The role of environmental gradients and microclimates in structuring communities and functional groups of lizards in a rainforest-savanna transition area

Alan F. Souza-Oliveira[1], Gabriela Zuquim[2,3], Lidia F. Martins[1], Lucas N. Bandeira[1], Luisa Maria Diele-Viegas[4], Victor H.G.L. Cavalcante[5], Fabricio Baccaro[6], Guarino Rinaldi Colli[5], Hanna Tuomisto[3] and Fernanda P. Werneck[1]

[1] Coordenação de Biodiversidade, Instituto Nacional de Pesquisa da Amazonia, Manaus, Amazonas, Brazil
[2] Section for Ecoinformatics and Biodiversity, Department of Biology, Aarhus University, Aarhus, Denmark
[3] Department of Biology, University of Turku, Turku, Finland
[4] Department of Biology, University of Maryland, College Park, United States of America
[5] Departamento de Zoologia, Universidade de Brasília, Brasília, Distrito Federal, Brazil
[6] Departamento de Biologia, Universidade Federal do Amazonas, Manaus, Amazonas, Brazil

Corresponding author
Alan F. Souza-Oliveira,
alanfilipe123@gmail.com

ABSTRACT

Environmental heterogeneity poses a significant influence on the functional characteristics of species and communities at local scales. Environmental transition zones, such as at the savanna-forest borders, can act as regions of ecological tension when subjected to sharp variations in the microclimate. For ectothermic organisms, such as lizards, environmental temperatures directly influence physiological capabilities, and some species use different thermoregulation strategies that produce varied responses to local climatic conditions, which in turn affect species occurrence and community dynamics. In the context of global warming, these various strategies confer different types of vulnerability as well as risks of extinction. To assess the vulnerability of a species and understand the relationships between environmental variations, thermal tolerance of a species and community structure, lizard communities in forest-savanna transition areas of two national parks in the southwestern Amazon were sampled and their thermal functional traits were characterized. Then, we investigated how community structure and functional thermal variation were shaped by two environmental predictors (*i.e.*, microclimates estimated locally and vegetation structure estimated from remote sensing). It was found that the community structure was more strongly predicted by the canopy surface reflectance values obtained *via* remote sensing than by microclimate variables. Environmental temperatures were not the most important factor affecting the occurrence of species, and the variations in ecothermal traits demonstrated a pattern within the taxonomic hierarchy at the family level. This pattern may indicate a tendency for evolutionary history to indirectly influence these functional features. Considering the estimates of the thermal tolerance range and warming tolerance, thermoconformer lizards are likely to be more vulnerable and at greater risk of extinction due to global warming than thermoregulators. The latter, more associated with open environments, seem to take advantage of their lower vulnerability and occur in both habitat types across the transition, potentially out-competing and further increasing the risk of extinction and vulnerability of forest-adapted thermoconformer lizards in these transitional areas.

INTRODUCTION

Investigating the factors that determine the structure of biological communities and their composition has been a longstanding interest in ecology (*Ricklefs, 1987*; *Huston, 1999*), with many implications for understanding biodiversity patterns and conservation. Different processes acting at different spatial and temporal scales often interact to structure diversity and community assembly. Historical processes (*e.g.*, extinction, speciation, and dispersal in response to tectonic, eustatic, climatic, and oceanographic events) have a more substantial influence at the global and regional levels, while ecological processes (*e.g.*, species interactions, disturbance, and dispersal and drift along environmental gradients) have greater importance at local levels (*Cavender-Bares et al., 2009*; *Algar, Kerr & Currie, 2011*; *Rapacciuolo & Blois, 2019*). Local effects tend to be particularly relevant particularly for taxonomic groups with relative dispersal limitations and an intrinsic association with environmental variables. This is especially the case of groups such as lizards and other ectothermic organisms (*Pianka & Vitt, 2003*; *Lewthwaite, Debinski & Kerr, 2017*). At finer scales, factors such as edaphic characteristics (*Whitney & Alonso, 1998*; *Pepper & Keogh, 2021*), vegetation structure (*Jellineck, Driscoll & Kirkpatrick, 2004*; *Tews et al., 2004*) and microhabitat availability (*Garda et al., 2013*) are very influential because environmental heterogeneity can provide shelter, breeding and thermoregulation sites, and modulate biotic interactions. Moreover, environmental variations along ecological gradients or habitat transitions (*e.g.*, savanna-forest ecotones) bring about different selection pressures for maintaining populations (*Chevin, Lande & Mace, 2010*; *Seebacher, White & Franklin, 2015*), which generate regions of physiological and ecological tension that can interfere with the functional characteristics of the species and filter species occurrences (*Liautaud, Barbier & Loreau, 2020*).

Functional aspects of species have recently gained importance in community ecology studies (*Mouillot et al., 2011*), and are often combined with new tools and metrics to investigate species diversity and the encompassing environmental variations. Remote sensing, for instance, provides global and easily accessible data that serve as a proxy for vegetation structure and composition at different spatial scales (*Tuomisto et al., 2003a*; *Tuomisto et al., 2003b*; *Tuomisto et al., 2019*; *Turner et al., 2003*; *Salovaara et al., 2005*; *Rocchini et al., 2018*). On the other hand, microclimate variables that are remotely inferred using modeling (*Algar, Morley & Boyd, 2018*) or directly measured on the ground with data loggers (*Alvarenga et al., 2017*) can provide greater refinement and accuracy in quantifying microhabitat variations (*Milling et al., 2018*). Together, functional traits, remote sensing, and microclimate variables can help to better characterize species-environment interactions and distribution of organisms (*Petchey & Gaston, 2002*; *Maximiano et al., 2020*).

Temperature is a significant driver of biodiversity in multiple spatial and temporal dimensions (*Waldock, Dornelas & Bates, 2018*) since it directly affects species distribution and physiological traits, and the activity, growth, and reproduction of individuals

(*Savage et al., 2004*; *Angilletta, 2009*). Lizards, for example, can vary the efficiency of their essential physiological functions according to environmental temperatures (*Angilletta, 2009*). The influence of environmental temperatures on physiological traits can be described using the shape of thermal performance curves. Their limits represent the minimum and maximum body temperatures supported by the individuals (*i.e.,* the critical temperatures that limit their physiological functions), and the range between these limits represents their thermal tolerance; and the maximal point in of the curve is related to the optimal temperature at which the animal can achieve its maximum performance (*Huey & Slatkin, 1976*; *Deutsch et al., 2008*; *Grigg & Buckley, 2013*; *Taylor et al., 2020*). Ectotherms modulate their body temperature according to the environment in two primary ways. Active thermoregulators, such as heliothermic organisms, actively maintain their body temperatures (Tb) within a specific range that is close to the optimum of their physiological performance (*Huey & Slatkin, 1976*; *Angilletta, 2009*), while thermoconformers passively align their Tb with the environmental temperature and usually present a broader range of optimal physiological temperatures (*Angilletta, 2009*). Environmental characteristics can also restrict or expand the species' thermal abilities. For example, the low availability of sunlight spots in forest environments may cause species of forest lizards to have more restricted thermoregulation skills than those associated with open areas and even the thermoconformers (*Huey et al., 2009*; *Piantoni et al., 2019*).

