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Disentangling the effects of environmental and geographic distances on lizard assemblages in Amazonian forests

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Abstract

Aim: Distinguishing ecological and evolutionary processes that structure assemblages can provide a comprehensive vision of the variation in species turnover in heterogeneous regions. However, the causes of spatial variation in organism assemblies in most of the Amazon still require further studies. In view of this, our objective was to determine the relative roles of species interactions, categorical and continuous environmental filters and isolation by distance in the taxonomic and functional composition of lizard assemblages.

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Location: Amazonian rainforest.

Taxon: Lacertilia.

Methods: We sampled 14 sites along 880km in the Madeira-Purus interfluvial region, central-south-western Amazonia. We used multiple linear models applied to distance matrices, spatial correlograms and partitioned variance to distinguish the effects of geographical distances from environmental distances on lizard assemblages. Additionally, to better understand the effects of environmental gradients and forest type on species traits, we used a combination of RLQ and fourth-corner analysis.

Results: Variance in taxonomic distance was mainly explained by a continuous environmental gradient that selects different species. Although we found no evidence of overdispersion or clustering of traits, functional distance was mainly explained by forest type and precipitation. The weak effect of geographical distance on lizard assemblages suggests that different environmental conditions have selected distinct subsets of species and functional traits.

Main Conclusions: We showed that the structural heterogeneity along an environmental gradient in Amazonia has a significant impact on the taxonomic and functional composition of lizard assemblages. Environmental filtering along the interfluvial region has caused species turnover and determined differences in the functional characteristics found between assemblages in dense and open forests. These results are relevant for conservation since local species or trait subsets change across the landscape and are therefore irreplaceable in the case of local extinction.

KEYWORDS

beta diversity, environmental filtering, functional traits, spatial autocorrelation, Squamata, taxonomic diversity

1 | INTRODUCTION

One of the main goals of community ecology is to investigate changes in species and trait richness and composition along environmental gradients. Non-random subsets from more diverse species pools emerge in response to environmental filtering (Kraft et al., 2007), competition (Santos et al., 2009; Vernes et al., 2005; Vitt et al., 2000), limited dispersal and demographic stochasticity (Hubbell, 2001). Distinguishing ecological and evolutionary processes and mechanisms structuring assemblages is not an easy task (Cadotte & Tucker, 2017), because they generally result from hierarchically related environmental and historical factors (e.g. Dias-Terceiro et al., 2015; Peixoto et al., 2020). However, regardless of the ecological and evolutionary processes behind non-random assemblages, testing spatial heterogeneity in assemblage taxonomic and functional structure is useful for determining levels of biotic complementarity and redundancy between sites (Diaz & Cabido, 2001; McGill et al., 2006), which makes it an efficient approach to conservation of local assemblies (Bueno et al., 2012; Faria et al., 2019; Fraga et al., 2011).

Species turnover is associated with elevation and environmental variation in western Amazonia near the Andes (Noriega & Realpe, 2018). However, the causes of spatial variation in organismal assemblages in the greater part of lowland Amazonia remain controversial. Large rivers, which block dispersal and gene flow (Cracraft, 1985; Ron, 2000), can generate complementary assemblages on opposite banks of rivers (Borges & Da-Silva, 2012; Juen & De-Marco, 2012; Ribas et al., 2012), but some studies have already shown that, for some taxa, there is little variation in communities along the banks, even though these rivers are considered the limits of endemism for well-studied groups, such as birds (Santorelli-Jr et al., 2018).

Even in areas with no apparent dispersal barriers, neutral processes can generate differences in assemblages that are separated by large distances (Hubbell, 2001), but the degree to which species turnover relates to neutral processes or to environmental filters that vary with distance has been disputed (Qian & Ricklefs, 2012). While neutral processes are expected to result in changes in the composition of communities, these changes should not result in consistent differences in the functional characteristics of assemblages because the neutral theory considers all species to be functionally equivalent.

Many studies have shown turnover of species assemblages in Amazonia (e.g. Fraga et al., 2018; Rojas-Ahumada et al., 2012), but the scale of those studies was too limited to detect neutral effects due to dispersal limitation. To increase the geographical coverage in an area with no obvious dispersal barriers, a multidisciplinary effort has been applied to provide an efficient sampling design to quantify dissimilarities among assemblages based on standardized sampling plots installed along the Madeira-Purus interfluvial region, in the Midwestern Amazonia (PPBio, 2020). The plot array covers 880km of lowland Amazonian rainforest and strong gradients in climate and vegetation structure, with the vegetation predominantly consisting of Dense Ombrophilous Forest (DOF) and Open Ombrophilous Forest (OOF). Both are evergreen rainforests that differ mainly by the denser understorey in the DOF, due to higher densities of shrubs, herbs, ferns, palm trees, epiphytes and lianas. Additionally, climatic seasonality is slightly more pronounced in OOF, where firstorder streams can dry completely during the low-rainfall season (IBGE, 1997). These forest types also represent different portions of gradients in soil texture, vegetation cover and climate. Combinations of those gradients have been shown to be related to dissimilarities among assemblages of plants (Bernardes & Costa, 2011), fish (Barros et al., 2013), snakes (Fraga et al., 2018) and bats (Marciente et al., 2015).

Lizards are considered model organisms for ecological studies because the functional significance of their morphological and behavioural traits has been studied intensively (Garland Jr & Losos, 1994; Gomes et al., 2016) and they are usually easy to sample. As most species are use only a small portion of the available thermal and vegetation structure gradients, they are considered to be sensitive indicators of variation in environmental conditions (Sinervo et al., 2010). In Amazonia, lizard assemblage structure may be predicted by gradients that determine the availability of foraging, resting, refuge and thermoregulation sites, such as canopy openness and light incidence (Lobão, 2008; Moraes, 2008), leaf-litter depth (Bittencourt, 2008; Pinto, 2006), prey availability (Lobão, 2008; Moraes, 2008), soil clay content (Pinto, 2006), elevation and slope (Lobão, 2008; Moraes, 2008), distance from waterbodies (Faria et al., 2019) and edge effects (Almeida-Corrêa et al., 2020). Since values of those gradients are not evenly distributed over heterogeneous landscapes, they may cause spatial mosaics of habitat guality and different local subsets of species and functional traits.

While distinguishing ecological and evolutionary processes behind species turnover may not be simple, dispersion or concentration of functional traits among assemblages has been used to infer the relative strengths of competition or environmental filters in assemblage structure (Faith, 1992; Winter et al., 2013). These analyses are often undertaken using phylogenetic proximity as a surrogate for similarity in functional traits because phylogenetic lineages often conserve similar functional traits (e.g. Fraga et al., 2018). However, they can be carried out using direct measures of differences in functional traits, since the traits measured explicitly carry a phylogenetic signal (Adams, 2014). This can be a useful strategy for conservation because phylogenetic diversity estimates may capture less functional diversity than sets of species randomly selected from a pool (Mazel et al., 2018).

We modelled our hypotheses on assemblage-level dissimilarities considering different ways to disentangle environmental distances from geographic distances. One of the main problems in distinguishing neutral effects resulting from geographic distance (Hubbell, 2001) from environmental filters is that sites separated by distances that are sufficient to cause measurable differences in assemblages usually also differ in environmental characteristics (Qian & Ricklefs, 2012). Similarity in taxonomic compositions of lizard assemblages could come about because the environment filters out species with certain functional traits (whether morphological or physiological), that may also vary with geographical distance (Fluck et al., 2020). In this case, we ask whether there should be strong correlations between differences in mean community trait characteristics and differences in environmental conditions. Alternatively, if species with all traits are present in all assemblages, the species composition of the entire assemblage is selected by environment or by geographically structured historical factors (e.g. barriers or different dispersal centres). In this case, there will be little correlation between differences in mean community trait characteristics and environment, despite the strong relationship between environment and taxonomic composition.

