Journal of Biogeography

WILEY

Journal of Biogeography

RESEARCH ARTICLE OPEN ACCESS

Biodiversity Frontiers: Insights From Brazil's Natural Laboratories

Environmental Filtering Dominates Over Dispersal Limitation in Structuring Highly Mobile Tropical Communities

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Received: 13 October 2025 | **Revised:** 19 March 2026 | **Accepted:** 20 May 2026

Keywords: Amazonia | community assembly | distance-decay | environmental filtering | macroecology | tropical biodiversity | β-diversity

ABSTRACT

Aim: To disentangle the relative roles of environmental filtering (niche processes) and dispersal limitation (neutral processes) in structuring communities of a highly mobile tropical taxon, and to assess the implications for biodiversity patterns at broad spatial scales.

Location: Brazilian Amazon.

Time Period: 2011–2019.

Major Taxa Studied: Fruit-feeding butterflies (Nymphalidae).

Methods: We surveyed 182 species across 148 plots spanning 730,000 km^2 and a broad climatic, edaphic and vegetational gradient. We used Generalized Linear Mixed-effects Models (GLMMs), ordination methods and variance partitioning to quantify the unique and shared contributions of environmental and spatial predictors to species richness and composition. We also used distance–decay models to compare isolation-by-distance versus isolation-by-environment.

Results: Species richness increased with solar radiation, temperature and precipitation, and with distance from the equator. Environmental gradients, particularly climatic and soil variables, explained more variation in species turnover than geographic distance. For this highly dispersive group, the unique effect of dispersal limitation was weak, even across continental scales.

Main Conclusions: Our findings provide rare, large-scale empirical evidence that niche-based processes can dominate over neutral dynamics, even for organisms with high dispersal capacity and at broad spatial scales. By disentangling environmental and spatial effects, we show that climate, soil and vegetation are primary predictors of β-diversity in a mobile tropical taxon, challenging assumptions that dispersal limitation necessarily strengthens with spatial extent. Because these predictors are sensitive to global change, our results offer a general framework for predicting macroecological biodiversity responses in mobile taxa and species-rich ecosystems worldwide.

1 | Introduction

The spatial distribution of a species is often limited by dispersal and environmental constraints, as well as biotic interactions. These factors may act, together or separately, to influence species distributions at different spatial scales. At wider geographic scales, the spatial distribution of species is the result of synergistic effects of dispersal limitation, which impedes species from occurring everywhere (Hubbell 2001; Warren et al. 2014), and environmental constraints, which result in patchy distributions of locally adapted species (Tuomisto et al. 2003).

Dispersal limitation is a neutral process, in which the species dispersal ability (i.e., the ability to move between sites) determines which species will be able to occur at local scales, depending on the geographical distance between sites (Hubbell 2001). Conversely, environmental filtering is a niche process, in which species distribution depends on how well their ecological requirements and functional traits match the available environmental conditions (e.g., Zirbel et al. 2017). Although changes in species assemblages are frequently associated with geographical distance (e.g., Svenning et al. 2011) and environment (e.g., Hawkins et al. 2003), attributing the patterns to ecological processes is often challenging. This is because environmental predictors, such as vegetation, soil features and climate, are often spatially structured, which may hamper the disentangling of the effects of neutral and niche processes (Leibold and Mikkelson 2002; Tuomisto et al. 2003; Zuquim et al. 2012).

There has been a long debate on the role of environmental and dispersal limitation in explaining the composition of Amazonian species, without a clear consensus on which factors are more important (e.g., plants, Tuomisto et al. 2016; termites, Dambros et al. 2017; ants, Guilherme et al. 2022; harvestmen, Dambros et al. 2025; birds, Maximiano et al. 2020; multi-taxa, Dambros et al. 2020). For instance, geographical distance tends to affect more strongly the compositional dissimilarity of birds, fish and palm trees, than environmental difference, suggesting that these groups are more limited by dispersal than environmental constraints (Dambros et al. 2020). On the other hand, for taxa with higher dispersal ability, such as bats, butterflies and ferns, geographical distance tends to have weaker effects (Dambros et al. 2020), and environmental conditions are more likely to affect the distribution of these species. Therefore, niche and neutral processes are not mutually exclusive, and their relative roles in shaping beta-diversity patterns remain debated, particularly since their significance can vary among taxa and spatial scales (Matthews and Whittaker 2014; Dambros et al. 2020).

Butterflies are abundant animals in tropical forests (Freitas et al. 2006). Environmental gradients, such as topography and vegetation structure, are tightly associated with species distributions at local scales (Ribeiro and Freitas 2012; Graça et al. 2016; Rabelo et al. 2021). On the other hand, climate was found to play an important role in determining the patterns of butterfly distribution at regional to continental spatial scales (Menéndez et al. 2007; Stefanescu et al. 2011; Santos et al. 2020). Unlike many vertebrate species, butterflies can disperse quickly and over large distances (Penz et al. 2015). Although several genera are widely distributed, species richness is typically highest in tropical regions (Legg 1978; Bonebrake et al. 2010; Raven et al. 2020), indicating that large-scale climatic gradients likely play an important role in shaping butterfly distributions. To the best of our knowledge, only a single study has explored the influence of environmental gradients for Amazonian butterflies at broad spatial scales. Dambros et al. (2020) found that soil features and climate, together with geographical distance, all appear to influence the distribution of Amazonian butterflies. These effects are likely indirect, as soil properties influence vegetation structure and host plant availability (Quesada et al. 2009), which are key determinants of butterfly communities (DeVries 1985). However, they were unable to disentangle the individual effects or quantify the unique contribution of each factor, probably due to the spatial structure and/or narrow coverage of environmental gradients.

We investigated how butterfly species richness and composition are associated with spatial predictors and environmental gradients (climate, soil and vegetation) at broad geographic scales in Amazonia. We also quantified the relative contributions of geographical position and environmental gradients to species richness and turnover. Finally, we evaluated how species composition similarity between pairs of sites varies in relation to geographical distance and environmental difference. We test the hypothesis that niche-based processes would be more strongly associated with butterfly diversity and community assembly, given the high dispersal ability of Amazonian butterflies (Penz et al. 2015), their dependence on host plants (DeVries 1985) and the importance of proper climatic conditions, such as temperature and solar radiation, for body temperature regulation and flight activity (Turner et al. 1987). Therefore, we expected that species richness would be more strongly associated with environmental gradients than geographic predictors. In particular, large-scale climatic gradients, such as temperature, precipitation and solar radiation may influence butterfly communities by affecting vegetation productivity, host plant availability and microclimatic conditions that regulate butterfly activity and thermoregulation. We also expected that environmental variables, especially climate, might be more strongly associated with changes in species composition than geographic constraints. Finally, we expected to find a stronger decay in species composition similarity with increasing environmental difference than with increasing geographical distance, suggesting that butterfly distribution is mainly driven by niche rather than neutral processes.