The effects of climate change might be negative (*e.g.*, lead to range loss, local extinction), positive (*e.g.*, cause range expansion), or neutral for lizard species worldwide (*Diele-Viegas et al., 2020*) and may end up enabling warm-adapted, open-habitat competitors to invade forests and change community dynamics (*Huey et al., 2009*). Due to climate change, the thermal limits of tropical lizards will probably be exceeded in the following decades, making them and the tropical region particularly vulnerable to climate change (*Deutsch et al., 2008*; *Sinervo et al., 2010*; *Diele-Viegas et al., 2020*). Additionally, assessing the warming tolerance of these species can serve as a crucial proxy for evaluating vulnerability at both the population and community levels (*Anderson, Meiri & Chapple, 2022*). Therefore, expanding the understanding of the diversity of lizards and how physiological challenges in forest-savanna ecotones affect community assembly can help forecast the impacts of climate change on tropical biodiversity. The Amazon basin is a large mosaic composed of diverse landscapes (*Tuomisto et al., 2019*; *Silva-Souza & Souza, 2020*) that range from flooded and non-flooded forests to open ecosystems such as white-sand ecosystems (*Adeney et al., 2016*; *García-Villacorta, Dexter & Pennington, 2016*) and savanna enclaves (*Ab'Sáber, 2002*). This heterogeneity of habitats favors a high diversity of species in various taxonomic groups, and promotes the emergence of subpopulations through habitat specificity (*Tuomisto, Ruokolainen & Yli-Halla, 2003*; *Pomara, Ruokolainen & Young, 2014*; *Menger et al., 2017*). Nevertheless, it is unknown how species composition and thermal traits of species at local scales are related to micro- and macro-climatic variables. It may be particularly relevant in these Amazonian landscapes with forest, and savanna vegetation abruptly replaced.

Therefore, using new tools such as functional quantification *via* ecophysiology traits and environmental classification through remote sensing and micro-climate variables, we seek to test the following hypothesis and predictions: (i) The high environmental

variation hypothesis suggests that the local occurrence of species and the assembly of lizard communities along a natural forest-savanna gradient in the Amazon are influenced by the high environmental heterogeneity. In line with this hypothesis, we predict that both micro-climatic and canopy reflectance variables will explain the turnover of lizard species composition, and indicate the influence of ecological factors on species assembly; (ii) The thermal trait variation hypothesis proposes that there are variations in these functional features across communities along the forest-savanna gradient, and that this variation is related to the different environmental characteristics along this gradient. Based on this hypothesis, we predict that species that are restricted to savanna and forest areas will exhibit distinct thermal functional variations, specifically, forest lizards, due to their more limited thermoregulation skills; (iii) The final hypothesis is the variation in vulnerability hypothesis, which suggests that there are implications for climate change vulnerability at the community level, and that these implications differ between savanna and forest communities. Consistent with this hypothesis, we predict that community vulnerability, assessed by species' warming tolerance (WT), varies across habitats. In particular, given the higher prevalence of thermoconformers in forest environments, we expect them to display greater vulnerability to climate change compared to thermoregulatory species, which are more commonly found in savanna areas.

METHODS

Study area

This study was carried out in two protected areas of the southwestern Brazilian Amazon: the Campos Amazônicos National Park (CANP) and the Mapinguari National Park (MNP) (Fig. 1). CANP is on the right (eastern) bank of the Madeira River in the municipality of Manicoré, Amazonas (8°30′S, 61°40′W) and has a total area of 961,318 ha (ICMBio, 2009). The area was sampled for 15 days in November 2017, at the beginning of the rainy season. The landscape consists mainly of extensive natural savannas, which consist of scattered trees amid a layer of grasses and shrubs. These savannas are presumably relics from the expansion of the Cerrado over the Amazon during the Quaternary interglacial periods (Josué Azevedo et al., 2020). The CANP also includes smaller areas of closed-canopy *terra-firme* forests, which are characterized by larger trees and a shaded understory. Deforestation due to livestock farming, gold mining, logging, and fire has impacted some areas of the park and its surroundings (ICMBio, 2009). With about 1,776,914 ha, the Mapinguari National Park (MNP), located on the left bank (western) bank of the Madeira River in the municipality of Humaitá (7°53′S, 63°51′W), was also sampled over 15 days in November and December 2017, at the beginning of the rainy season. MNP also features extensive savannas that, unlike those of CANP, are associated with geological events that affected sedimentation patterns, thus creating sharp edaphic boundaries (Rossetti et al., 2019). MNP faces similar threats as a result of current human pressure.

Sampling

In each area, the lizard community was sampled using pitfalls traps. Each trap consisted of four 35 L buckets buried at ground level forming a "Y" shape, with one bucket at each
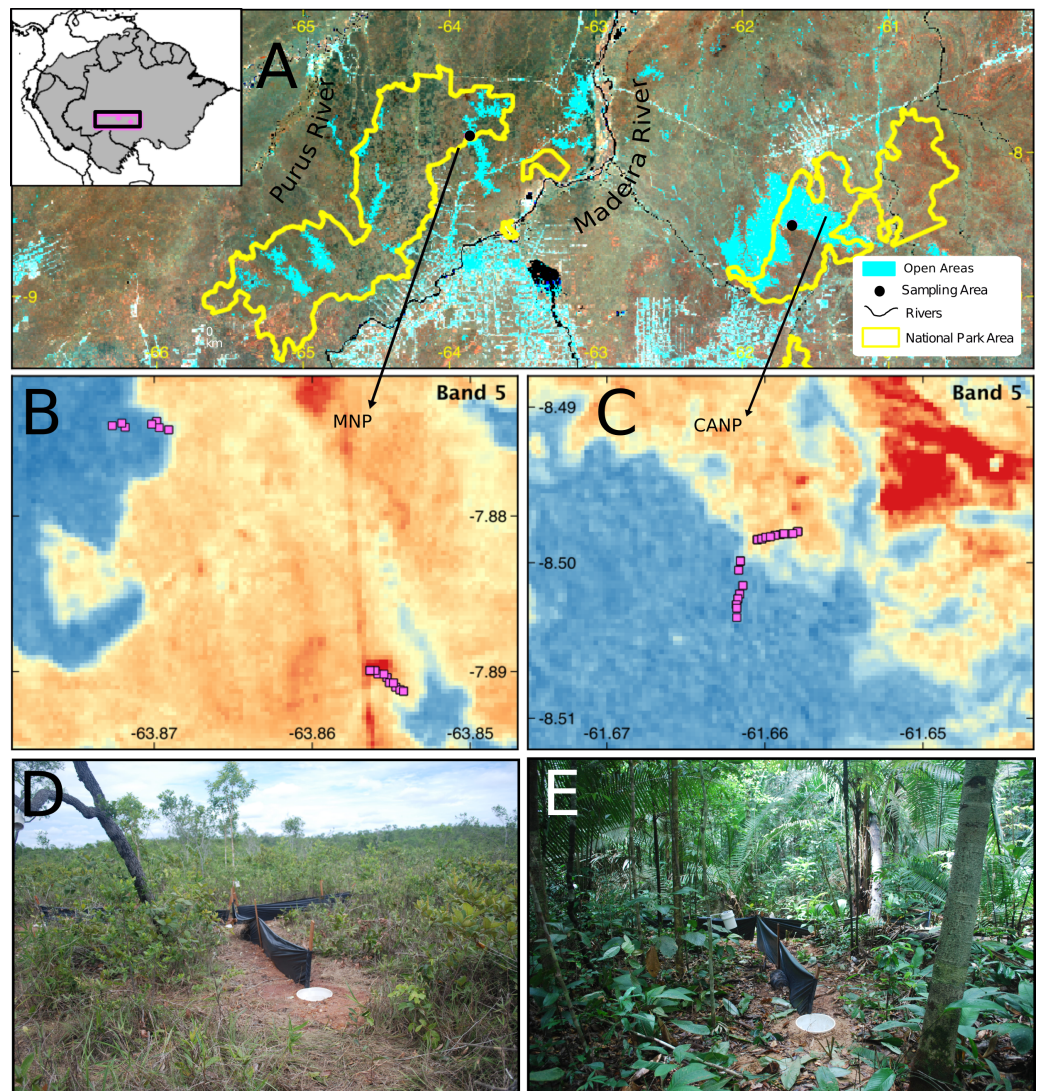
Figure 1 **Sampling area in different perspectives and images of the trap set in the two sampled habitat types.** (A) Location and limits of the Campos Amazônicos National Park (CANP) and the Mapinguari National Park (MNP). (B–C) Design and arrangement of plots in the different types of habitats in each of the parks based on the reflectance values of Landsat Band-5. The reddish tones represent open areas, and the blueish one indicates forest areas; the pink squares are the location of the pitfall traps. Pitfall traps in savanna (D) and forest (E) environments.