In this paper, we investigate how environmental gradients (forest type, vegetation cover, soil texture, climate) and geographic distance influence lizard species composition and functional traits (morphology, thermoregulation, foraging mode) in the Amazonian rainforest. Our main objective was to distinguish the effects of dispersal limitation and environmental filters on the taxonomic and functional compositions of assemblages.

MATERIALS AND METHODS 2

Sampling sites are located along in the interfluve between the Madeira and Purus rivers, central-southwestern Brazilian Amazonia.

-WILEY-The study area covers rainforests crossed by the BR-319 federal highway, which connects Manaus to Humaitá, in the state of Amazonas, and on the west bank of the upper Madeira River, Rondônia state. The topography of the region is relatively flat and low (30-60 m a.s.l.), and according to a classification proposed by the Brazilian Institute of Geography and Statistics (IBGE, 1997), the vegetation is predominantly covered by Dense Ombrophilous Forest and Open Ombrophilous Forest.

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We sampled 14 sites (sites are made of aggregated plot replicates, which we will call modules from now on), which were installed according to the RAPELD (Brazilian acronym for rapid survey plus long-term ecological research) method (Magnusson et al., 2005, 2013). Each module is composed of two main 5-km long trails, parallel and separated by 1 km. We sampled nine modules within DOF and five modules within OOF (see Figure 1). Each module contains 10 250 m-long, 10-m wide plots, following natural altitudinal contours to minimize environmental heterogeneity within plots.

We found active or resting lizards using a combination of visual search (Campbell & Christman, 1982) along the centre line of each plot and leaf-litter sweeping and shelter inspection within a range of 1m from the centre line of the plot. We collected data in 2010 between the late dry season and the middle of the rainy season (September-December). Leaf-litter sweeping and shelter inspection were used to



FIGURE 1 RAPELD sampling modules along the BR-319 federal highway (M1-M11) and the upper Madeira River (M12-M15) in Brazilian Amazonia. The module M8 (in red) was not sampled because it was flooded during the rainy season. Different colours show patches of natural or anthropogenic landscapes, as detailed in the inset legend.

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detect sheltered lizards and compensate for possible effects of seasonal changes in weather over the sampling period on the activity of some species. Fossorial species are under-sampled in this study, since we did not use pitfall traps, which are inefficient in places with high water tables or rocky ground. We applied each method over 60min per plot, with two simultaneous observers, 10m apart, and we pooled the data from both observers to compose each sample.

Logistical constraints prevented us from obtaining temporal sampling repetitions and may have reduced our ability to find rare or very cryptic species. However, our data resulted from 140 sampling plots with a sample effort equivalent to 16,800 h× observers. When species were difficult to identify in the field, we collected a maximum of three specimens and killed them using a lidocaine-based anaesthetic, fixed them in 10% formaldehyde and stored them in 70% ethanol. The specimens were deposited in the herpetological section of the zoological collections of the Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil.

2.1 | Measuring taxonomic and functional trait distances

To quantify lizard assemblages we adopted the taxonomic nomenclature recognized by the Reptile Database (Uetz et al., 2020). Some species we sampled may be part of complexes composed of multiple evolutionary lineages, but due to the lack of robust evidence to differentiate them based on morphology or geographic distribution, we considered them as single taxonomic entities. Exceptionally, the Blue-Lipped Lizard *Plica umbra* contains two subspecies (*P. umbra umbra* and *P. umbra ochrocollaris*) that have been considered distinct evolutionary lineages (Oliveira et al., 2016). We estimated taxonomic distances among paired modules using the Bray–Curtis index, implemented in the VEGAN R-package (Oksanen et al., 2020).

To quantify lizard assemblages based on functional traits, we selected traits that potentially represent interactions among lizards, biotic and abiotic habitat elements. We used morphometric traits reported in previous studies (Gómez-Ortiz & Moreno, 2017; Peña-Joya et al., 2020) because they can suggest important aspects of the diet of the species (e.g. prey size), habitat use and ability to disperse, forage, thermoregulate and escape from predators (Vitt, 1991; Vitt et al., 1997). We used a digital calliper to measure snout-vent length (SVL), head width, head height, anterior limb length (hereafter arm length), and posterior limb length (hereafter leg length). We measured 5–15 individuals per species and transformed average values in proportions relative to SVL to reduce the effect of size. We used foraging mode (active, sedentary ambush, active ambush), because this trait reflects levels of exposure to predators, feeding frequency, fat accumulation rate and consequently defensive behaviour, which can impact reproductive success (Vitt, 1991). We gathered information about interactions between species and microhabitat (terrestrial, arboreal, cryptic, scansorial) and thermoregulation (heliotherm and non-heliotherm) because these traits represent direct interactions between species and the available habitats (Vitt et al., 2001).

We obtained species-level data on foraging mode, thermoregulation and interactions between species and microhabitat from the literature (Ávila-Pires, 1995; Vitt et al., 2008). We encoded all categorical traits in binary data as suggested by Petchey et al. (2007).

To estimate functional distances among paired modules, we used continuous trait means weighted by species abundance, implemented in the FD R-package (Laliberté et al., 2014). For the binary traits, we weighted by proportions of each trait relative to the total species abundance per module. We estimated functional distances using the Gower index implemented in the VEGAN R-package (Oksanen et al., 2020), because this index has been described as efficient for mixed datasets composed of continuous, categorical and binary variables (Petchey et al., 2007).

2.2 | Phylogenetic signal and trait dispersion

In addition to the ecological background for the choice of functional traits measured in this study, we quantified the phylogenetic signal carried by each trait. This gives an indication of the processes that structure a community. The phylogenetic relationships were based on a well-supported phylogenetic tree proposed by Pyron et al. (2013), which was based on 12 concatenated genes (five mitochondrial and seven nuclear). We calculated *K* statistics based on Brownian motion (Blomberg et al., 2003), using the PICANTE R-package (Kembel et al., 2010) to calculate the strength and statistical support of the phylogenetic signal carried by each trait.

Since all traits measured in this study are dependent on phylogenetic relationships among the species sampled (see Figure S1), and that traits driving assemblage structure are conserved over the phylogeny (Cavender-Bares et al., 2009), our inferences based on functional distances can be interpreted from an evolutionary perspective. Additionally, we used the phylosor (1-phylosor) function of the PICANTE R-package to estimate phylogenetic distances based on fractions of branch-length shared among paired modules. By applying a simple linear regression given by *functional distance* = a + b (*phylogenetic distance*), we found a positive relationship ($r^2 = 0.40$, p < 0.00001), which indicates that functional distance is a good proxy for phylogenetic distance in our study system, consistent with snake assemblages in Amazonia (Fraga et al., 2018).

We determined whether the phylogenetic (and therefore functional) structure of lizard assemblages is characterized by phylogenies more dispersed or clustered across modules than expected by chance. We used NRI and NTI, which compare observed and random values generated by a null model of mean pairwise distances (MPD) and mean nearest-neighbour distances (MNTD) respectively (Webb et al., 2002). Both indices return positive values for assemblages composed of more related species than expected by chance, and negative values for species more distant than expected by chance. We implemented NRI and NTI in the PICANTE R-package (Kembel et al., 2010), using a null model that randomizes the assemblage data with the independent swap algorithm (Gotelli & Entsminger, 2003),

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maintaining species occurrence frequency and richness. The *p*-values obtained were derived from 999 randomizations.

2.3 | Environmental gradients

To measure environmental variables in the study area, we collected information on vegetation cover and soil structure, such as the basal area of trees and clay content in the soil. Basal area is a measure of vegetation cover based on the cross-sectional area of trees at chest height, and we used the data collected over the study area by Schietti et al. (2016). Clay content in the soil was measured using a standard protocol based on particle selection, which is part of the environmental sampling protocols of the Biodiversity Research Program (PPBio). Further details on methods and references can be found at: https://ppbiodata.inpa. gov.br/metacatui/data.