2 | Material and Methods

2.1 | Sampling Design and Data Collection

Sampling covered a broad geographic scale across Amazonia (Figure 1). This area encompasses a gradient of contrasting environmental variables (climate, vegetation and soil), as well as a gradient of geographical distances between sampling plots. We surveyed butterflies between April 2011 and December 2019 in 148 sampling plots, located in 19 sampling grids with 5 to 24 plots each (Figure 1). Sampling grids were established by researchers from the Brazilian Biodiversity Research Program (PPBio), which is a long-term ecological programme that aims to compare the distribution of multiple taxa using standardized protocols (Magnusson et al. 2005). Plots (sample units)

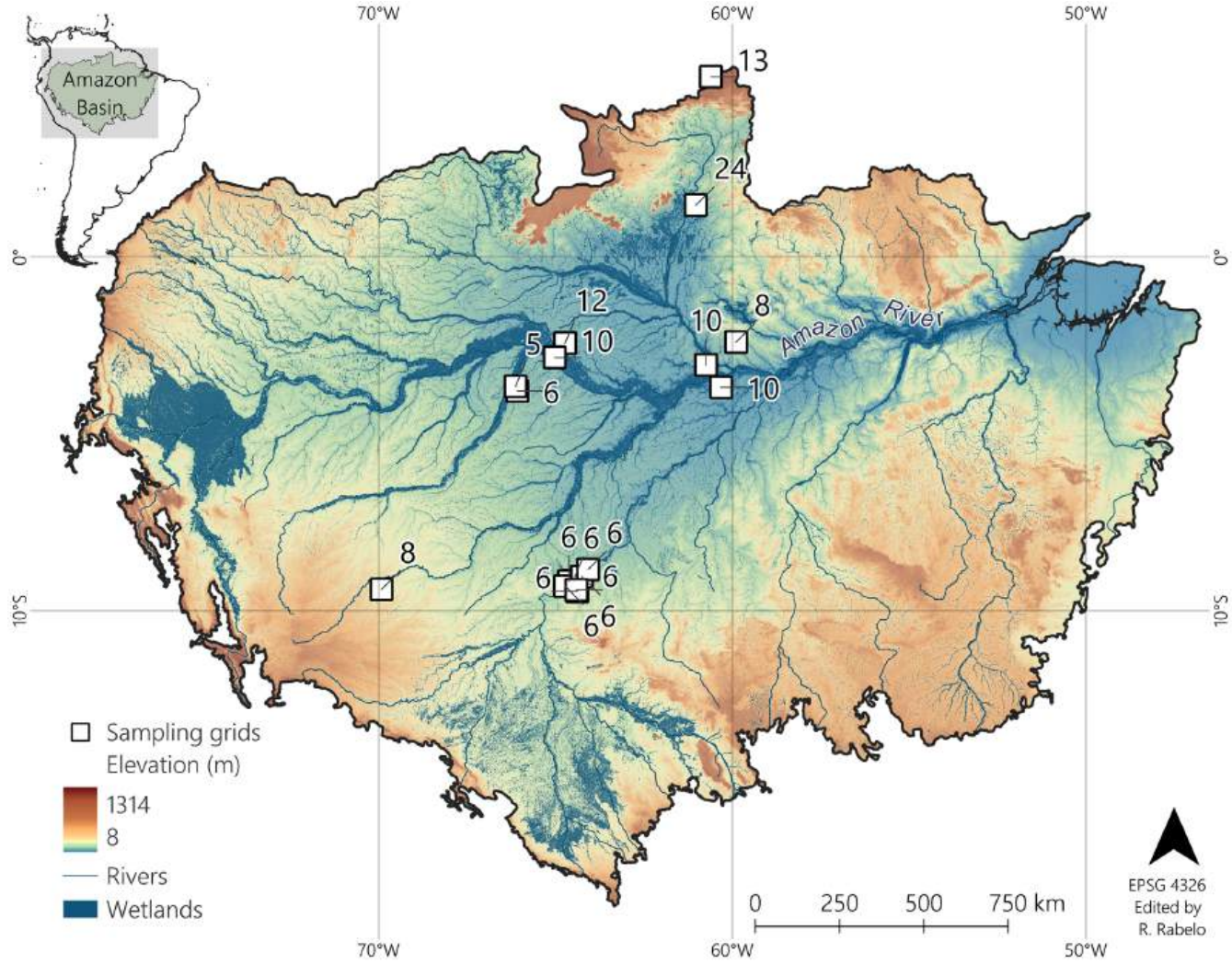

FIGURE 1 | Distribution of 148 sampling plots across Amazonia. White squares show the location of sampling grids and adjacent numbers indicate the number of sampling plots surveyed at each grid.

consisted of 250-m long transects, separated by at least 500 m from the nearest plot. The distance between grids varied from 8 to ~1910 km, and grids were spread over an area encompassing about 730.000 km^2. Most plots were located in tall, dense, lowland *terra-firme* tropical forests, but some were placed in seasonally flooded *várzea* forests, and a few were established in cloud forests in the Guayana Highlands and white-sand forests with simpler vegetation structure (locally known as *Campinas* and *Campinaranas*). Therefore, our sample size is more than three times larger and spans a much broader environmental gradient than that of previous studies (Dambros et al. 2020).

Butterfly surveys were conducted via passive sampling with Van Someren-Rydon baited traps, thus we studied only the guild of fruit-feeding butterflies. We placed from four to eight equally-spaced butterfly bait traps in each plot, hanging half of the traps in tree branches in the understorey (1.5–2 m high) and the other half in the canopy (15–20 m high). We baited the traps with a mixture of sugar-cane juice and bananas fermented for 48-h (Freitas et al. 2014) and checked them every 24 h to record captures and replace the bait. We left the traps active from five to eight consecutive days. All captured butterflies were collected for posterior identification and the specimens were deposited in the entomological collections of the National Institute of Amazonian Research, Mamirauá Sustainable Development Institute, University of São Paulo, and the Federal University of Rio Grande do Sul. We evaluated whether differences in sampling effort among plots influenced observed species richness. Sampling effort was weakly and non-significantly correlated with richness (Pearson $r = 0.06$, $p = 0.45$, Figure S1), indicating that variation in effort did not bias richness estimates across plots. We excluded plots with very low sampling completeness (≤ 2 individuals recorded) from subsequent analyses, as they do not provide reliable estimates of species richness and can generate extreme dissimilarities in composition analyses. This resulted in a final dataset of 138 plots used in all analyses.