end and another in the center, interconnected by 6 m-long and 0.8 m-high black tarp drift fences (*e.g.*, *Werneck, Colli & Vitt, 2009*; *Garda et al., 2013*). To maximize lizard captures, funnel traps (1 × 0.3 × 0.6 m minnow traps) were placed along the drift fences, one at each side, totaling six funnel traps. Hereafter, each set of pitfall and funnel traps is referred to a sampling plot (Fig. 1). In total, 25 plots were installed in each area along a transect, at least 50 m apart, to avoid spatial autocorrelation. To sample the environmental gradients

in each park, approximately half of the plots were installed in open areas and the other half in *terra-firme* or lowland forest areas.

All individuals collected in the field were euthanized after collection of thermal traits (see below) using a lethal injection of thiopental. Following this, all specimens were fixed in 10% formalin and stored in 70% alcohol. Vouchers were deposited in the Amphibians and Reptiles Collection of the National Institute for Amazonian Research (INPA-H) and tissue samples were deposited in the Genetic Resources-*Herpetofauna* Collection (INPA-HT). All specimens were collected under permit # 57707-2, which was issued by ICMBio.

Predictor variables
Micro-climatic variables
In each sample plot, a data-logger (Onset HOBO U23 Pro v2 temperature/relative humidity data logger) was installed to record the air temperature and relative humidity every minute during the 15-day sampling period. Data were collected as previously described in *Alvarenga et al. (2017)*. In general, 14 micro-climatic variables were derived of which seven are related to humidity, such as absolute maximum relative humidity (Hmaxa), absolute minimum relative humidity (Hmina), absolute standard deviation of relative humidity (Hsda), maximum relative humidity (Hmax), mean relative humidity (Hmean), minimum relative humidity (Hmin), standard deviation of relative humidity (Hsd). In addition, more seven were derived from air temperature absolute maximum temperature (Tmaxa), absolute minimum temperature (Tmina), absolute standard deviation of temperature (Tsda), maximum temperature (Tmax), mean temperature (Tmean), minimum temperature (Tmin), standard deviation of temperature (Tsd).

Remote-sensing environmental variables
A remote-sensing dataset of canopy surface reflectance was used as a proxy for floristic and edaphic patterns (*Tuomisto et al., 2019*; *Van doninck et al., 2020*; *Zuquim et al., 2021*). We used a Landsat TM/ETM+ image composite that is already available (*Van doninck & Tuomisto, 2018*). It is based on cloud-free observations acquired over the ten-year period 2000–2009. Bands 4, 5, and 7 were used since they had been deemed informative in earlier studies (*Van doninck & Tuomisto, 2018*; *Van doninck et al., 2020*). The median reflectance values corresponding to a 15 by 15-pixel window centered on the coordinates of each plot (450-m window, given the original image resolution of 30 m) were extracted for each band. Non-forested pixels were masked using an unsupervised k-means clustering with a post-classification interpretation based on visual inspection of spectral signature and spatial distribution. Median reflectance values were obtained separately for forested and non-forested pixels within the window, and the number of pixels in each category (out of the total of 225) was registered.

Species functional traits
For each sampled species, thermal biology was characterized using at least five captured specimens. The individual body mass was measured with a scale and then the snout-vent length (SVL) was measured with a digital caliper to represent the body size. To estimate the preferential temperature (T_{pref}), the lizards were placed on a wooden thermal gradient

(1 m long and 40 cm wide) for 1 h. One end of the gradient had a frozen gel pack, and the other had a heating lamp (∼100 W full spectrum). The lizards' body temperatures were recorded every 3–5 min, with a one mm thermocouple attached with tape to their abdomen and connected to a data logger and the T_{pref} was estimated as the mean of all records. The second experiment measured the critical minimum (CT_{min}) and maximum (CT_{max}) temperatures of the lizards. For this, the lizards were placed first in a container to avoid direct contact with the material and then the container was placed in an icebox (CT_{min}) or a thermal box with a heating lamp (∼100 W) (CT_{max}) until the animal lost its locomotor response capacity, *i.e.,* when the animal was placed in the supine position and could not return to the upright position. The body temperature measured at this moment was regarded as the CT_{min} or Ct_{max} (*e.g.,* *Taylor et al., 2020*). Finally, we subtracted the values for CT_{min} from CT_{max} ($CT_{max}-CT_{min}$) to obtain the thermal tolerance range (TTR), which represents the individuals' thermal amplitude, and also subtracted the mean CT_{max} from the mean maximum ambient temperature ($CT_{max}-T_{max}$) to obtain the warming tolerance (*Deutsch et al., 2008*). Ecophysiology data was collected following standard protocols (*e.g.,* *Angilletta, 2009*; *Diele-Viegas et al., 2018*; *Pontes-da-Silva et al., 2018*; *Caetano et al., 2020*), under authorizations from the Commission of Ethics and Animal Use of the University of Brasília (33786/2016) and INPA (029/2014). Species were classified as thermoregulators or thermoconformers based on *Diele-Viegas et al. (2018)*. We did not classify any species, nor did we use any criteria based on our data to classify the thermoregulation mode of the species.