To quantify heterogeneity in precipitation across the study area, we selected variables available in the WORLDCLIM database (Fick & Hijmans, 2017), which comprised interpolated surfaces from mean values over 50 years (1950–2000), and we extracted values per centroid geographic coordinates of each module using the DIVA-GIS software (Hijmans et al., 2012). The mean annual rainfall had the greatest amplitude (1930–2624 mm), so we used it as a proxy for the heterogeneity in precipitation in the study area (see Table S1).

Due to the high multicollinearity among environmental variables, both climatic and structural (Pearson r = 0.78-0.92, variance-inflation factor = 5.59-15.52), it was not possible to use them as independent variables in multiple parameter linear models. Therefore, to estimate the effects of environmental heterogeneity on taxonomic and functional distances, we converted basal area, soil clay content and precipitation into a matrix of Euclidean distances among paired modules. We call this an environmental gradient, which represents a distance-based estimate of the continuous spatial environmental heterogeneity by forest type, mainly on the basis of understorey openness (DOF and OOF). Subsequently, we performed a principal coordinate analysis (PCoA) applied to the functional distance and forest-type matrices.

2.4 | Effects of environmental and geographical distances on lizard assemblages

We undertook all analyses in R 4.0.2 (R Core Team, 2020), whose results can be seen in Figures S2 and S3. We used linear multiple regression on distance matrices to determine the effects of the environmental gradient, geographical distance and differences between forest types (DOF and OOF) on differences in taxonomic and functional lizard assemblages, separately. To evaluate the effects of geographical distance on the relationships between taxonomic or functional distances and environmental distances, we used partial multivariate correlograms, which we implemented in the ECODIST

R-package (Goslee & Urban, 2007). We constructed spatial correlograms using taxonomic or functional distances as response matrices, environmental distances as an ancillary matrix, 1000 permutations and 10 classes of geographical distance.

We additionally used partial correlations based on type III sums of squares to partition the variance in the taxonomic distance estimates between unique contributions of environmental gradient, geographical distance, forest type and unexplained variance. All the data used in this study can be found in the Supporting Information.

2.5 | Environmental filtering of species traits

To further investigate how environmental gradients affect the functional traits of species, we applied a complementary, categorical approach (Dray et al., 2007). RLQ is a co-inertia analysis that relates environmental data (R) to functional traits (Q) using species relative abundances (L) as a link (Southwood, 1977).

We implemented RLQ in the ADE4 R-package (Dray & Dufour, 2007), which performs a correspondence analysis on the L matrix and evaluates covariance between the R and Q matrices using a Hill-Smith PCA. To quantify environmental variation throughout the study area we applied a PCA on clay soil content, basal area and precipitation, and represented these gradients as three principal components axes. We did this separately for overall, arboreal and terrestrial assemblages, but in all cases, the first principal component axis mainly represented precipitation (99% of the captured variance), the second axis represented clay content (98%) and the third axis represented precipitation (99%). We also added forest type as a predictor variable and ran the analyses with species abundances standardized by the square root of total abundance, as implemented by the Hellinger standardization available in the VEGAN R-package (Oksanen et al., 2020). Then, we tested two combined null hypotheses, namely (i) distribution of species with fixed traits is not influenced by environmental variables and (ii) distribution of species along fixed environmental conditions is not influenced by species traits, for which we assessed coefficients based on 49,999 permutations (Farneda et al., 2015; Núñez et al., 2019).

To evaluate the effects of geographic distance on the relationships between species traits and environmental gradients, we used partial multivariate correlograms, which we implemented in the <u>PGIRMESS</u> R-package (Giraudoux, 2018). We constructed spatial correlograms based on 999 permutations, using the RLQ axes 1 and 2 as response variables and 10 classes of geographic distance.

3 | RESULTS

We found 27 species of lizards of 17 genera distributed in nine families (Table S2). Gymnophthalmidae was the richest family in the sample, represented by seven species. Among the most frequently sampled species were *Norops fuscoauratus* (85% of the modules,

n = 12), Chatogekko amazonicus (78%, n = 11) and Ameiva ameiva (71%, n = 10). Respectively, these species are a small arboreal anole, a tiny leaf litter gecko and a large terrestrial teiid.

3.1 | Phylogenetic structure of lizard assemblages

There was no evidence of phylogenetic overdispersion, based on either NTI and NRI (p > 0.8 in all cases), and little evidence of phylogenetic clustering, since values more positive than chance (p < 0.05) were generated for only two modules, and only when considering the entire functional tree (Figure 2). These findings indicate that neither environmental filters nor competitive interactions could be predicted by phylogenetic proximity.

3.2 | Effects of an environmental gradient and spatial autocorrelation

Although we expected a strong relationship between geographic distance and species composition of assemblages, taxonomic distance was not associated with either geographic distance or forest type. Taxonomic distance was associated only with environmental distance in all multiple linear models. Geographic distance did not affect taxonomic or functional similarity of assemblages in any model (Table S3), but forest type and the environmental gradient had independent effects on functional distances (see Figures S2 and S3).



FIGURE 2 Nearest Taxon Index (NTI) and Net Relatedness Index (NRI) values estimated for 14 sampling modules along the Amazonian Madeira-Purus interfluve. Positive values indicate lizard assemblages more clustered by phylogenetic proximity than chance, negative values indicate assemblages more overdispersed than chance. The phylogenetic hypothesis used is based on five mtDNA and seven nuclear gene fragments (Pyron et al., 2013).

Taxonomic and functional distances were not independent, but 26% positively related for the overall assemblages, 12% for arboreal assemblages and 22% for terrestrial assemblages (p < 0.0001 in all cases). Therefore, to better understand the independent correlations among variables, we carried out partial Mantel tests on all combinations of distance matrices. There were statistically significant partial correlations ($r_m = 0.21-61$) for all variables, but correlations with geographic distance after controlling for differences in environment or assemblage distances were generally weaker and mostly statistically not significant (Table S4). Terrestrial assemblages showed relatively strong effects of geographic distance, and although controlling for geographic distance, functional or taxonomic distances did not remove the effects of the other variables.

Species differed in their abundance along the environmental gradient (Figure 3a), such as *Loxopholis* and *Dactyloa* tended to cluster at one end of the gradient, but species of other genera, such as *Kentropyx* and *Norops*, occurred at opposite ends of the gradient or were spread along it. The assemblage-level trait means also differed along this gradient (Figure 3b), but most traits were more abundant in areas with more dense forest (Figure 3c). The PCoA showed that the difference in the trait means weighted by species proportional abundance were high enough to generate two distinct clusters that correspond to forest types (Figure 3d). For this analysis, we did not encode categorical traits as binary, to avoid inflating the variances captured.

The Mantel-based correlograms (see Figure 4) showed no spatial autocorrelation in taxonomic distance across 10 geographic distance classes (p > 0.1 in all cases). For functional distances, regardless of the assemblage coverage (overall, arboreal or terrestrial), there was positive spatial autocorrelation in only one distance class ($r_m = 0.68$ -0.76, p < 0.02 in all cases). This finding suggests that at Euclidean distances of approximately 178 km, lizard assemblages tend to be more functionally similar than chance, although spatial autocorrelation in smaller distances was not detected. A cluster analysis based on similarities among modules in the measured environmental gradient revealed that some pairs of modules 170–200 km apart are more environmentally similar to each other than geographically closer modules. Therefore, the spatial autocorrelation detected probably reflects similar habitat conditions which are not continuously distributed across the landscape.

Weak effects of geographic distance on taxonomic and functional distances were supported by partitioned variances among predictor variables. Unexplained proportions of variance were relatively high for functional distances (63%–91%). However, the variances explained by geographical distance were usually lower than environmental gradient or forest type in all models (see Figure S4).