We gathered climatic, edaphic and vegetation data for every plot location from GIS online databases. For extracting such data, we used the geographic coordinates corresponding to the centroid of each sampling plot. We obtained data of mean annual temperature and annual precipitation at ~1-km resolution from WorldClim version 2.1 (http://www.worldclim.org; Fick and Hijmans 2017). We also converted WordClim monthly data of solar radiation from 1970 to 2000 into mean annual solar radiation. We used two variables describing soil

texture (percentage of sand and clay), which are related to soil drainage, obtained from SoilGrids database (http://www.soilgrids.org) at 250-m resolution. We also used one soil chemical variable related to nutrient availability (soil cation concentration), obtained from a modelled raster layer based on direct soil measurements and estimates derived from soil-indicator plant species (Zuquim et al. 2019). These soil variables were included because soil texture and nutrient availability are known to influence vegetation structure, plant community composition, and host plant availability in Amazonian forests (Quesada et al. 2009), which in turn can affect butterfly communities (DeVries 1985; Graça et al. 2016). Soil cation concentration was log-transformed in subsequent analyses. To account for differences in vegetation structure, we obtained data on percentage of tree cover at 1-km resolution derived from the NOAA's Advanced Very High Resolution Radiometer data (AVHRR; http://earthexplorer.usgs.gov) and canopy height derived from spaceborne LiDAR and cloud-free MODIS at 500-m resolution (https://daac.ornl.gov; Sawada et al. 2015).

2.2 | Data Analysis

Our modelling approach was designed to evaluate the relative association between environmental gradients and spatial predictors with patterns of butterfly richness and composition at broad spatial scales. Because environmental and spatial variables are often spatially structured and potentially correlated, our analyses aim to quantify the relative predictive contribution of these sets of variables rather than infer direct causal mechanisms. Accordingly, we interpret model coefficients and variance partitioning results as indicating statistical associations between predictors and community patterns. This framework is commonly used in macroecology and biogeography to evaluate the relative importance of environmental and spatial structure in shaping biodiversity patterns across large spatial extents.

Before evaluating the relationships of spatial and environmental variables with species richness and composition, we first investigated the multicollinearity among predictor variables based on the variance inflation factor (VIF) through a stepwise procedure, using a correlation threshold of 0.7 and a VIF threshold of 10 (Figure S2). Latitude and mean annual solar radiation were highly correlated ($r = 0.88$). As solar radiation is known to strongly affect butterfly distributions (Turner et al. 1987), we kept this variable in subsequent analyses and substituted the whole value of latitude for its modulus value to avoid collinearity problems, since these two variables were weakly correlated ($r = -0.48$). Therefore, the modulus of latitude, which was used as one of the spatial predictors, also represented the distance from the Equator. All environmental and spatial variables were standardized before analyses to zero mean and unit variance.

We used the number of observed species per plot (estimate of species richness) as a response variable in a Generalized Linear Mixed-effects Model (GLMM) with Poisson distribution, using the environmental variables as predictor variables and the identity of grids as a random factor. We also included latitude and longitude among predictors to account for spatial gradients. We compared models containing all possible combinations of uncorrelated predictor variables with the corrected Akaike Information Criterion (AICc). When more than one model was indicated as equally plausible (i.e., delta AICc < 2; Burnham and Anderson 2002), we chose the model with strongest variables effects. We used the Moran's *I* index to calculate spatial autocorrelation of the residuals in the selected model. We finally quantified the amount of variance in butterfly species richness associated with spatial and environmental factors using variance partitioning to separate the variation in species richness explained uniquely by: (1) environmental variables (environment); (2) latitude and longitude, possibly caused by neutral processes or variables that cause clumping not included in the analysis ('space'); (3) both environment and 'space' (environment + 'space'); and (4) unexplained variation not associated with clumping (residual). We used the 'varpart' function from 'vegan' package (Oksanen et al. 2025) to perform the variance partitioning.

To disentangle the relative role of dispersal and environmental filters on species composition, we first used an abundance-based species-site matrix in a Principal Coordinate Analysis (PCoA), based on the Horn-Morisita dissimilarity index. Before proceeding to the matrix ordination, we standardized abundances in the cells by dividing by the total abundance in each plot (total of matrix rows) to obtain their relative abundance. The first two PCoA axes were used to represent species composition (or species turnover) in GLMMs, using spatial coordinates and environmental variables as predictor variables, and grids as a random factor. We compared alternative models including different combinations of predictor variables with the corrected Akaike Information Criterion (AICc) to identify the models that best predict variation in species composition. When more than one model was ranked among the best models (i.e., delta AICc < 2), we chose the model with strongest variables effects. We used the Moran's *I* to calculate spatial autocorrelation of the residuals in the selected model. We also estimated the amount of variance in the first two PCoA axes representing butterfly species composition associated with spatial coordinates and environmental variables using variance partitioning.

We also used a distance-based approach to evaluate how geographical and environmental distances affect butterfly compositional similarity between sites. While the PCoA approach addressed whether the response variable varies directly in relation to predictors, in the distance-based method we tested what factors are associated with the compositional dissimilarity between sampling plots: isolation by distance or by environmental difference. In this approach, the response variable was a pairwise dissimilarity matrix using 1-Jaccard index, which compared species composition between sites, and cell values represented the degree of compositional dissimilarity. Predictor variables consisted of distance matrices quantifying the geographical distance and the degree of environmental difference between pairs of sites. Geographical distance values were logarithmically transformed prior to analysis to account for the tendency of lower distance decay at larger distances (Hubbell 2001; Tuomisto et al. 2003). We calculated the environmental-distance matrices based on Euclidean distances independently considering the whole set of environmental variables. We tested whether dissimilarity in

butterfly composition was related to geographic distance or environmental difference using Multiple Regression on distance Matrices (MRM). Before running the model, we checked for the correlation between geographical and environmental distances ($r = 0.66$). The MRM models were implemented using functions adapted from Dambros et al. (2020), which align predictor matrices with the response matrix and standardize distance variables prior to model fitting. We evaluated the relative contribution of geographic and environmental distances using variance partitioning of the MRM models. Statistical significance of model coefficients was assessed using permutation tests. Because *p*-values are estimated using permutations, this approach does not require the assumption of normally distributed residuals. All analyses were carried out in the R version 4.5.1 (R Development Core Team 2025) using 'vegan' (Oksanen et al. 2025) and 'ecoDist' (Goslee and Urban 2007) packages, as well as functions created in Dambros et al. (2020) to automate the process of running multiple regression models on distance matrices. R code for running the analyses is available in Supporting Information S2.

3 | Results

We captured 2683 individuals belonging to 182 species in the 138 sampled plots, in a total sampling effort of 717,340 trap-days. The number of species per plot varied from 1 to 29, with a median of 6 species per plot (first and third quartile were 5 and 9, respectively). Singletons and doubletons were represented by 36 (~20%) and 24 (~13%) species, and species-accumulation curves did not approach an asymptote (Figure S3).