Statistical analyses

To describe the variations in microclimate and canopy reflectance among the plots along the forest-savanna transition, a principal components analysis (PCA) of the correlation matrix was used.

The Bray–Curtis dissimilarity index was calculated based on abundance data in order to investigate dissimilarity in species composition within and between the two sampled areas. This measure represents the compositional turnover between the two sites and varies from 0 (the two sites have the same composition) to 1 (the two sites are entirely different and do not share any species). However, when calculated for two plots that do not share species, the index result will necessarily be equal to one, no matter how large the actual dissimilarity between them is. To mitigate this problem, the step-across or extended dissimilarity method was used (*De'ath, 1999*). Measures of extended dissimilarity can be obtained through one or more intermediate sampling units that share species with the non-species sharing samples. The value is calculated by adding the dissimilarity of these intermediate sample units. This procedure allows the dissimilarity between samples that do not share species to continue to grow as the ecological distance between them increases and facilitates the interpretation of ecological gradients in high-turnover data (*De'ath, 1999*; *Tuomisto, Ruokolainen & Ruokolainen, 2012*).

To investigate the first hypothesis of high environmental variation, a principal coordinates analysis (PCoA) was performed to visualize the composition dissimilarities as quantified using the extended Bray–Curtis dissimilarity, both for the two areas/national
parks together and for each area separately. Multiple regressions were also performed to investigate which group of environmental variables (*i.e.,* micro-climatic or canopy reflectance) best explain the compositional turnover of the lizards (the first two axes of the PCoA), using the stepwise method based on the significance of the variables. To avoid redundant variables in the models, the correlation among all variables within each class of predictors (micro-climatic and vegetation structure estimated from canopy reflectance) was calculated. Pairs of variables with Pearson's R of >0.7 were evaluated and subsequently removed or maintained in the model considering previous knowledge of lizard ecology and species-environmental relationships. After assessing the Pearson correlation among environmental predictors, four variables were retained for the subsequent multiple regressions: two micro-climatic (T_{min} and H_{max}) variables and two variables based on canopy reflectance (Landsat Band 4 and Band 5) variables.

In order to investigate the second hypothesis regarding the variations in thermal traits, a PCoA based on Euclidean distance was used to summarize changes in the functional dissimilarity of the thermal traits for the lizards along the forest-savanna gradient. To this end, the community weighted mean (CWM) of each functional trait T_{pref}, CT_{min}, and CT_{max} was first calculated as the mean of the functional traits of the species weighted by the frequency of the species in each plot, thus enabling an evaluation of functional dissimilarity comparable to taxonomic dissimilarity. In addition, a PERMANOVA was used using the first two axes of the PCoA analyzed with CWM data as a function for both habitat types (forest-savanna) and the two national parks (MNP and CANP). These analyses were performed using the *vegan (Oksanen et al., 2019)* and *FD* packages (*Laliberté, Legendre & Shipley, 2015*) of the R statistical environment (*R Core Team, 2020*).

To investigate the third and last hypothesis regarding the variation in vulnerability and analyze the pattern of warming tolerance (WT) and the range of thermal tolerance (TTR) of the species, a Shapiro test was performed to analyze the normality of predictive parameters (*i.e.,* means of TTR and WT). The Shapiro test was also performed to assess whether they differ between habitat type and thermoregulation mode. When normality could not be assumed, a non-parametric Kruskal–Wallis test of differences between habitats and thermoregulation mode was performed. Finally, these results were used to qualitatively assess the vulnerability of species to global warming in the sampled areas. These analyses were performed using the R statistical environment's *base* package (*R Core Team, 2020*).

RESULTS

Environmental variations: microclimates and vegetation structure

The principal component analysis based on microclimate variables and Landsat bands demonstrated that the plots could be divided into three groups. One group contained all the savanna plots, regardless of which national park was considered. The second group contained the forest plots of CANP, and the third group contained the forest plots of MNP (Fig. 2). All the forest plots were associated with high values of Landsat Band 4 and mean (H_{mean}) and minimum (H_{min}) relative humidity. When considering each national park that was sampled, a dichotomy associated with PC axis 2 axis was apparent (Fig. 2). The values
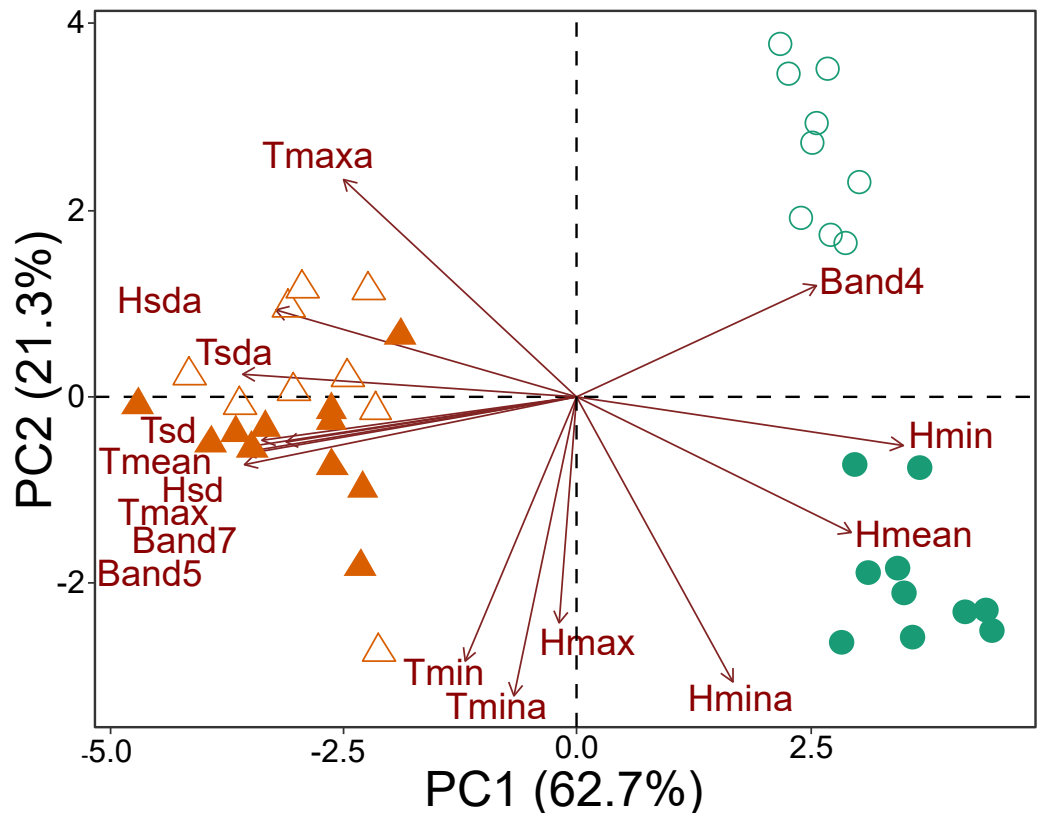
Figure 2 **Multivariate ordination of the environmental variables, including micro-climatic and canopy reflectance/vegetation structure variables.** Triangles: savanna plots; circles: forest plots. Open symbols represent sampling plots of the CANP and closed symbols represent plots of the MNP.

of minimum (T_{min}) and absolute minimum (T_{mina}) temperature, and maximum (H_{max}) and minimum absolute (H_{mina}) humidity presented the strongest contributions. The forest plots of CANP had higher Band 4 reflectance values and lower minimum temperatures than the forest plots of MNP. In turn, savanna plots were more associated with high maximum (T_{max}) and mean (T_{mean}) temperatures, as well as with high reflectance values of Landsat Bands 5 and 7. The savanna plots were characterized by higher values of absolute maximum temperature and higher temperatures.

