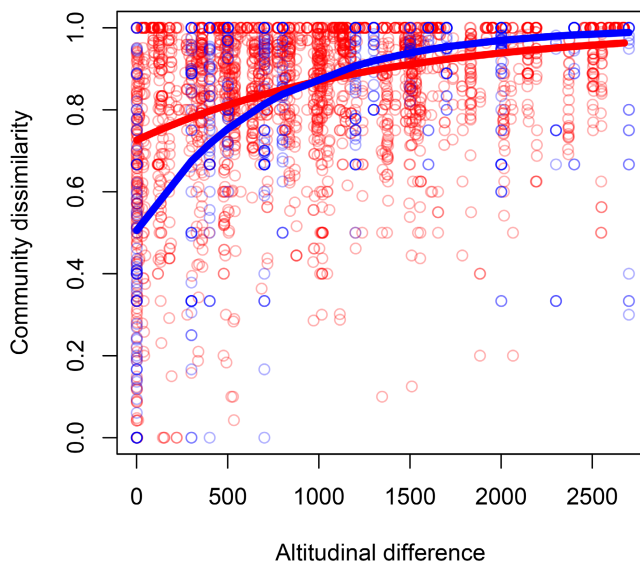


FIGURE 4 Relationship between community dissimilarity (β_{bc-bal}) and altitudinal difference in the Amazon (blue) and the Atlantic Forest (red). Curves represent the fitted negative exponential functions.

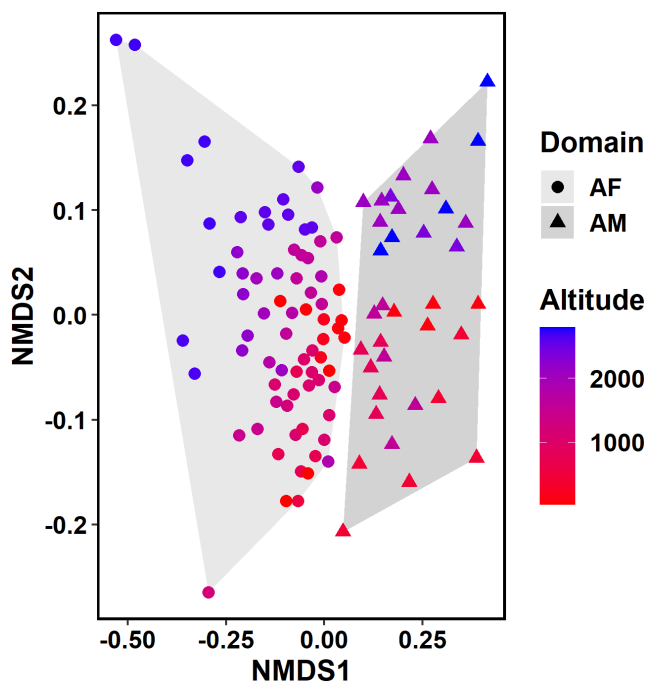


FIGURE 5 Non-metric multidimensional scaling (NMDS) of abundance-based dissimilarity (β_{bc-bal}) of madicolous communities in the mountains of the Atlantic Forest (AF) and Amazon (AM) biomes. The balanced variation in abundance of madicolous insect community was investigated in 109 sites distributed from the base to the summit. Elevation is represented as a colour gradient.

hypothesis (MPHT, Janzen, 1967). Remarkably, this prediction holds even at a relatively small latitudinal range in the Neotropical region. Our results reveal outstanding differences in the spatial structure of these aquatic communities not only at the larger scale

(i.e. marked differences in community composition between the Amazon and the Atlantic Forest mountains) but also at the smaller one (i.e. strong replacement of individuals of one species by individuals of another species within each region). We also have evidence that the factors driving these biodiversity patterns differed in each mountain range, with altitude and environmental predictors being more relevant in the Amazon than in the Atlantic Forest mountains. Taken altogether, these findings support the MPHT hypothesis as the spatial turnover of communities in the Amazon mountain is more related to environmental and elevational gradients, suggesting that species ranges are more constrained by the local conditions at lower latitudes than at higher latitudes. According to Janzen's hypothesis, climatic variation along elevational gradients represents an effective barrier for the dispersal of tropical organisms as they are adapted to thermal uniformity (Janzen, 1967). Here, we show that, despite the relatively short latitudinal distance between the Amazon and the Atlantic Forest (less than 25°), elevational gradients were indeed a more important driver of community turnover at the Amazon than at the Atlantic Forest mountains. This implies that, for a similar elevational gradient, more species reached their environmental limits and were replaced by others at lower latitudes than at higher latitudes.