3.1 | Species Richness

The selected model for explaining species richness in relation to predictor variables (Table S1) explained 22% of the variation in species richness. Spatial predictors (|latitude|) and climatic predictors (solar radiation, temperature and rainfall) were the most important variables in the complete model, with a sum of weights above 0.45 in the AIC selection procedure (Figure S4). Butterfly species richness was higher in areas with higher solar radiation, temperature and precipitation (Table 1; Figure 2). Species richness was also affected by spatial predictors (i.e., |latitude|), reaching higher mean richness in plots further from the Equator (Table 1; Figure S5). There was no spatial autocorrelation in model residuals (Moran's *I*: obs.: −0.0004; exp.: −0.007; $p = 0.22$), and environmental variables had the largest unique contribution to explain species richness (Figure 3).

3.2 | Species Composition

The first two axes of PCoA ordination of plots explained 21% of the variation in species composition. Geographic position (|latitude| and longitude), rainfall and canopy height were the most important variables in the complete model for PCoA 1, with sum of weights above 0.5 in the AIC selection procedure (Figure S6). In addition to these variables, soil cation concentration, temperature and solar radiation were also important to explain butterfly composition captured by PCoA 2 (Figure S6). All these variables were included in the selected models, and explained 59% of the variation in the species composition summarized in PCoA 1 and PCoA 2 (Figure 3). According to the selected models (Table S2), butterfly species composition was associated with both environmental (rainfall, solar radiation, soil cation concentration and canopy height) and spatial predictors (Table 1, Figure 2). Model residuals did not show spatial structure for PCoA 1 (Moran's *I*: obs.: −0.001; exp.: −0.007; $p = 0.28$), nor PCoA 2 (Moran's *I*: obs.: −0.005; exp.: −0.007; $p = 0.23$). Variance partitioning showed that environmental variables had the largest unique contribution to explain butterfly species turnover, whereas geographic position was less important (Figure 3). To evaluate the robustness of the results to the ordination method, we also performed the community analyses using Non-Metric Multidimensional Scaling (NMDS) instead of PCoA and found qualitatively similar results (Figure S7; Table S3).

There was a weak decay in species compositional similarity between sites with increasing geographical distance, but with several deviations of this general trend at some intervals of geographical distance (see splines in Figure 4A). Such deviations in the main trend coincided with increases in environmental similarity with increasing geographical distance (Figure 4C). Butterfly compositional similarity showed a clearer decreasing trend with increasing environmental distance, with no major reversals in the main trend (Figure 4B). Both environmental ($\beta = 0.22$; $p < 0.01$) and geographical ($\beta = 0.18$; $p < 0.01$) distances showed a significant association with the decay in compositional similarity. However, variance partitioning showed that

TABLE 1 | Coefficients from selected generalized linear mixed-effects models (GLMMs) for the effects of geographic position and environmental variables on species richness and composition.

	Species richness	Species composition (PCoA 1)	Species composition (PCoA 2)
Intercept	−3.05	1.33	**6.29**
Tree cover (%)	—	—	—
Canopy height	—	**−0.06**	**0.04**
Clay content	—	—	—
Sand content	—	—	—
Log(soil cation concentration)	—	—	**0.18**
Mean annual temperature	**0.47**	—	—
Annual precipitation	**0.32**	**−0.11**	—
Mean annual solar radiation	**0.82**	—	**−0.13**
|Latitude|	**0.25**	**−0.03**	0.01
Longitude	−0.06	0.03	**0.10**

Note: Model for species richness was performed considering a Poisson distribution. Species composition represents the species turnover, which was summarized by two axes of a PCoA ordination based on a Horn-Morisita index. Model selection was based on AICc (Tables S1 and S2) and only variables included in the best model are shown. Bold coefficients represent significant values at $p < 0.05$. (—) Indicates variables not included in the selected model.

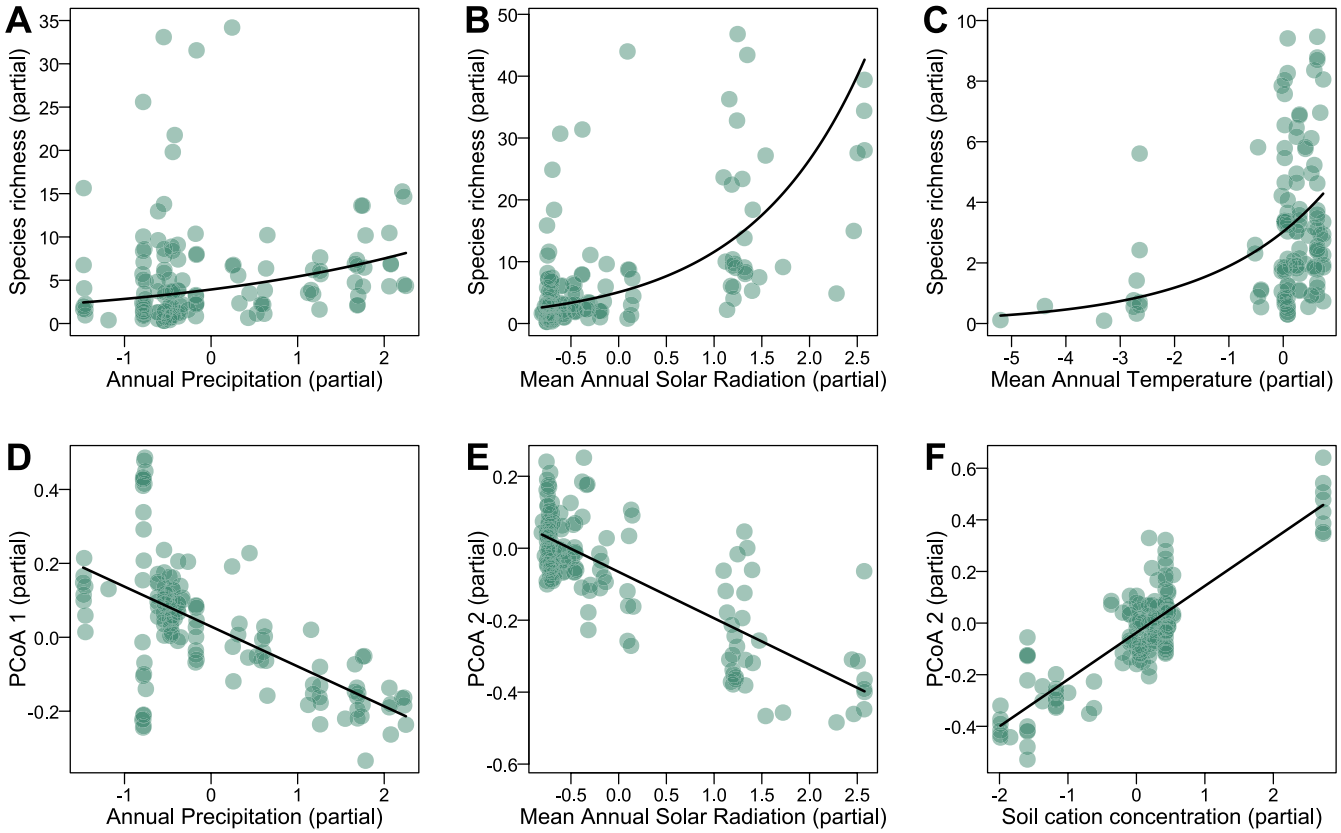

FIGURE 2 | Independent responses of species richness and composition (y-axes) to environmental variables (x-axis). Graphs represent the partial responses according to Generalized Linear Mixed-effects Models (GLMMs). Upper graphs show the response of species richness to annual precipitation (A), mean annual solar radiation (B) and mean annual temperature (C). Lower graphs show the response of species composition, which was summarized by the first two axes of a Principal Coordinate Analisys (PCoA 1 and 2), to annual precipitation (D), mean annual solar radiation (E) and soil cation concentration (F).