Taxonomic composition and community structure

A total of 149 individuals were captured in both national parks, representing 17 lizard species in eight different families. *Kentropyx altamazonica* (35 individuals), followed by *Cercosaura olivacea* (25) and *Copeoglossum nigropunctatum* (24), were the most common species (Table 1). Despite two-thirds of the individuals originating from savanna plots (savanna: 100 individuals, forest: 49), the forest plots exhibited a higher species count (savanna: 10, forest: 12). However, it is crucial to acknowledge that this result may be biased due to the difference in the number of plots between the savanna and forest habitats. CANP had a greater abundance and richness of species, with eight species occurring only
Table 1 **Checklist of the species collected in the two parks (CANP, Campos Amazônicos National Park; MNP, Mapinguari National Park) with respective sampling abundances by habitat, thermoregulation mode, and the species' habitats of occurrence.** (TR) thermoregulator; (TC) thermoconformer. Thermoregulatory information follows *Diele-Viegas et al. (2018)*.

Taxon	PNCA		PNM		Thermoregulation mode	Habitat of occurrence
	Savanna	Forest	Savanna	Forest		
Squamata						
"Sauria"						
Dactyloidae						
Anolis fuscoauratus (D'Orbigny, 1837)	–	1	–	3	TC	Forest
Anolis tandai (Ávila-Pires, 1995)	–	2	–	–	TC	Forest
Diploglossidae						
Ophiodes sp.	–	–	2	–	TC	Open areas
Gymnophthalmidae						
Cercosaura anordosquama (Sturaro et al. 2018)	1	3	–	–	TC	Forest
Cercosaura olivacea (Gray, 1845)	16	1	8	–	TC	Open areas
Cercosaura eigenmanni (Griffin, 1917)	1	–	–	–	TC	Forest
Iphisa elegans (Gray, 1851)	–	1	–	–	TC	Forest
Loxopholis percarinatum (Müller, 1923)	–	2	–	–	TC	Forest
Hoplocercidae						
Hoplocercus spinosus (Fitzinger, 1843)	3	–	–	–	–	Open areas
Scincidae						
Copeoglossum nigropunctatum (Spix, 1825)	–	2	19	3	TR	Forest/Open areas
Manciola guaporicola (Dunn, 1935)	4	–	–	–	–	Open areas
Sphaerodactylidae						
Chatogekko amazonicus (Andersson, 1918)	–	–	–	4	TC	Forest
Teiidae						
Ameiva ameiva (Linnaeus, 1758)	2	–	16	4	TR	Forest/Open areas
Kentropyx altamazonica (Cope, 1875)	25	8	1	1	TR	Open areas
Kentropyx calcarata (Spix, 1825)	–	9	–	2	TR	Forest
Salvator merianae (Duméril & Bibron, 1839)	2	–	–	–	TR	Open areas
Tropiduridae						
Plica umbra (Linnaeus, 1758)	–	2	–	1	TC	Forest
Total richness	8	10	5	7		
Total abundance	54	31	46	18		

in this area, of which four were exclusive of to the savanna plots (*Cercosaura eigenmanni, Hoplocercus spinosus, Manciola guaporicola* and *Salvator merianae*), three were exclusive to forest plots (*Anolis tandai, Iphisa elegans* and *Loxopholis percarinatum*), and one occurred in plots of both habitats (*Cercosaura anordosquama*) (Table 1). Two species were sampled only in the MNP, one in the savanna plots (*Ophiodes* sp.) and the other in the forest plots (*Chatogekko amazonicus*).

The PCoA analyses showed two distinct groups in terms of species composition when considering the environmental gradient, both when evaluating all the sampling plots of the two parks together (Fig. 3A) and plots from each park separately (Figs. 3B–3C). The
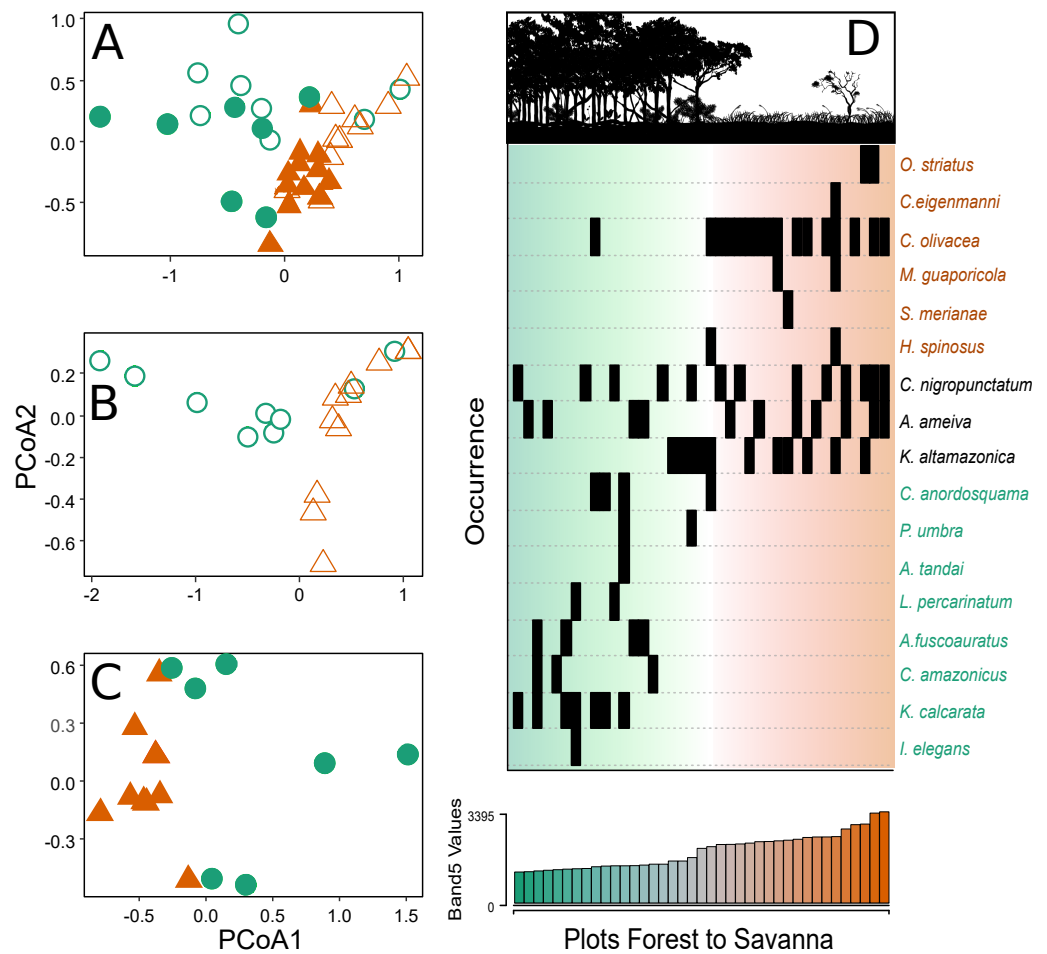
Figure 3 Principal coordinate analysis depicting the species turnover between plots along the environmental gradient. (A) Plots in the CANP and MNP, (B) plots in the CANP, and (C) plots fin the MNP. (D) Direct ordination of the species by occurrence along the gradient of Landsat Band 5 values. Triangles = savanna plots, circles = forest plots. Open symbols represent sampling plots in the CANP, and closed symbols represent plots in the MNP.