Following Janzen's premises, climatic stability at low latitudes would result in stronger species turnover in community composition along elevational gradients, given that organisms are expected to have narrower thermal tolerances and hence be highly influenced by environmental variation along elevational gradients. Indeed, the climate at the lowlands of the Amazon is characterized by high and constant annual precipitation and mean temperature is higher than 26°C, in contrast to the climate in the Atlantic Forest, where temperature ranges are wider while mean temperature does not usually surpass 20°C (Alvares et al., 2013). In accordance with Janzen's hypothesis, our results show that environmental predictors and altitude explained community variation better in the Amazon mountain (explaining 30% and 20% of the variation, respectively) than in the Atlantic Forest mountains (explaining 13% and 12%, respectively).

Spatial predictors also contributed to explaining a large fraction of the variation in community composition in both regions. This is likely associated to the characteristics of these aquatic systems as well as the limited dispersal ability of madicolous insects (Poff et al., 2006). In general, aquatic insects from lotic ecosystems can both actively (e.g. through drift, upstream movement or adult's flight, Petersen et al., 2004) and passively disperse (e.g. within mosses transported by the wind (Bitušik et al., 2017) or birds (Green and Sánchez, 2006)). However, madicolous species are expected to be weak dispersers given that dispersal is limited to the adults' flight. Moreover, madicolous habitats are structurally simple and lack connectivity, thus limiting the probability of migration from one habitat to another, as it occurs in other isolated waterbodies, such as headwater streams, which present high beta diversity (Sarremejane et al., 2017). Similar biodiversity patterns, with spatial variables being correlated to community dissimilarity,

have been reported for other dispersal-limited taxa in the Atlantic Forest, such as rodents and marsupials (Dambros et al., 2022; Varzinczak et al., 2019). Thus, our results suggest that habitat connectivity and dispersal ability also influence community assembly in these systems.

Another key prediction of the MPHT is an increase of community dissimilarity with altitude difference, and the rate of that increase should be higher at lower latitudes. While we observe that community dissimilarity increases with altitude difference in both regions, the relationship is tighter and steeper in the Amazon than in the Atlantic Forest, as expected. Taking into account that both regions show high multiple-site dissimilarity in community composition, these findings indicate that madicolous communities can also present high turnover of species at higher latitudes and this would be driven by factors not exclusively related to the climate variability hypothesis. When Janzen first proposed the MPHT hypothesis, he did it based on data from the United States and Costa Rica, respectively, at latitudes 40°N and 10°N. Similarly, studies that later confirmed this pattern attempted to compare the tropical and the northern temperate region (Gill et al., 2016; McCain, 2009; Polato et al., 2018; Shah et al., 2017). Our results evidence that the predictions of the MPHT also hold for mountain ranges in the Southern Hemisphere, even at a relatively small latitudinal range. However, given the high community dissimilarity observed in the region at the highest latitude, we should also consider that the MPHT can result in weaker patterns in the Southern Hemisphere than in the Northern Hemisphere.

Climatic variation seems to be more pronounced in the Northern Hemisphere, due to lower winter temperatures, which are buffered in the South Hemisphere by the ocean proximity (Chown et al., 2004; Montaña-Centellas et al., 2021). We found that differences in community composition in the Atlantic Forest were partly driven by spatial predictors, with longitude having a significant contribution to the most parsimonious model. The coastal position of the Atlantic Forest results in an environmental gradient from east to west, suggesting that proximity to the ocean can influence the variation in community composition in that region. Even though the studied communities in the Atlantic Forest mountains are not directly influenced by seawater, we believe that sites closer to the coast are more prone to suffer from oceanic influence, such as higher annual rainfall (Oliveira-Filho & Fontes, 2000) and/or deposition of dissolved or particulate matter brought by wind (Padial et al., 2021). This is especially important for the studied communities at low to intermediate elevations, which are geographically closer to the sea. Nevertheless, most of the variation in community composition in the Atlantic Forest communities could not be explained by the predictors we considered, so further investigation is needed to reveal the drivers of community dissimilarity in this mountain range.