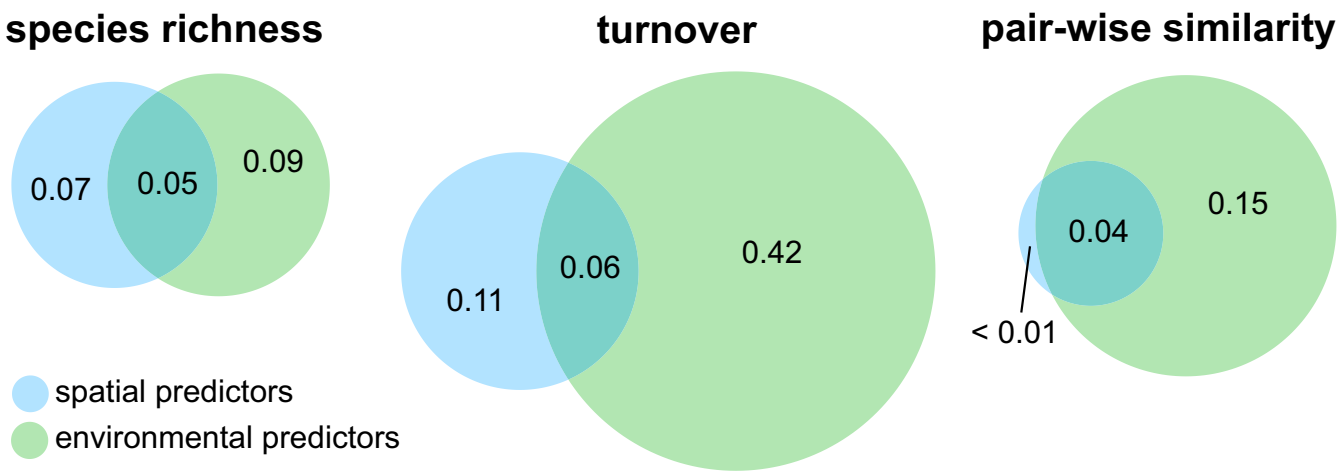

FIGURE 3 | Relative contribution (R^2) of environmental and spatial factors to explain butterfly richness, turnover and pair-wise similarity in Amazonia. Compositional turnover was measured by two axes of a Principal Coordinate Analysis (PCoA), based on the Horn-Morisita similarity index. For species richness and turnover, environmental predictors correspond to the environmental variables included in selected models, whereas spatial predictors correspond to latitude and longitude of sampling plots, and relative contributions were determined using Generalized Linear Mixed-effects Models (GLMMs) and variance partitioning. For pair-wise similarity, compositional similarity was measured by 1-Jaccard index, environmental predictors correspond to environmental difference, spatial predictors correspond to geographical distance between pairs of sites, and their contribution was determined using multiple regressions on distance matrices and variance partitioning. Values show the amount of variance that was uniquely or jointly explained by the components.

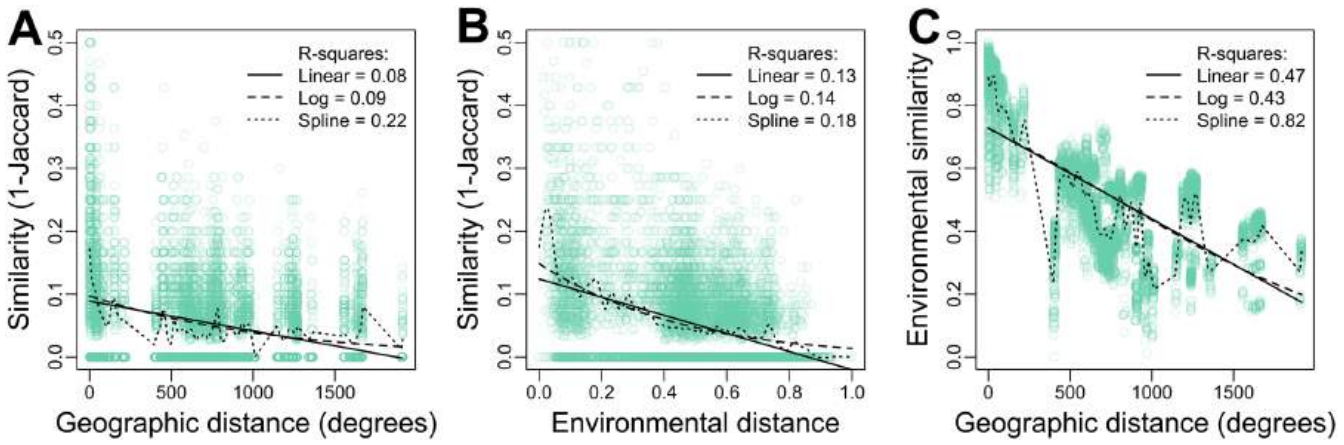

FIGURE 4 | Decay of compositional similarity with geographical distance and environmental difference among 138 sample plots. Each point represents a pair of sites being compared. Butterfly species similarity (Jaccard index) between sites is plotted against their geographical (A) and environmental (B) distances. Environmental similarity between sites is plotted against their geographic distance (C). Environmental similarity is the complement of the environmental distance. Linear, logarithm and flexible splines curves are shown to represent changes in the average similarity with increasing distance. Flexible spline function gives the most accurate representation of changes in average similarity.

environmental distance had the largest unique contribution to explain the butterfly compositional similarity, whereas geographical distance had nearly no unique contribution (Figure 3).