3.3 | Environmental filtering for the composition of assemblages and species traits

The RLQ axes 1 and 2, respectively, captured 88.7% and 10.6% of the variance in trait-environment relationships for overall



FIGURE 3 Direct ordination of sampling modules along an environmental gradient or forest types within the Madeira-Purus interfluve. (a) Ordination along an environmental gradient showing the variation in the absolute abundance of lizard species (height of the columns). (b) Ordination along an environmental gradient showing the variation in the functional trait means weighted by proportional species abundance. (c) Ordination along two categorical forest levels (dense and open) showing the variation in weighted functional trait means. (d) Distribution of modules along two principal coordinate analysis (PCoA) axes summarizing functional distances among pairs of modules. Numbers in parentheses are proportional variances captured by each PCoA axis in relation to the original distances. Ellipses delimit 95% inertia.

assemblages, 89% and 10.9% for arboreal assemblages and 98.6% and 1.1% for terrestrial assemblages. For the overall assemblages, the Hill-Smith PCA summarizing the R matrix captured 47% of the variance in the environmental variables along its axis 1, which was mainly associated with differences in forest type and precipitation between sampling modules (Figure 5). According to the distribution of traits along the axis 1 derived from the Hill-Smith PCA applied to the Q matrix (which captured 48% of the original variance) and the

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FIGURE 4 Spatial correlograms based on partial Mantel tests applied to lizard taxonomic and functional distances among 14 paired modules along the Madeira-Purus interfluve, Brazilian Amazonia. Each Euclidean distance class is equivalent to approximately 89 km.

fourth-corner analysis, some variables affected certain characteristics, and these correlations are shown by the positive or negative sign. Thus, relationships were found for head length and width (+), arm length (+), and the occurrence of species with cryptic habits (+). The Hill–Smith PCA axes 2 applied on the matrices R and Q captured 30% and 29% of the original variances, respectively, and separated sampling modules by differences in clay content in the soil and basal area, differences in lizard body colour, thermoregulation mode and SVL. However, the combination of RLQ and fourth-corner analysis did not detect any significant relationship between species traits and environmental variables represented along this axis.

For the arboreal assemblages, the Hill–Smith PCA summarizing the R matrix captured 49% of the variance observed in the environmental variables in its axis 1, which separated sampling modules mainly by soil-clay content, forest type and precipitation. Combining the Hill–Smith PCA axis 1 applied to the matrix Q (which captured 61% of the original variance in the species traits) and the fourthcorner analysis revealed that these variables mainly affected arm length (+) and body colour (+ for brown colour, – for green colour). No relationship between species traits and environmental variables was detected along the RLQ axis 2.

For terrestrial assemblages, the Hill-Smith PCA summarizing the R matrix captured 42% of the variance observed in environmental variables in its axis 1, which separated sampling modules mainly by forest type and precipitation. Combining Hill-Smith PCA axis 1 applied on matrix Q (which captured 99% of the original variance in species traces) and the fourth-corner analysis revealed that these variables mainly affected SVL (-), length and head width (+), arm and leg length (+), occurrence of cryptic (+), heliotherm (-), non-heliotherm (+), brown-coloured (+) and greencoloured (-) species. No relationship between species traits and environmental variables was detected along RLQ axis 2. Detailed results from the RLQ+fourth-corner analysis can be found in Table S5. Spatial autocorrelation tests revealed that relationships between environmental variables and lizard species traits can be more similar than expected by chance (Figure 6). However, this finding is only applied when these relationships are represented by the RLQ axis 1, and within Euclidean distances less than 270 km. Complete results of spatial autocorrelation tests can be found in Table S6.

4 | DISCUSSION

Phylogenetic similarity is often used to predict the effects of environmental filters or competitive interactions on assemblage spatial structure (Fraga et al., 2018; Webb et al., 2002). The NRI and NTI estimates showed no evidence of lizard assemblages structured by phylogenetic clustering or overdispersion. This finding may be just a statistical artefact caused by the high sensitivity of these indices to the pool size of species that contribute to local assemblage (Kraft et al., 2007), or the evenness in which taxa are distributed over a phylogeny (Coronado et al., 2015). Alternatively, environmental filtering and competition associated with the frequency at which traits occur in an assemblage operate through adaptive pressure over generations, which cannot be detected without explicit identification of genetic loci under selection pressure. Additionally, NRI and NTI were particularly inefficient to detect assemblage structure in our study because the distributions of some species or functional traits were clumped along the environmental gradient while others were widely dispersed, indicating that the occurrence of both processes in the assemblages could impede the identification of significant effects of phylogenetic relatedness on assemblage structure under a neutral scenario.

Separating effects of distance and environment on assemblage composition is often difficult, and there is probably no universal solution applicable to all cases. Similarity species composition of assemblages tend to decrease with distance, but this depends on the dispersal ability of the species (Hubbell, 2001). Environment tends to vary stochastically over short distances, but small distances are unlikely to affect dispersal (Ricklefs & Lovette, 1999). Over larger distances, there tend to be large environmental gradients in climate and vegetation structure, and this induces collinearity in predictors of distance and environment (Qian & Ricklefs, 2012). At intermediate distances (<178 km), our results showed that most of the variance in assemblage dissimilarities caused by geographic distances reflects discontinuous environmental similarities along the interfluve.

Amazonian squamates tend to have wide distributions (Ávila-Pires, 1995; Nogueira et al., 2019; Ribeiro-Júnior & Amaral, 2016) and probably have high-dispersal ability across generations, as observed by some genetic analyses for some snake species in the Madeira-Purus Interfluve (Fraga et al., 2017). In spite of this we found that although some geographic distance should be expected to affect functional and taxonomic distances among paired lizard assemblages, the measured environmental gradient was generally a more powerful predictor of taxonomic distances and forest type was a better predictor of functional distances.



FIGURE 5 Outputs from a RLQ+ fourth-corner analysis applied to estimate the effects of environmental variables on lizard species traits along the Madeira-Purus interfluve, Brazilian Amazonia. The biplots show Hill-Smith PCAs (principal component analysis) summarizing environmental gradients and species traits, where vectors denote distances and directions from the centroid. The columns containing rectangles show positive (red), negative (blue) or non-significant (grey) relations between axes summarizing environmental variables and species traits. The analyses were run separately for assemblages composed of all sampled species (overall), only arboreal species and only terrestrial species.

The similarity in composition of assemblages was explained by differences in environmental gradients. The environment seems to have a strong effect, with influence on morphological and physiological traits for some species in this locality. Although most of the species sampled in this study are widely distributed across Amazonia (Ávila-Pires, 1995; Ribeiro-Júnior, 2015; Vitt et al., 2008), they were locally restricted to fractions of environmental gradients. Lizard species turnover along environmental gradients has been demonstrated in different regions within

Amazonia, especially related to distance from water courses (Faria et al., 2019; Moraes et al., 2016; Pinto, 2006). In such a case, local trait similarity within each forest type apparently results from density-dependent dispersal, since individuals tend to colonize neighbouring patches of similar habitats as population growth renders habitats nearly saturated (Holyoak et al., 2005). This may indicate general unsuitability for lizards, or competition with other groups that eat invertebrates, such as frogs and birds, in particular segments of environmental gradients.

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FIGURE 6 Spatial correlograms applied to test spatial autocorrelation in relationships between environmental variables and lizard species traits along the Madeira-Purus interfluve, Brazilian Amazonia, as estimated by a RLQ+fourth-corner analysis. Red circles are cases of significant spatial autocorrelation. Each distance class covers approximately 89km.

The environmental heterogeneity within the Madeira-Purus interfluvial region predicts spatial structure of lizard assemblages, mainly for terrestrial species through biotic complementarity among forest types or precipitation. Different forest types have emerged along the interfluve mainly as a consequence of the geomorphological modelling resulting from the Andean orogenesis (Bispo et al., 2009; Hoorn et al., 2010), which has generated certain biogeographic regions in relation to lizard functional traits, and species associations. The vegetation structure for the lizards is directly responsible for the supply of microhabitats and availability of food, besides acting for the regulation of the air temperature, and affecting direct solar incidence in forests (Silva & Araújo, 2008), and therefore may influence demographic patterns in assemblages. These thermoregulatory requirements are important for the physiological processes in tropical lizards, because they maintain several biological aspects of the species (Bergallo & Rocha, 1993; Huey & Slatkin, 1976; Ortega & Pérez-Mellado, 2016; Pontes et al., 2018). Dense and very humid forests usually contain highly stratified vegetation cover, which should generate more stable microenvironments and select for traits such as arboreality and passive thermoregulation (Magnusson & Silva, 1993). In contrast, OOF has relatively low plant density in the understorey, lower canopy levels and relatively low average rainfall, possibly making these environments conducive for occupation by heliothermic species (Silva & Araújo, 2008).