savanna plots were more similar to each other in terms of species composition than the plots of the forest area.

After a single round of the multivariate stepwise multiple regressions, the simple model containing the variable Band 5 was selected ($P < 0.001$, $R^2 = 0.335$). This result indicates that canopy reflectance of short-wave infrared radiation (Band 5) is the best predictor of species turnover along the forest-savanna gradient when considering all park plots together (Fig. 3A). The direct ordination of species composition based on occurrence in the plots also demonstrated substantial turnover associated with values of the Landsat Band 5 (Fig. 3D).
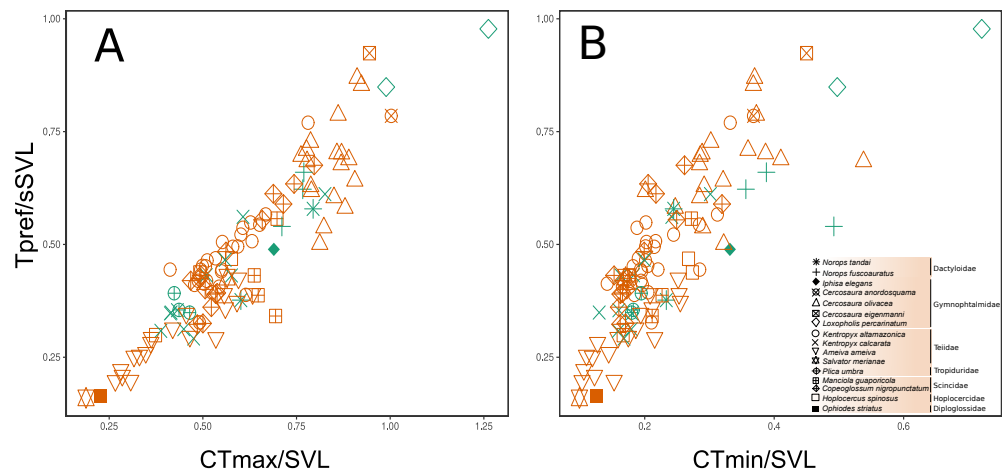
Figure 4 Functional space of the sampled communities based on the thermal traits of the species and family level. The preferred temperature (T_{pref}) axis weighted by body size (SVL) varies correlated to the maximum critical temperature (CT_{max} and minimum critical temperature (CT_{min}) axes, both weighted by body size (SVL). The weighting of the variables by body size (SVL) was used to remove the effect of this parameter on the thermal temperature traits. (A–B) is the space considering the savanna-forest transition (reddish = savanna; greenish = forest). The thermal trait values can be found in the Supplementary File.

Thermal ecology

A strong correlation was found between the three functional traits evaluated, in which T_{pref} and CT_{max} had the highest values ($r = 0.921$, $P < 0.0001$), followed by CT_{max} vs. CT_{min} ($r = 0.825$, $P < 0.0001$) and, finally, T_{pref} vs. CT_{min} ($r = 0.817$, $P < 0.0001$). This indicates that any possible selection of one thermal trait will likely affect the evolution of all those considered here. In addition, this collinearity could represent a shared phylogenetic history among the species. Despite the large overlap, there was a subtle difference between the two habitats in the functional strategies of individuals (Figs. 4A–4B). Except for *Loxopholis percarinatum,* species that occur in the forest plots have a range of lower to intermediate values for these key thermal physiology traits. On the other hand, species that occur in the savanna plots occupy a much wider trait space (Figs. 4A–4B). The species with lower values for CT_{min}, CT_{max}, and T_{pref} were *Ophiodes* sp. (Diploglossidae), *Salvator merianae, Ameiva ameiva, Kentropyx calcarata* (Teiidae), followed by species with intermediate values *K. altamazonica* (Teiidae), *Hoplocercus spinosus* (Hoplocercidade), *Copeoglossum nigropunctatum, Manciola guaporicola* (Scincidae), *Plica umbra* (Tropiduridae), *Anolis fuscoauratus, A. tandai* (Dactyloidae) and *Iphisa elegans* (Gymnophthalmidae). Finally, the species with the highest values for the three traits were *Cercosaura olivacea, C. anordosquama, C. eigenmanni* and *Loxopholis percarinatum* (Gymnophthalmidae) (Figs. 4A–4B). All ecothermal data, both weighted by SVL, mass, and the raw data for species and individuals are available in the supplementary material.

The principal coordinate analysis showed no clear pattern of dissimilarity between CWM values taking into account the two habitat types (Fig. 5). However, when we considered
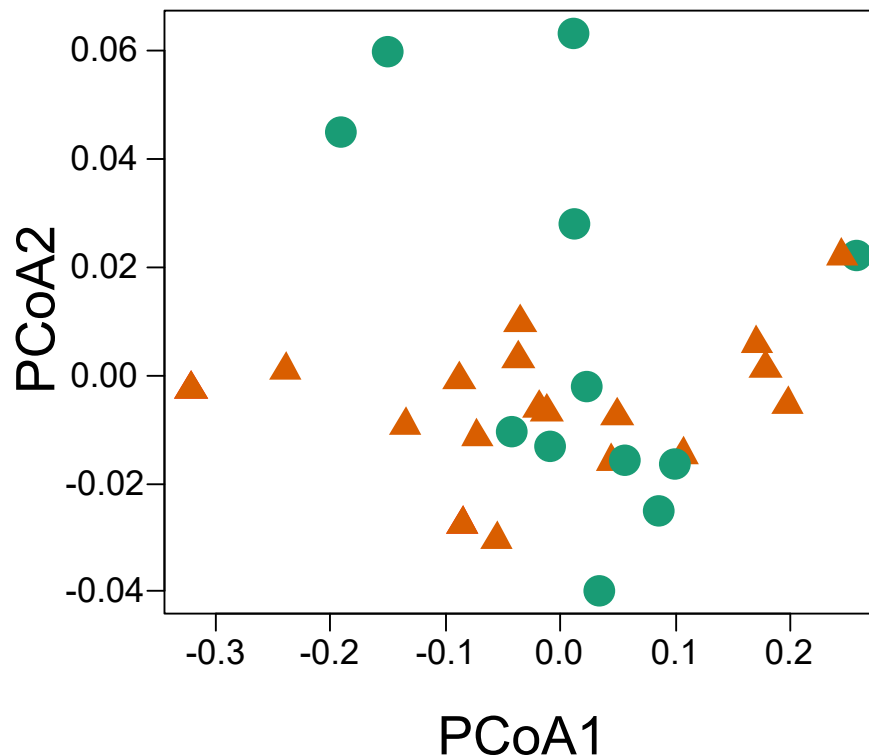
Figure 5 Principal coordinate analysis based on the dissimilarity of the community weighted means (CWM) of thermal traits of lizards from two parks in the southwestern Amazon. Red triangles represent savanna plots; green circles represent forest plots.