4 | Discussion

4.1 | The Role of Spatial and Environmental Factors

We found that environmental factors, especially temperature and solar radiation, are important predictors of butterfly species richness. These findings are consistent with the expectation that species with higher dispersal ability are more strongly affected by local environmental conditions (Hubbell 2005). Regional patterns of butterfly richness are often explained by climatic variables and richness tends to be higher in warm and more humid regions (Hawkins and Porter 2003; White and Kerr 2006; Menéndez et al. 2007; Stefanescu et al. 2011), although few studies have investigated such broad-scale patterns in the Neotropics (but see Rosser et al. 2012, Doré et al. 2022). As ectothermic organisms, adult butterflies depend on warm temperatures and high solar radiation to maintain their normal activity (Turner et al. 1987). Therefore, warm temperatures and high solar radiation increase butterfly metabolic rates, which in turn may increase rates of genetic divergence and speciation, increasing overall diversity towards the tropics (Allen et al. 2006).

Our findings are also consistent with previous studies that reported species turnover along environmental gradients in Amazonia across multiple taxa and environmental contexts (e.g., Tuomisto et al. 2003; Zuquim et al. 2012; Dias-Terceiro et al. 2015; Dambros et al. 2017; Fluck et al. 2020; Guilherme et al. 2022). Such turnover is often interpreted as reflecting niche partitioning, in which species are associated with different portions of environmental gradients (Leibold and Mikkelson 2002), although other processes such as dispersal limitation or historical factors may also contribute to spatial patterns in community composition. In this context, the strong association between butterfly turnover and environmental gradients observed in our study suggests that environmental filtering likely plays an important role in structuring these communities. Although our analyses identify statistical predictors of butterfly richness and turnover, disentangling the causal mechanisms linking environmental gradients and butterfly communities would require experimental or trait-based approaches. In particular, traits related to thermoregulation, flight morphology, and host plant specialization may influence how butterfly species respond to climatic and environmental gradients, representing promising avenues for future research. Additionally, although our analyses focused on continuous environmental gradients, major Amazonian forest types such as *terra-firme*, *várzea*, *campina* and *campinarana* integrate multiple environmental characteristics and may provide a useful framework for interpreting biodiversity patterns in conservation contexts.

Plant diversity and host plant availability are also likely to influence butterfly communities, given the strong dependence of butterfly larvae on specific host plants and the importance of vegetation resources for adult butterflies (DeVries 1985; Graça et al. 2016). Although plant diversity was not directly measured across all plots in this study, we found a significant association of butterfly turnover with vegetation structure (canopy height) and a strong association with soil fertility. Soil properties and climate are known to influence vegetation composition, structure and productivity across Amazonian landscapes (Quesada et al. 2009). These environmental variables may therefore partly capture spatial variation in plant communities (Zuquim et al. 2012, 2019) that indirectly affects butterfly diversity and composition. Future studies integrating plant community data and butterfly traits could help clarify how host plant availability mediates the relationship between environmental gradients and butterfly community assembly.

Butterfly richness and composition were also associated with spatial predictors, although their relationships tended to be relatively less important than the environment. Species richness increased with distance from the Equator, and species composition was associated with latitude and longitude. Despite these relationships, geographic positioning alone was less important

in explaining butterfly turnover. We found a clear, although weak, decay in butterfly compositional similarity with increasing geographical distance, which indicates that isolation by long geographical distances in Amazonia may limit the dispersal of many organisms. However, the unique contribution of geographical distance to explain butterfly compositional similarity was nearly absent. This decay in compositional similarity with geographical distance may represent the relationship of environmental differences between sites (Tuomisto et al. 2003). Therefore, our findings are in accordance with the expectation that butterflies have high dispersal capacity, thereby being less likely to be limited by dispersal, even at broad scales.

4.2 | Interaction Between Environment and Space

Spatial and environmental factors often interact to explain species distribution because environmental gradients are inherently spatially structured, which can make it difficult to disentangle their independent effects. For instance, the trend of decreasing compositional similarity between sites with their geographical distance presented deviations at some intervals of geographical distances, which reflected the increase in both environmental similarity and geographical distance. In addition, butterfly richness tended to increase with distance from the Equator and species composition (PCoA 2) changed from East to West (although our sampled longitudinal gradient spanned only ~10°). The highest species richness in the Northern portion of our study extent coincided with areas where solar radiation reaches the highest values in our sampled gradient (see Figure S2). On the other hand, the richest assemblages in the southern region of our sampling extent are located in areas with more fertile soils (Zuquim et al. 2019), as well as with persistent orographic rainfall due to the Andes (Hooghiemstra and Van Der Hammen 1998). Therefore, the increasing species richness with latitude to the North likely reflects changes in solar radiation, whereas the increased richness to the South may reflect the increased soil fertility and climatic stability due to persistent rainfall towards the Andes.

We found that both spatial and environmental predictors affect butterfly richness and composition, including in the distance-based approach, in which we evaluated the response of compositional similarity to geographical and environmental distances. However, variance partitioning showed that environmental predictors had a higher relative contribution to explain butterfly richness and, especially, turnover. Although environmental features are often spatially structured, hampering the estimation of individual relationships of environment and space, we did not find a strong correlation between these variables in our study. Our findings have broader relevance beyond Amazonian butterflies. Mobile taxa, such as birds and bats, or even sessile organisms, such as plants, often face similar interactions between dispersal capacity and environmental heterogeneity (Dambros et al. 2020). Our results support the general prediction from community assembly theory that niche-based filtering can dominate even for highly dispersive organisms, challenging assumptions that large spatial extents necessarily strengthen dispersal limitation. Moreover, because the dominant predictors we identified are climatic, shifts in temperature, precipitation and solar radiation under climate change are likely to have profound impacts on the composition and richness of mobile tropical communities worldwide.

5 | Conclusions

Here we evaluate how environmental and dispersal filters affect the distribution of Amazonian fruit-feeding butterflies to better understand the relative importance of niche-based and neutral processes at broad spatial scales. We found that environmental gradients, particularly climatic and soil factors, are strongly associated with species turnover, indicating that butterflies are specialized to different parts of these gradients (i.e., niche partitioning). This strong environmental relationship likely reflects the close association of butterflies with vegetation and primary productivity, as well as their ectothermic physiology, which makes them highly dependent on suitable climatic conditions for normal activity. Although geographic distance also contributed to predict species turnover, this relationship was comparatively weaker, suggesting that dispersal limitation plays a smaller role, even across the vast spatial extent of this study. By disentangling the relative contributions of environmental and spatial processes in a highly mobile tropical taxon, our findings reveal that environmental conditions predominantly shape species distributions, highlighting the dominance of niche-based mechanisms over neutral dynamics, even across continental scales. This study advances our ability to predict macroecological biodiversity responses to future environmental changes in tropical and other species-rich regions. Our results also highlight the importance of conserving a wide range of environmental conditions across tropical landscapes, as maintaining environmental heterogeneity is likely critical for sustaining butterfly diversity.