The effect of clay content on arboreal species may be an indirect effect, because soil texture affects invertebrate prey density and water retention (Menger et al., 2017). In Amazonia, soils with higher clay content have been associated with lower groundwater (Schietti et al., 2016), which may contribute to the pattern of co-occurrence of the species locally. Precipitation, however, is almost never evaluated in the studies of the spatial structure of assemblages of Amazonian lizards (Pinto, 2006; Vitt, 1991), but it is also an important factor for the climatic conditions of the environment, necessary for thermoregulation of the species, apart from influencing invertebrates that compose diet of several species (Rutschmann et al., 2016).

Our RLQ and fourth-corner analyses showed that head and limb size are highly associated with habitat use, probably because larger heads and longer limbs, respectively, generate greater ability to explore food resources and reach high speeds and higher locomotor performance in open forests (Vitt et al., 1997). In fact, it is widely known that relationships between morphological traits and environmental conditions can affect the permanence of species in habitats because they determine the ability to explore available resources (Caldwell & Vitt, 1999). Similarly, environmental conditions can select body colours through the efficiency of thermoregulation, intraspecific communication and evasion of predators under different background colours (Diamond & Bond, 2013). Specifically in our study system, our models have shown that brown species tend to occur more often in open forests, while green species tend to occur more often in dense forests. This finding may be related to the higher density of green moss in tree trunks in dense forests, which generate a background colour that should give camouflage advantages to green species. Therefore, the spatial distribution of colour morphs in our study area seems to be mediated by predation pressure, although this result could only be detected when we split the data into terrestrial and arboreal assemblages.

Although large Amazonian rivers are commonly reported as vicariant barriers promoting biodiversity in Amazonia (Antonelli et al., 2010; Boubli et al., 2015; Haffer, 1997; Ribas et al., 2012; Simões et al., 2008; Smith et al., 2014), the current habitat heterogeneity within the Madeira-Purus interfluve, which is hierarchically dependent on historical processes operating at wider spatial scales (Peixoto et al., 2020), efficiently predicts lizard assemblages. Future studies should investigate physiological traits, such as temperature sensitivity and resistance to desiccation, or genetic loci under adaptive selection to assess whether climatic seasonality creates enough stress for ecophysiological barriers to inhibit some evolutionary lineages, which would limit phylogenetic and functional diversity (Coronado et al., 2015; Miller et al., 2013; Qian et al., 2013) within open forests.

Conducting multi-faceted biodiversity assessments can provide a comprehensive vision of the organization of ecological communities over space and time, so our results are relevant for conservation because they show complementary biodiversity among sites that reflect the level of complexity of this interfluvial region, which has several distinct ecoregions based on bioclimatic variables, drainage density, altitude and slope (Ximenes et al., 2021). Since local species or trait subsets change across the landscape, the local lizard diversity is often unique, and therefore irreplaceable in the case of local extinction and degradation (Pressey et al., 1993). This is a special concern in the Madeira-Purus interfluve because the forests covering this region have been drastically disturbed by a federal highway crossing several reserves (Fearnside & Graça, 2006) and large This study is the first to evaluate environmental effects on Amazonian lizard assemblages from different geographical scales and identify that the structural heterogeneity along an environmental gradient has a significant impact on the taxonomic and functional composition of lizard assemblages. Environmental filtering related to vegetation types, precipitation and edaphic gradients along the Madeira-Purus interfluvial has caused species turnover, and determined the differences found between assemblages in dense and open forests.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Further details on methods, environmental gradients and references can be found at Data Bank|ppbio.inpa.gov.br/inicio.

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REFERENCES

Adams, D. C. (2014). A generalized K statistic for estimating phylogenetic signal from shape and other high-dimensional multivariate data.

Systematic Biology, 63, 685-697. https://doi.org/10.1093/sysbio/ syu030

Almeida-Corrêa, T., Frazão, L., Costa, D. M., Menin, M., & Kaefer, I. L. (2020). Effect of environmental parameters on squamate reptiles in an urban forest fragment in Central Amazonia. *Acta Amazonica*, 50, 239–245. https://doi.org/10.1590/1809-4392201904423

rnal of geograp<u>hy</u>

- Antonelli, A., Quijada-Mascareñas, A., Crawford, A. J., Bates, J. M., Velazco, P. M., & Wüster, W. (2010). Molecular studies and phylogeography of Amazonian tetrapods and their relation to geological and climatic models. In C. Hoorn & F. P. Wesselingh (Eds.), *Amazonia, landscape and species evolution* (Vol. 1, pp. 386–403). Blackwell Publishing.
- Ávila-Pires, T. C. S. (1995). *Lizards of Brazilian Amazonia (Reptilia: Squamata)* (1st ed.). Zoologische Verhandeligen Leiden.
- Barros, D. F., Albernaz, A. L. M., Zuanon, J., Espírito-Santo, H. M. V., Mendonça, F. P., & Galuch, A. V. (2013). Effects of isolation and environmental variables on fish community structure in the Brazilian Amazon Madeira-Purus interfluve. *Brazilian Journal* of Biology, 73, 491–499. https://doi.org/10.1590/S1519-69842 013000300005
- Bergallo, H. G., & Rocha, C. F. D. (1993). Activity pattern and body temperature of 405 two sympatric lizards with different foraging tactics in southeastern Brazil. *Amphibia Reptilia*, 4, 312–315.
- Bernardes, C., & Costa, F. R. C. (2011). Environmental variables and piper assemblage composition: A mesoscale study in the Madeira-Purus interfluve, Central Amazonia. *Biota Neotropica*, 11, 83–91. https:// doi.org/10.1590/S1676-06032011000300006
- Bispo, P. C., Valeriano, M. M., & Kuplich, T. M. (2009). Relation of local geomorphometric variables with the vegetation of the Madeira-Purus interfluve (AM/RO). Acta Amazonica, 39, 81–90. https://doi. org/10.1590/S0044-59672009000100008
- Bittencourt, S. (2008). Insularização como agente de fragmentação florestal em comunidades de lagartos da Amazônia Central. (Master thesis). Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia. https://bdtd.inpa.gov.br/handle/tede/1846
- Blomberg, S. P., Garland, T., & Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution*, 57, 717–745. https://doi.org/10.1111/j.0014-3820.2003. tb00285.x
- Borges, S. H., & Da-Silva, J. M. (2012). A new area of endemism for Amazonian birds in the Rio Negro Basin. *The Wilson Journal Ornithology*, 124, 15–23. https://doi.org/10.1676/07-103.1
- Boubli, J. P., Ribas, C., & Alfaro, J. W. L. (2015). Spatial and temporal patterns of diversification on the Amazon: A test of the riverine hypothesis for all diurnal primates of Rio Negro and Rio Branco in Brazil. *Molecular Phylogenetics and Evolution*, 82, 400–412. https:// doi.org/10.1016/j.ympev.2014.09.005
- Bueno, A. S., Bruno, R. S., Pimentel, T. P., Sanaiotti, T. M., & Magnusson, W. E. (2012). The width of riparian habitats for understory birds in an Amazonian forest. *Ecological Applications*, 22, 722–734. https:// doi.org/10.2307/41416795
- Cadotte, M. W., & Tucker, C. M. (2017). Should environmental filtering be abandoned? *Trends in Ecology & Evolution*, 32, 429–437. https://doi. org/10.1016/j.tree.2017.03.004
- Caldwell, J. P., & Vitt, L. J. (1999). Dietary asymmetry in leaf litter frogs and 426 lizards in a transitional northern Amazonian rain forest. *Oikos*, 84, 383–397.
- Campbell, H. W., & Christman, S. P. (1982). Field techniques for herpetofaunal community analysis. In N. J. Scott (Ed.), *Herpetological communities: A symposium of the Society for the Study of Amphibians and Reptiles and the Herpetologist's league* (Vol. 1, pp. 193–200). Department of Interior, Fish and Wildlife Service, Wildlife Research Report.
- Cavender-Bares, J., Kozak, K. H., Fine, P. V. A., & Kembel, S. W. (2009). The emerging of community ecology and phylogenetic biology. *EcologyLetters*, 12, 693–715. https://doi.org/10.1111/j.1461-0248.2009.01314.x