the same analysis and explored the dissimilarity of the functional traits between the two parks, we were able to recover a dissimilar pattern between them. When running the PERMANOVA, we were able to observe a significant relationship of dissimilarity between the two national parks with respect to the composition of functional traits of the sampled individuals ($P = 0.013$, $R^2 = 0.159$, permutations 999).

The Kruskal–Wallis test showed that there was no significant difference in mean TTR between the two types of habitats or between thermoregulation modes (Chi-squared = 20.953; $P = 0.399$; $df = 20$ and Chi-squared = 29.086; $P = 0.3072$; $df = 26$, respectively). However, the two thermoregulatory behaviors differed in the breadth of the thermal ranges (Fig. 6A). Thermoconformers (TC) had a much broader and more generalized TTR, regardless of habitat type; while, thermoregulators (TR) had a narrower TTR, varying slightly in more specific temperature values (Fig. 6A).

The CT_{max}, when subtracted from the maximum temperature of the environment, resulted in a smaller margin for the thermoconformers than the thermoregulators (Fig. 6B). However, forest thermoconformers had a smaller safety margin for CT_{max} in relation to thermoregulators, indicating a narrow warming tolerance (Table 2). For thermoregulators, the type of habitat made no difference to the individual's warming tolerance.
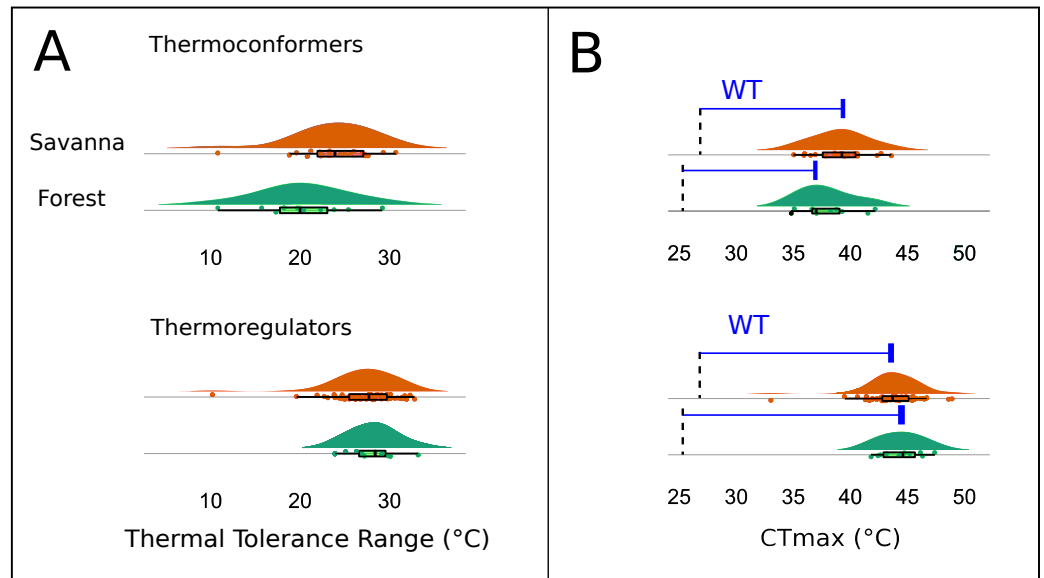
Figure 6 **Thermal and warming tolerance of the lizard community across two habitat types and their thermoregulatory modes.** (A) Thermal tolerance range (TTR) of the lizard species considering habitat type and thermoregulation mode. (B) Frequency of the critical maximum temperature (CT_{max}) of the species considering the two types of habitats and the thermoregulation behavior. The dotted line indicates the mean maximum temperature recorded in the respective environments, and the difference between the bar and the curves is the warming tolerance (WT) (blue bar).

Table 2 **Mean CT_{max} and maximum environmental temperature (T_{max}) values and warming tolerance (WT) by habitat type and thermoregulation mode for lizard species in the two sampled parks.**

	Thermoconformers		Thermoregulators	
	Forest	**Savanna**	**Forest**	**Savanna**
MCTmax (°C)	37.9	39.1	44.4	43.8
Mtmax (°C)	29.55	29.54	29.55	29.54
WT (°C)	11.35	9.56	17.85	14.26

DISCUSSION

Environmental variations

The environmental transition along the savanna-forest ecotone corresponds to clear microclimate and canopy surface reflectance differences in the sampled areas. Moreover, as shown by the variation along the PC 2 axis (Fig. 2), there is a clear distinction between the parks' habitat characteristics. This result may be inherent due to differences in their geological formation histories (see *Rossetti et al., 2019*; *Ruokolainen et al., 2019*; *Josué Azevedo et al., 2020*), which would be responsible for a floristic and micro-climate turnover between both environments. In general, forest areas are cooler, with significant variation in air humidity and higher reflectance of the near-infrared Landsat Band 4. The low and highly variable relative humidity in these forest environments compared to the same habitat type in the center of the biome seems to be a characteristic of this habitat type in the southwestern

portion of the Amazon, especially for areas that border savanna environments and are susceptible to fire (*Brando et al., 2014*). The savanna plots, in turn, are environments with higher temperatures, greater incidence of sunlight, greater stability in relative humidity, and higher reflectance of Landsat Bands 5 and 7 (Fig. 2).

In vegetated areas, the surface reflectance registered by satellites depends on the kinds of functional plant properties that typically vary among edaphically determined vegetation types, such as the degree of woodiness and the amount and structure of photosynthetic leaf tissue (*Tuomisto et al., 2003a*; *Tuomisto et al., 2019*; *Serbin & Philip, 2020*). Band 4, for example, registers wavelengths in the near infrared (0.77–0.90 µm), whose reflectance depends on photosynthetic activity and biomass, with the highest reflectance values associated with forest environments, in which trees accumulate more biomass than the smaller plants in open areas. Bands 5 (short-wave infrared, 1.55–1.75 µm) and 7 (also short-wave infrared, 2.09–2.35 µm) indicate leaf water content, which is typically lower in woody plants (such as trees) than in herbaceous plants (such as savanna grasses and sedges). (*e.g.*, *Schwieder et al., 2016*). Therefore, our results reinforce the use of these variables as good alternatives that more accurately provide the limit between the vegetative types of savanna and forest, in addition to demonstrating the variability that exists within these environments (Fig. 2).