Author Contributions

Rafael M. Rabelo: conceptualization – lead, data curation, data analysis and interpretation – lead, writing – original draft, writing – review and editing. **Cristian Dambros:** data analysis and interpretation – support, writing – review and editing. **Márlon B. C. S. Graça:** data curation, data interpretation, writing – review and editing. **Geanne C. N. Pereira:** data curation, data interpretation, writing – review and editing. **Isabela F. Oliveira:** data curation, data interpretation, writing – review and editing. **Tarik Godoy Dangl Plaza:** data curation, data interpretation, writing – review and editing. **William E. Magnusson:** conceptualization – support, data analysis and interpretation – support, writing – review and editing. All authors contributed to the final manuscript and approved the submitted version.

Acknowledgements

We thank the logistical support from Mamirauá Institute, from the ICMBio, from the National Institute for Amazonian Biodiversity (CENBAM), and from the Departamento de Mudanças Climáticas e Unidades de Conservação (DEMUC-AM). We thank Thamara Zacca for help in species identification. The Mamirauá Institute and the Program for Biodiversity Research (PPBio) provided support during analyses and data storage. We also thank two anonymous reviewers who provided important comments that substantially improved the manuscript. The Article Processing Charge for the publication of this research was

funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614).

Funding

This research was funded by the National Council for Scientific and Technological Development (CNPq, 142352/2017-9 and 441260/2023-3), Mamirauá Institute for Sustainable Development (Instituto Mamirauá-OS/MCTI), Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), Gordon and Betty Moore Foundation, Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES—PROEX #0742/2020) and Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM-PAPAC #005/2019).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data used in this work is available at the Knowledge Network for Biocomplexity repository (DOI: https://doi.org/10.5063/F1KK999R). The R code used for data analysis is available in Supporting Information Data S1 .

References

Allen, A. P., J. F. Gillooly, V. M. Savage, and J. H. Brown. 2006. "Kinetic Effects of Temperature on Rates of Genetic Divergence and Speciation." *Proceedings of the National Academy of Sciences of the United States of America* 103: 9130–9135.

Bonebrake, T. C., T. Fartmann, and H. Van Dyck. 2010. "More Than Just Indicators: A Review of Tropical Butterfly Ecology and Conservation." *Biological Conservation* 143: 1831–1841.

Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach*. 2nd ed. Springer.

Dambros, C. S., E. L. Abbad, P. A. Garcia, and A. L. Tourinho. 2025. "River Barriers and Spatial Constraints: Unveiling the Factors Shaping Species Distribution in the Amazonian Rainforest." *Journal of Biogeography* 52: e70064.

Dambros, C. S., J. W. Morais, R. A. Azevedo, and N. J. Gotelli. 2017. "Isolation by Distance, Not Rivers, Control the Distribution of Termite Species in the Amazonian Rain Forest." *Ecography* 40: 1242–1250.

Dambros, C. S., G. Zuquim, G. M. Moulatlet, et al. 2020. "The Role of Environmental Filtering, Geographic Distance and Dispersal Barriers in Shaping the Turnover of Plant and Animal Species in Amazonia." *Biodiversity and Conservation* 29: 3609–3634.

DeVries, P. J. 1985. "Hostplants Records and Natural History Notes on Costa Rican Butterflies (Papilionidae, Pieridae & Nymphlidae)." *Journal of Research on the Lepidoptera* 24: 290–333.

Dias-Terceiro, R. G., I. L. Kaefer, R. de Fraga, M. C. de Araújo, P. I. Simões, and A. P. Lima. 2015. "A Matter of Scale: Historical and Environmental Factors Structure Anuran Assemblages From the Upper Madeira River, Amazonia." *Biotropica* 47: 259–266.

Doré, M., K. Willmott, B. Leroy, et al. 2022. "Anthropogenic Pressures Coincide With Neotropical Biodiversity Hotspots in a Flagship Butterfly Group." *Diversity and Distributions* 28: 2912–2930.

Fick, S. E., and R. J. Hijmans. 2017. "WorldClim 2: New 1-km Spatial Resolution Climate Surfaces for Global Land Areas." *International Journal of Climatology* 37: 4302–4315.

Fluck, I. E., N. Cáceres, C. D. Hendges, M. N. Brum, and C. S. Dambros. 2020. "Climate and Geographic Distance Are More Influential Than Rivers on the Beta Diversity of Passerine Birds in Amazonia." *Ecography* 43: 860–868.

Freitas, A. V. L., C. A. Iserhard, J. P. Santos, et al. 2014. "Studies With Butterfly Bait Traps: An Overview." *Revista Colombiana de Entomologia* 40: 203–212.

Freitas, A. V., I. R. Leal, M. Uehara-Prado, and L. Iannuzzi. 2006. "Insetos como Indicadores de Conservação da Paisagem." In *Biologia da Conservação e Manejo da Vida Silvestre*, 357–384. UFPR.

Goslee, S. C., and D. L. Urban. 2007. "The Ecodist Package for Dissimilarity-Based Analysis of Ecological Data." *Journal of Statistical Software* 22: 1–19.

Graça, M. B., J. W. Morais, E. Franklin, P. A. C. L. Pequeno, J. L. P. Souza, and A. S. Bueno. 2016. "Combining Taxonomic and Functional Approaches to Unravel the Spatial Distribution of an Amazonian Butterfly Community." *Environmental Entomology* 45: 301–309.

Guilherme, D. R., P. A. C. L. Pequeno, F. B. Baccaro, E. Franklin, C. R. dos Santos Neto, and J. L. P. Souza. 2022. "Direct and Indirect Effects of Geographic and Environmental Factors on Ant Beta Diversity Across Amazon Basin." *Oecologia* 198: 193–203.

Hawkins, B., B. A. Hawkins, R. Field, et al. 2003. "Energy, Water, and Broad-Scale Geographic Patterns of Species Richness." *Ecology* 84: 3105–3117.

Hawkins, B. A., and E. E. Porter. 2003. "Water-Energy Balance and the Geographic Pattern of Species Richness of Western Palearctic Butterflies." *Ecological Entomology* 28: 678–686.

Hooghiemstra, H., and T. Van Der Hammen. 1998. "Neogene and Quaternary Development of the Neotropical Rain Forest: The Forest Refugia Hypothesis, and a Literature Overview." *Earth-Science Reviews* 44: 147–183.

Hubbell, S. P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press.

Hubbell, S. P. 2005. "Neutral Theory in Community Ecology and the Hypothesis of Functional Equivalence." *Functional Ecology* 19: 166–172.

Legg, G. 1978. "A Note on the Diversity of World Lepidoptera (Rhopalocera)." *Biological Journal of the Linnean Society* 10: 343–347.

Leibold, M. A., and G. M. Mikkelson. 2002. "Coherence, Species Turnover, and Boundary Clumping: Elements of Meta-Community Structure." *Oikos* 97: 237–250.

Magnusson, W. E., A. P. Lima, R. Luizão, et al. 2005. "RAPELD: A Modification of the Gentry Method for Biodiversity Surveys in Long-Term Ecological Research Sites." *Biota Neotropica* 5: 21–26.