12 | Journal of Biogeogra

- Coronado, E. N. H., Dexter, K. G., Pennington, R. T., Chave, J., Lewis, L. J., Alexiades, M., Alvarez, E., de Oliveira, A. A., Amaral, I. L., Araujo-Murakami, A., Arets, E. J. M. M., Aymard, G. A., Baraloto, C., Bonal, D., Brienen, R., Cerón, C., Valverde, F. C., Di Fiore, A., Farfan-Rios, W., ... Phillips, O. L. (2015). Phylogenetic diversity of Amazonian tree communities. *Diversity and Distributions*, *2*1, 1295–1307. https://doi.org/10.1111/ddi.12357
- Cracraft, J. (1985). Historical biogeography and patterns of differentiation within the south American avifauna: Areas of endemisms. Ornithological Monographs, 36, 49–84. https://doi.org/10.2307/40168278
- Diamond, J., & Bond, A. B. (2013). *Concealing coloration in animals*. Belknap Press. An Imprint of Harvard University Press.
- Dias-Terceiro, R. G., Kaefer, I. L., Fraga, R., Araújo, M. C., Simões, P. I., & Lima, A. P. (2015). A matter of scale: Historical and environmental factors structure anuran assemblages from the upper Madeira River, Amazonia. *Biotropica*, 47, 259–266. https://doi.org/10.1111/ btp.12197
- Diaz, S., & Cabido, M. (2001). Vive la difference: Plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, 16, 646–655. https://doi.org/10.1016/S0169-5347(01)02283-2
- Dray, S., & Dufour, A. B. (2007). The ade4 package: Implementing the duality diagram for ecologists. *Journal of Statistical Software*, 22, 1–20.
- Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity. Biological Conservation, 61, 1–10. https://doi.org/10.1016/0006-3207 (92)91201-3
- Faria, A. S., Menin, M., & Kaefer, I. L. (2019). Riparian zone as a main determinant of the structure of lizard assemblages in upland Amazonian forests. *Austral Ecology*, 44, 850–858. https://doi. org/10.1111/aec.12754
- Farneda, F. Z., Rocha, R., López-Baucells, A., Groenenberg, M., Silva, I., Palmeirim, J. M., Bobrowiec, P. E. D., & Meyer, C. F. J. (2015). Trait-related responses to habitat fragmentation in Amazonian bats. *Journal of Applied Ecology*, 52, 1381–1391. https://doi. org/10.1111/1365-2664.12490
- Fearnside, P. M. (2014). Impacts of Brazil's Madeira river dams: Unlearned lessons for hydroelectric development in Amazonia. *Environmental Science & Policy*, 38, 164–172. https://doi.org/10.1016/j. envsci.2013.11.004
- Fearnside, P. M., & Graça, P. M. L. A. (2006). BR-319: Brazil's Manaus-Porto Velho highway and the potential impact of linking the arc of deforestation to Central Amazonia. *Environmental Management*, 38, 705–716. https://doi.org/10.1007/s00267-005-0295-y
- Fick, S. E., & Hijmans, R. J. (2017). Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas. *The International Journal of Climatology*, 37, 4302–4315. https://doi.org/10.1002/ joc.5086
- Fluck, I. E., Cáceres, N., Hendges, C. D., Brum, M. N., & Dambros, C. S. (2020). Climate and geographic distance are more influential than rivers on the beta diversity of passerine birds in Amazonia. *Ecography*, 43, 1–9. https://doi.org/10.1111/ecog.04753
- Fraga, R., Ferrão, M., Stow, A. J., Magnusson, W. E., & Lima, A. P. (2018). Different environmental gradients affect different measures of snake β-diversity in the Amazon rainforests. *PeerJ*, 6, e5628. https://doi.org/10.7717/peerj.5628
- Fraga, R., Lima, A. P., & Magnusson, W. E. (2011). Mesoscale spatial ecology of a tropical snake assemblage: The width of riparian corridors in Central Amazonia. *Herpetology Journal*, 21, 51–57.
- Fraga, R., Lima, A. P., Magnusson, W. E., Ferrão, M., & Stow, A. J. (2017). Contrasting patterns of gene flow for Amazonian snakes that actively forage and those that wait in ambush. *Journal of Heredity*, 108, 524–534. https://doi.org/10.1093/jhered/esx051
- Garland, T., Jr., & Losos, J. B. (1994). Ecological morphology of locomotor performance in squamate reptiles. In P. C. Wainwright & S. M. Reilly (Eds.), *Ecological morphology: Integrative organismal biology* (pp. 240– 302). University of Chicago Press.

- Giraudoux, P. (2018). Pgirmess: Spatial analysis and data mining for field ecologists. R Package Version 1.6.9. https://cran.r-project.org/ package=pgirmess
- Gomes, V., Carretero, M. A., & Kaliontzopoulou, A. (2016). The relevance of morphology for habitat use and locomotion in two species of wall lizards. *Acta Oecologica*, 70, 87–95.
- Gómez-Ortiz, Y. G., & Moreno, C. E. (2017). La diversidad funcional en comunidades animales: Una revisión que hace énfasis en los vertebrados. *Animal Biodiversity and Conservation*, 40, 165–174.
- Goslee, S. C., & Urban, D. L. (2007). The ecodist package for dissimilaritybased analysis of ecological data. *Journal of Statistical Software*, 22, 1–19. https://doi.org/10.18637/jss.v022.i07
- Gotelli, N., & Entsminger, G. L. (2003). Swap algorithms in null model analysis. *Ecology*, 84, 532–535.
- Haffer, J. R. (1997). Alternative models of vertebrate speciation in Amazonia: An overview. *Biodiversity and Conservation*, *6*, 451-476.
- Hijmans, R. J., Guarino, L., & Mathur, P. (2012). DIVA-GIS version 7.5. http://www.diva-gis.org
- Holyoak, M., Leibold, M. A., & Holt, R. D. (2005). Metacommunities: Spatial dynamics and ecological communities. University of Chicago Press.
- Hoorn, C., Wesselingh, F. P., ter Steege, H., Bermudez, M. A., Mora, A., Sevink, J., Sanmartín, I., Sanchez-Meseguer, A., Anderson, C. L., Figueiredo, J. P., Jaramillo, C., Riff, D., Negri, F. R., Hooghiemstra, H., Lundberg, J., Stadler, T., Särkinen, T., & Antonelli, A. (2010). Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science*, 330, 927-931. https://doi. org/10.1126/science.1194585
- Hubbell, S. P. (2001). The unified neutral theory of biodiversity and biogeography. Princeton University Press.
- Huey, R. B., & Slatkin, M. (1976). Costs and benefits of lizard thermoregulation. Quarterly Review of Biology, 51, 363–384. https://doi. org/10.1086/409470
- IBGE. (1997). Instituto Brasileiro de Geografia e Estatística. Recursos Naturais e Meio Ambiente: Uma visão Do Brasil. http://biblioteca. ibge.gov.br
- Juen, L., & De-Marco, P. (2012). Dragonfly endemism in the Brazilian Amazon: Competing hypotheses for biogeographical patterns. *Biodiversity and Conservation*, 21, 3507–3521. https://doi. org/10.1007/s10531-012-0377-0
- Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P., & Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26, 1463–1464. https://doi.org/10.1093/bioinformatics/btq166
- Kraft, N. J. B., Cornwell, W. K., Webb, C. O., & Ackerly, D. D. (2007). Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *The American Naturalist*, 170, 271–283. https://doi.org/10.1086/519400
- Laliberté, E., Legendre, P., Shipley, B., & Laliberté, M. E. (2014). Package 'FD'. Measuring functional diversity from multiple traits, and other tools for functional ecology. https://mran.microsoft.com/snapshot/2014-11-17/web/packages/FD/FD.pdf
- Lobão, P. S. P. (2008). Associações no uso do habitat por cinco espécies de lagartos amazônicos. (Master thesis). Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia. https:// bdtd.inpa.gov.br/handle/tede/731
- Magnusson, W. E., & Silva, E. V. (1993). Relative effects of size, season and species on the diets of some Amazonian savanna lizards. *Journal of Herpetology*, *27*, 380–385.
- Magnusson, W. E., Braga-Neto, R., Pezzini, F., Baccaro, F., Bergallo, H., Penha, J., Rodrigues, D., Verdade, L. M., Lima, A., Albernaz, A. L., Hero, J.-M., Lawson, B., Castilh, C., Drucker, D., Franklin, E., Mendonça, F., Costa, F., Galdino, G., Castley, G., ... Mendes Ponte, A. R. (2013). Biodiversidade e Monitoramento Ambiental Integrado: o sistema RAPELD na Amazônia (1st ed.). Áttema.