The complex past events that occurred in South America may have also contributed to the observed patterns of community dissimilarity. For example, climatic instability in the eastern part of the continent during the interglacial–glacial periods led to the fragmentation of suitable habitats and isolation of populations

(Carnaval et al., 2009; Haffer, 1969; Leite et al., 2016; Rahbek et al., 2019), and has been used to explain the narrow geographic ranges in other taxonomic groups in the Atlantic Forest mountains (Santos et al., 2020; Thomé et al., 2020). These climatic events were also responsible for past connections between the Amazon and the Atlantic Forest, as evidenced in many biogeographic studies (Costa, 2003; Batalha-Filho et al., 2013; Ledo & Colli, 2017). In spite of this, we found that the Atlantic Forest and the Amazon mountains currently share few madicolous species, since the taxonomic composition notably diverged between both regions. As evidenced by the ephemeropteran genus *Massartella*, the geoclimatic events that occurred after the last connection between both regions were responsible for subsequent diversification processes that separated lineages from the Amazon and the Atlantic Forest (Gatti et al., 2022). Additionally, regarding the high dependence of madicolous insects on humid substrates, the existence of a vast territory of dryland and sparse vegetation between both rain forests (Oliveira-Filho & Ratter, 1995) may act as a barrier to the current dispersal of the species.

Our results indicate that the structure of the madicolous insects' communities in two relatively close Neotropical mountain ranges can be explained in light of the Climatic Variability Hypothesis. Environmental and altitudinal predictors had a larger contribution to variation in community composition at the low-latitude mountain range than at the high-latitude one. Although we found high community dissimilarity in the Atlantic Forest, this might result from factors not directly related to the climatic-physiological predictions derived from the MPHT Jansen's hypothesis because altitude and environmental conditions were poor correlates of community turnover in these mountains. We also found that madicolous communities were highly spatially restricted, being probably limited by weak short and long-distance dispersal due to the low connectivity among madicolous habitats and the low dispersal ability of most species. These findings highlight the conservation value of tropical mountain ecosystems, since the limited distribution of these taxa makes them severely vulnerable to habitat change and global warming. Considering that the average global temperature will increase and that temperature and rainfall will be less constant in the short term (Garcia et al., 2014), understanding the relationship between biotic communities and the environment is urgently needed. Furthermore, the Amazon and the Atlantic Forest are among the most diverse biomes in the world, harbouring a megadiverse fauna and flora (Mittermeier et al., 2005; Myers et al., 2000) and yet most of this diversity remains unexplored. Our results provide further support to the high conservation value of mountain communities of the Amazon and the Atlantic Forest, showing the existence of very restricted insect communities in these vulnerable madicolous habitats.

ACKNOWLEDGEMENTS

We are indebted to Prof. Dr Gilmar P. Neves for the valuable help in fieldwork. We thank Yanomami people from Maturacá Village and to the Yanomami Association of the Cauaburis River and Tributaries

(AYRCA) for allowing our entry into their territory and for providing great assistance in the Amazon expedition. We are indebted to AAEP/FUNAI (n. 47/AAEP/PRES/2019) and ICMBio for the permissions granted to this research (n. 40423-4 and 65851-1). We thank Prof. Dr. Victor Saito for helping in fieldwork at Pedra da Mina Mountain and Dr. Danilo Naliato for preparing the map. We are grateful to Prof. Dr. Susana Trivinho-Strixino for grating laboratory structure and for the fruitful discussions on the aquatic insects. This study was funded by São Paulo Research Foundation – FAPESP (processes number 2018/11068-9, 2020/01762-5 and 2022/12640-3). CJEL wish to acknowledge the financial support from the Brazilian National Research Council (CNPq; grant 302751/2019-0). We are also grateful for the insightful and constructive comments and suggestions made by the Associate Editor (Sabine Rumpf) and two anonymous reviewers.

FUNDING INFORMATION

This study was funded by São Paulo Research Foundation – FAPESP (processes number 2018/11068-9 and 2020/01762-5 and 2022/12640-3).

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13747>.

DATA AVAILABILITY STATEMENT

All data that support the findings of this study are openly available in Dryad at <https://doi.org/10.5061/dryad.83bk3j9vs>.

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BIOSKETCHES

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Author Contributions: E.M.S. and C.J.E.L. conceived the study and generate the data. E.M.S. drafted the manuscript. C.G.R. and A.B. advised on statistical methods and helped in manuscript writing. All authors revised the manuscript.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Shimabukuro, E. M., Gómez-Rodríguez, C., Lamas, C. J. E., & Baselga, A. (2023). Mountain passes are higher at low latitudes for madicolous insect communities of the Neotropical region. *Diversity and Distributions*, 29, 1118–1128. <https://doi.org/10.1111/ddi.13747>