Matthews, T. J., and R. J. Whittaker. 2014. "Neutral Theory and the Species Abundance Distribution: Recent Developments and Prospects for Unifying Niche and Neutral Perspectives." *Ecology and Evolution* 4: 2263–2277.

Maximiano, M. F. A., F. M. d'Horta, H. Tuomisto, G. Zuquim, J. Van Doninck, and C. C. Ribas. 2020. "The Relative Role of Rivers, Environmental Heterogeneity and Species Traits in Driving Compositional Changes in Southeastern Amazonian Bird Assemblages." *Biotropica* 52: 946–962.

Menéndez, R., A. González-Megías, Y. Collingham, et al. 2007. "Direct and Indirect Effects of Climate and Habitat Factors on Butterfly Diversity." *Ecology* 88: 605–611.

Oksanen, A. J., F. G. Blanchet, M. Friendly, et al. 2025. "vegan: Community Ecology Package."

Penz, C., P. DeVries, J. Tufto, and R. Lande. 2015. "Butterfly Dispersal Across Amazonia and Its Implication for Biogeography." *Ecography* 38: 410–418.

Quesada, C. A., J. Lloyd, M. Schwarz, et al. 2009. "Regional and Large-Scale Patterns in Amazon Forest Structure and Function Are Mediated

by Variations in Soil Physical and Chemical Properties." *Biogeosciences Discussions* 3: 3993–4057.

R Development Core Team. 2025. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.

Rabelo, R. M., G. C. N. Pereira, J. Valsecchi, and W. E. Magnusson. 2021. "The Role of River Flooding as an Environmental Filter for Amazonian Butterfly Assemblages." *Frontiers in Ecology and Evolution* 9: 693178.

Raven, P. H., R. E. Gereau, P. B. Phillipson, C. Chatelain, C. N. Jenkins, and C. Ulloa Ulloa. 2020. "The Distribution of Biodiversity Richness in the Tropics." *Science Advances* 6: eabc6228.

Ribeiro, D. B., and A. V. L. Freitas. 2012. "The Effect of Reduced-Impact Logging on Fruit-Feeding Butterflies in Central Amazon, Brazil." *Journal of Insect Conservation* 16: 733–744.

Rosser, N., A. B. Phillimore, B. Huertas, K. R. Willmott, and J. Mallet. 2012. "Testing Historical Explanations for Gradients in Species Richness in Heliconiine Butterflies of Tropical America." *Biological Journal of the Linnean Society* 105: 479–497.

Santos, J. P., T. Sobral-Souza, K. S. Brown Jr., M. H. Vancine, M. C. Ribeiro, and A. V. L. Freitas. 2020. "Effects of Landscape Modification on Species Richness Patterns of Fruit-Feeding Butterflies in Brazilian Atlantic Forest." *Diversity and Distributions* 26: 196–208.

Sawada, Y., R. Suwa, K. Jindo, et al. 2015. "A New 500-m Resolution Map of Canopy Height for Amazon Forest Using Spaceborne LiDAR and Cloud-Free MODIS Imagery." *International Journal of Applied Earth Observation and Geoinformation* 43: 92–101.

Stefanescu, C., J. Carnicer, and J. Peñuelas. 2011. "Determinants of Species Richness in Generalist and Specialist Mediterranean Butterflies: The Negative Synergistic Forces of Climate and Habitat Change." *Ecography* 34: 353–363.

Svenning, J. C., C. Fløjgaard, and A. Baselga. 2011. "Climate, History and Neutrality as Drivers of Mammal Beta Diversity in Europe: Insights From Multiscale Deconstruction." *Journal of Animal Ecology* 80: 393–402.

Tuomisto, H., G. M. Moulatlet, H. Balslev, et al. 2016. "A Compositional Turnover Zone of Biogeographical Magnitude Within Lowland Amazonia." *Journal of Biogeography* 43: 2400–2411.

Tuomisto, H., K. Ruokolainen, and M. Yli-Halla. 2003. "Dispersal, Environment, and Floristic Variation of Western Amazonian Forests." *Science* 299: 241–244.

Turner, J. R. G., C. M. Gatehouse, and C. A. Corey. 1987. "Does Solar Energy Control Organic Diversity? Butterflies, Moths and the British Climate." *Oikos* 48: 195–205.

Warren, D. L., M. Cardillo, D. F. Rosauer, and D. I. Bolnick. 2014. "Mistaking Geography for Biology: Inferring Processes From Species Distributions." *Trends in Ecology & Evolution* 29: 572–580.

White, P., and J. T. Kerr. 2006. "Contrasting Spatial and Temporal Global Change Impacts on Butterfly Species Richness During the 20th Century." *Ecography* 29: 908–918.

Zirbel, C. R., T. Bassett, E. Grman, and L. A. Brudvig. 2017. "Plant Functional Traits and Environments Conditions Shape Community Assembly and Ecosystem Functioning During Restoration." *Journal of Applied Ecology* 54: 1070–1079.

Zuquim, G., J. Stropp, G. M. Moulatlet, et al. 2019. "Making the Most of Scarce Data: Mapping Soil Gradients in Data-Poor Areas Using Species Occurrence Records." *Methods in Ecology and Evolution* 10: 788–801.

Zuquim, G., H. Tuomisto, F. R. C. Costa, et al. 2012. "Broad Scale Distribution of Ferns and Lycophytes Along Environmental Gradients in Central and Northern Amazonia, Brazil." *Biotropica* 44: 752–762.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** jbi70273-sup-0001-Supinfo01.R. **Figure S1:** Relationship between sampling effort (trap-days) and butterfly species richness per sampling unit. **Figure S2:** Pairwise correlation of predictor variables used multiple regression models. **Figure S3:** Species accumulation curve. **Table S1:** Ranking of models with different combinations of variables for predicting species richness according to AICc. **Figure S4:** Importance of predictor variables (sum of weights from the AIC selection procedure) in Generalized Linear Mixed-effect Models (GLMMs) for explaining butterfly species richness. **Figure S5:** Variation of species richness (y-axis) according to distance from Equator, in degrees (x-axis). **Figure S6:** Importance of predictor variables (sum of weights from the AIC selection procedure) in Generalized Linear Mixed-effect Models (GLMMs) for explaining butterfly species composition summarized with the first two axes of a Principal Coordinate Analysis (PCoA). **Table S2:** Ranking of models with different combinations of variables for predicting species composition (represented by PCoA 1 and 2) according to AICc. **Figure S7:** Importance of predictor variables (sum of weights from the AIC selection procedure) in Generalized Linear Mixed-effect Models (GLMMs) for explaining butterfly species composition summarized with a 2-dimension Nonmetric Multidimensional Scaling (NMDS). **Table S3:** Coefficients from selected Generalized Linear Mixed-effect Models for the effects of geographic position and environmental variables on composition.