- Magnusson, W. E., Lima, A. P., Luizão, R., Luizão, F., Costa, F. R. C., Castilho, C. V., & Kinupp, V. F. (2005). RAPELD: A modification of the gentry method for biodiversity surveys in long-term ecological research sites. *Biota Neotropica*, *5*, 1–6. https://doi.org/10.1590/ S1676-06032005000300002
- Marciente, R., Bobrowiec, P. E. D., & Magnusson, W. E. (2015). Groundvegetation cutter affects phyllostomid bat assemblage structure in lowland Amazonian forest. *PLoS ONE*, 10, e0129560. https://doi. org/10.1371/journal.pone.0129560
- Mazel, F., Pennel, M. W., Cadotte, M. W., Diaz, S., Riva, G. V. D., Grenyer, R., Leprieur, F., Mooers, A. O., Mouillot, D., Tucker, C. M., & Pearse, W. D. (2018). Prioritizing phylogenetic diversity captures functional diversity unrealiably. *Nature Communications*, 9, 1–9. https://doi. org/10.1038/s41467-018-05126-3
- McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends* in Ecology & Evolution, 21, 178–185. https://doi.org/10.1016/j. tree.2006.02.002
- Menger, J., Magnusson, W. E., Anderson, M. J., Schlege, M., Pe'er, G., & Henle, K. (2017). Environmental characteristics drive variation in Amazonian understorey bird assemblages. *PLoS ONE*, 12, e0171540. https://doi.org/10.1371/journal.pone.0171540
- Miller, E. T., Zanne, A. E., & Ricklefs, R. E. (2013). Niche conservatism constrains Australian honeyeater assemblages in stressful environments. *Ecology Letters*, 16, 1186–1194. https://doi.org/10.1111/ ele.12156
- Moraes, L. F. P. (2008). Diversidade beta em comunidades de lagartos em duas Ecorregiões distintas na Amazônia. (Master thesis). Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia. https://bdtd.inpa.gov.br/handle/tede/736
- Moraes, L. J., Pavan, D., Barros, M. C., & Ribas, C. C. (2016). The combined influence of riverine barriers and flooding gradients on biogeographical patterns for amphibians and squamates in south eastern Amazonia. *Journal of Biogeography*, 43, 2113–2124. https://doi. org/10.1111/jbi.12756
- Nogueira, C., Argôlo, A. J. S., Arzamendia, V., Azevedo, J. A., Barbo, F. E., Bérnils, R. S., Bolochio, B. E., Borges-Martins, M., Brasil-Godinho, M., Braz, H., Buononato, M. A., Cisneros-Heredia, D. F., Colli, G. R., Costa, H. C., Franco, F. L., Giraudo, A., Gonzalez, R. C., Guedes, T., Hoogmoed, M. S., ... Martins, M. (2019). Atlas of Brazilian snakes: Verified point-locality maps to mitigate the Wallacean shortfall in a megadiverse snake fauna. South American Journal of Herpetology, 14, 1–274. https://doi.org/10.2994/SAJH-D-19-00120.1
- Noriega, J. A., & Realpe, E. (2018). Altitudinal turnover of species in a neotropical peripheral mountain system: A case study with dung beetles (Coleoptera: Aphodiinae and Scarabaeinae). Environmental Entomology, 47(6), 1376–1387.
- Núñez, S. F., López-Baucells, A., Rocha, R., Farneda, F. Z., Bobrowiec, P. E. D., Palmeirim, J. M., & Meyer, C. F. J. (2019). Echolocation and stratum preference: Key trait correlates of vulnerability of insectivorous bats to tropical forest fragmentation. *Frontiers in Ecology and Evolution*, 7, 1–12. https://doi.org/10.3389/fevo.2019.00373
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2020). Vegan: Community ecology package. https://cran.r-project.org/web/packages/vegan/index.html
- Oliveira, D. P., de-Carvalho, V. T., & Hrbek, T. (2016). Cryptic diversity in the lizard genus *plica* (Squamata): Phylogenetic diversity and Amazonian biogeography. *Zoologica Scripta*, 45, 630–641. https:// doi.org/10.1111/zsc.12172
- Ortega, Z., & Pérez-Mellado, V. (2016). Seasonal patterns of body temperature and microhabitat selection in a lacertid lizard. *Acta Oecologica*, 77, 201e206. https://doi.org/10.1016/J.ACTAO.2016.08.006
- Peixoto, G. M., Fraga, R., Araújo, M. C., Kaefer, I. L., & Lima, A. P. (2020). Hierarchical effects of historical and environmental factors on lizard assemblages in the upper Madeira river, Brazilian

Amazonia. PLoS ONE, 15, e0233881. https://doi.org/10.1371/journ al.pone.0233881

geography

-WILEY

- Peña-Joya, K. E., Cupul-Magaña, F. G., Rodríguez-Zaragoza, F. A., Moreno, C. E., & Téllez-López, J. (2020). Spatio-temporal discrepancies in lizard species and functional diversity. *Community Ecology*, 21(1), 1–12. https://doi.org/10.1007/s42974-020-00005-8
- Petchey, O. L., Evans, K. L., Fishburn, I. S., & Gaston, K. J. (2007). Low functional diversity and no redundancy in British avian assemblages. *Journal of Animal Ecology*, 76, 977–988. https://doi. org/10.1111/j.1365-2656.2007.01271.x
- Pinto, M. G. M. (2006). Diversidade beta, métodos de amostragem e influência de fatores ambientais sobre uma comunidade de lagartos na Amazônia Central. (PhD dissertation). Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia. https:// bdtd.inpa.gov.br/handle/tede/947
- Pontes-da-Silva, E., Magnusson, W. E., Sinervo, B., Caetano, G. H., Miles, D. B., Colli, G. R., & Werneck, F. P. (2018). Extinction risks forced by climatic change and intraspecific variation in the thermal physiology of a tropical lizard. *Journal of Thermal Biology*, 73, 50-60. https://doi.org/10.1016/j.jtherbio.2018.01.013
- PPBio. (2020). Repository. ppbio.inpa.gov.br/en/repository
- Pressey, R. L., Humphries, C. J., Margules, C. R., Vane-Wright, R. I., & Williams, P. H. (1993). Beyond opportunism: Key principles for systematic reserve selection. *Trends in Ecology & Evolution*, 8, 124–128. https://doi.org/10.1016/0169-5347(93)90023-I
- Pyron, R., Burbink, F. T., & Wiens, J. J. (2013). A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. BMC Evolutionary Biology, 13, 1–53. https://doi. org/10.1186/1471-2148-13-93
- Qian, H., & Ricklefs, R. E. (2012). Disentangling the effects of geographic distance and environmental dissimilarity on global patterns of species turnover. *Global Ecology and Biogeography*, 21, 341–351. https://doi.org/10.1111/j.1466-8238.2011.00672.x
- Qian, H., Swenson, N. G., & Zhang, J. (2013). Phylogenetic beta diversity of angiosperms in North America. *Global Ecology and Biogeography*, 22, 1152–1161. https://doi.org/10.1111/geb.12076
- R Development Core Team. (2020). A language and environment for statistical computing. R Foundation for Statistical Computing. https:// cran.r-project.org
- Ribas, C. C., Aleixo, A., Nogueira, A. C. R., Miyaki, C. Y., & Cracraft, J. (2012). A palaeobiogeographic model for biotic diversification within Amazonia over the past three million years. *Proceedings of the Royal Society B: Biological Sciences*, 279, 681–689. https://doi. org/10.1098/rspb.2011.1120
- Ribeiro-Júnior, M. A. (2015). Catalogue of distribution of lizards (Reptilia: Squamata) from the Brazilian Amazonia. II. Gekkonidae, Phyllodactylidae, Sphaerodactylidae. *Zootaxa*, 3981, 1–55. https:// doi.org/10.11646/zootaxa.3981.1.1
- Ribeiro-Júnior, M. A., & Amaral, S. (2016). Diversity, distribution, and conservation of lizards (Reptilia: Squamata) in the Brazilian Amazonia. Neotropical Biodiversity, 2, 195–421. https://doi. org/10.1080/23766808.2016.1236769
- Ricklefs, R. E., & Lovette, I. J. (1999). The roles of Island area per se and habitat diversity in the species-area relationships of four lesser Antillean faunal groups. *Journal of Animal Ecology*, *68*, 1142–1160. https://doi.org/10.1046/j.1365-2656.1999.00358.x
- Rojas-Ahumada, D. P., Landeiro, V. L., & Menin, M. (2012). Role of environmental and spatial processes in structuring anuran communities across a tropical rain forest. *Austral Ecology*, *37*, 865–873. https://doi.org/10.1111/j.1442-9993.2011.02330.x
- Ron, S. R. (2000). Biogeographic area relationships of lowland neotropical rainforest based on raw distributions of vertebrate groups. *Biological Journal of the Linnean Society London*, 71, 379–402. https://doi.org/10.1111/j.1095-8312.2000.tb01265.x
- Rutschmann, A., Miles, D. B., Le-Galliard, G. F., Richard, M., Moulherat, S., Sinervo, B., & Clobert, J. (2016). Climate and habitat interact to

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> shape the thermal reaction norms of breeding phenology across lizard populations. *Journal of Animal Ecology*, *85*, 457–466. https://doi. org/10.1111/1365-2656.12473

- Santorelli-Jr, S., Magnusson, W. E., & Deus, C. P. (2018). Most species are not limited by an Amazonian river postulated to be a border between endemism areas. *Scientific Reports*, 8(1), 2294. https://doi. org/10.1038/s41598-018-20596-7
- Santos, E. S., Maia, R., & Macedo, R. H. (2009). Condition-dependent resource value affects male-male competition in the blue-black grassquit. *Behavioral Ecology*, 20, 553–559. https://doi.org/10.1093/ beheco/arp031
- Schietti, J., Martins, D., Emilio, T., Souza, P. F., Levis, C., & Baccaro, F. B. (2016). Forest structure along a 600 km transect of natural disturbances and seasonality gradients in Central-Southern Amazonia. *Journal of Ecology*, 104, 1335–1346. https://doi. org/10.1111/1365-2745.12596
- Silva, V. N., & Araújo, A. F. B. (2008). Ecologia dos lagartos brasileiros (1st ed.). Technical Books Editora.
- Simões, P. I., Lima, A. P., & Magnusson, W. E. (2008). Acoustic and morphological differentiation in the frog *Allobates femoralis*: Relationships with the upper Madeira River and other potential geological barriers. *Biotropica*, 40, 607–614. https://doi.org/10.1111/j.1744-7429.2008.00416.x
- Sinervo, B., Mendez-De-La-Cruz, F., Miles, D. B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., Lara-Resendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M. L., Meza-Lázaro, R. N., Gadsden, H., Avila, L. J., Morando, M., De la Riva, I. J., Sepulveda, P. V., Rocha, C. F. D., Ibargüengoytía, N., Puntriano, C. A., Massot, M., ... Sites, J. W., Jr. (2010). Erosion of lizard diversity by climate change and altered thermal niches. *Science*, *328*(5980), 894–899.
- Smith, A. L., Bull, C. M., Gardner, M. G., & Driscoll, D. A. (2014). Life history influences how fire affects genetic diversity in two lizard species. *Molecular Ecology*, 23, 2428–2441. https://doi.org/10.1111/mec.12757
- Southwood, T. R. E. (1977). Habitat, the templet for ecological strategies? Journal of Animal Ecology, 46(2), 337-365. https://doi. org/10.2307/3817
- Uetz, P., Freed, P., & Hošek, J. (2020). The Reptile Database. http://www. reptile-database.org
- Vernes, K., Pope, L. C., Hill, C. J., & Bärlocher, F. (2005). Seasonality, dung specificity and competition in dung beetle assemblages in the Australian wet tropics, North-Eastern Australia. *Journal of Tropical Ecology*, 21, 1–8.
- Vitt, L. J. (1991). Ecology and life history of the wide-foraging lizard Kentropyx calcarata (Teiidae) in Amazonian Brazil. Canadian Journal of Zoology, 69, 2791–2799. https://doi.org/10.1139/z91-393
- Vitt, L. J., Magnusson, W. E., Ávila-Pires, T. C. S., & Lima, A. P. (2008). Guide to the lizards of Reserva Adolpho Ducke (1st ed.). Central Amazonia. Áttema Design Editorial.
- Vitt, L. J., Sartorius, S. S., Ávila-Pires, T. C. S., & Espósito, M. C. (2001). Life on the leaf litter: The ecology of Anolis nitens tandai in the Brazilian Amazon. Copeia, 2, 401–412. https://doi.org/10.1643/0045-8511
- Vitt, L. J., Sartorius, S. S., Ávila-Pires, T. C. S., Esposito, M. C., & Miles, D. B. (2000). Niche segregation among sympatric Amazonian teiid lizards. *Oecologia*, 122, 410-420. https://doi.org/10.1007/s0044 20050047

- Vitt, L. J., Zani, P. A., & Lima, A. P. (1997). Heliotherms in tropical rain forest: The ecology of *Kentropyx calcarata* (Teiidae) and *Mabuya nigropunctata* (Scincidae) in the Curuá-una of Brazilian. Journal of Tropical Ecology, 13, 199–220. https://doi.org/10.1017/S0266 467400010415
- Webb, C. O., Ackerly, D. D., McPeek, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. Annual Review of Ecology, Evolution, and Systematics, 33, 475–505.
- Winter, M., Devictor, V., & Schweiger, O. (2013). Phylogenetic diversity and nature conservation: Where are we? Trends in Ecology & Evolution, 28, 199–204. https://doi.org/10.1016/j.tree.2012.10.015
- Ximenes, A. C., Amaral, S., Monteiro, A. M. V., Almeida, R. M., & Valeriano, D. M. (2021). Mapping the terrestrial ecoregions of the Purus-Madeira interfluve in the Amazon Forest using machine learning techniques. *Forest Ecology and Management*, 488, 118960. https:// doi.org/10.1016/j.foreco.2021.118960

BIOSKETCH

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SUPPORTING INFORMATION

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

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