Composition of lizard species

The taxonomic composition showed an evident dissimilarity between forest and savanna habitats under both configurations of analysis (the assemblages of the two parks together and separately). It is important to consider that the low abundance in the forest habitats, with only 49 individuals, could cause bias in the results, mainly in regards to comparisons within the two habitats in the same park. Such structuring was represented by a strong pattern of species turnover along the canopy reflectance gradient, which was the variable that explained this pattern best (Fig. 3D). This result corroborates our expectation that the lizard community would show considerable species turnover along the forest-savanna transition. A similar result was reported by *Vitt & Zani (1998)* in a forest-savanna in the northern Amazon, and indicates that this could be a general pattern.

The influence of environmental variables, such as canopy openness, number of trees, density vegetation, elevation and soil structure in structuring ectothermic vertebrate communities on a local scale has been reported for the mid-upper Madeira River (*e.g.*, *Garda et al., 2013*; *Dias-Terceiro et al., 2015*; *Peixoto et al., 2020*). The fact that temperature is not the main variable or determining factor for lizard assembly is intriguing (Fig. 3), as temperature often affects several physiological and behavioral activities of lizards and ectotherms in general (*Angilletta, 2009*). However, the discussion of the role of temperature in the presence of ectotherms and lizards themselves is still a question to be further investigated. *Kearney (2013)*, for example, comments that the activity time alone is not capable of determining the presence of an ectothermic species, while *Caetano et al. (2020)*, in a macro-climatic approach, argues that such a parameter is a better predictor than the temperature variable alone. If we consider Band 5 an indicator of such functional aspects of the vegetation that may be important for the lizards and that, in addition, there is a large

contribution of micro-climatic temperature variables, our result supports the idea that, despite not having a primary role, temperature has a greater contribution when the other factors that are correlated to it are taken into account. *Vitt & de Carvalho (1995)* also argue that climate alone is not determinant for the diversity of lizard species, especially for open areas, which have lower diversity that is inherently due to the lower structural diversity of the environment, and this may also explain the lower species richness that was found in the savanna.

Spatial heterogeneity of vegetation and vegetation cover are known to affect the occurrence and abundance of squamates in the tropics, as they are related to the availability of resources and sites for nesting, foraging, thermoregulation (*Vitt & Zani, 1998*; *Vitt et al., 2007*; *Pringle, Webb & Shine, 2003*; *Masseli et al., 2019*; *Mesquita et al., 2015*) and variation of light incidence, humidity and temperature (*Pringle, Webb & Shine, 2003*; *Peixoto et al., 2020*). The communities sampled herein are also affected by these factors since they are structured along a gradient of plant structure, which is represented by canopy reflectance, varying in the availability of open environments with a high incidence of light, temperature, and humidity, as well as forest environments with a lower incidence of direct light and milder temperatures. Furthermore, forest environments have a greater availability of microhabitats thanks to the vertical stratification; whereas, in the Cerrado biome (open areas), habitat stratification occurs horizontally over various types of vegetation (*Colli, Bastos & Araujo, 2002*; *Gainsbury & Colli, 2003*; *Nogueira, Valdujo & França, 2005*). The higher lizard richness that was recorded in forest plots (Table 1) may result from the fact that typical forest species do not usually disperse to savanna areas (*Vitt & de Carvalho, 1995*), while heliotherms from open areas, such as *Ameiva ameiva*, *Copeoglossum nigropunctatum*, and *Kentropyx altamazonica,* often use forest clearings formed by treefalls and forest edges, thus increasing the species richness of the forest habitat.

The difference in species richness and distribution between the parks may be related to historical factors that affect speciation and extinction, such as the different geological histories of these environments, especially in the savannas. *Gainsbury & Colli (2003)*, for example, argue that the lizard assemblages from savanna enclaves in the southwestern Amazon are structured by stochastic factors, particularly extinctions and isolation of these areas caused by the retraction of the Cerrado and the expansion of the forest in the Holocene. They also demonstrate that enclaves that are geographically distant from the core of the Cerrado have fewer species than those closer to the ecotone. Our results mirror this pattern, since the species richness of savanna areas in the CANP is higher than what is found in the MNP, which is further away from the core of the Cerrado and is also separated by the Madeira River, a critical biogeographic barrier for many species (*Peixoto et al., 2020*).

Thermal ecology and the implications of climate change for the community

No dissimilarity pattern of lizard thermal functional variation was found between the two forest-savanna habitat types. On the other hand, we did encounter a significant difference in dissimilarity between the national parks. Although it seems to contradict

initial predictions, this result makes sense if one considers that CT_{max}, T_{pref}, and CT_{min} are parameters that are normally under phylogenetic conservatism (*Grigg & Buckley, 2013*), as well as being correlated with each other and sharing phylogenetic histories (*Diele-Viegas et al., 2018*; Fig. 5). The thermal traits do not seem to be influenced by the environmental filtering promoted by the specific local conditions of the two habitat types (savanna-forest). Another possibility would be that the environmental filters are similar in both habitats, which is common at the local scale (*Kraft et al., 2015*). However, on a regional scale, the significant difference in dissimilarity of the thermal traits used to compare the two parks possibly reflects the influence of the inherent environmental filters of the different climatic and geological events that shaped the environment of these two parks (see *Josué Azevedo et al., 2020*; *Rossetti et al., 2019*). We encountered an apparent pattern of structure in the species' functional space at the family level, which reinforces a possible role of evolutionary history on the thermal traits of the lizards (*Bodensteiner et al., 2020*). This may be better observed with the inclusion of the taxonomic family as a structuring factor. It is important to report that we did not explicitly test historical factors, but we recommend such approaches in further work, given the trend found in our results. On a regional scale, the preferential temperature (T_{pref}) has been reported to be more affected by factors other than phylogeny, such as environmental temperatures, which makes it more prone to show greater phenotypic plasticity along environmental transitions (see *Diele-Viegas et al., 2018*; *Pontes-da-Silva et al., 2018*). However, on a local scale, we did not observe variations between habitats in T_{pref} among individuals of the species in both forest and savanna plots (*i.e., C. nigropunctatum, A. ameiva, K. altamazonica*). This result may reflect the high correlation between thermal features analyzed or their more active thermoregulation behavior attenuating this variation as they move between the two habitat types (*Huey et al., 2012*).

Tropical lizard species are considered especially vulnerable to global warming, as they experience environmental temperatures that are already close to or exceed their optimum temperatures and maximum performance (*Deutsch et al., 2008*; *Huey et al., 2009*; *Clusella-Trullas & Chown, 2014*). Furthermore, species adapted to warmer tropical environments can be asymmetrically affected in comparison to those associated with slightly cooler tropical climates, a typical scenario of transitional environments, such as savanna-forest transitions (*Huey et al., 2012*). In this context, thermoconformers, which were more common in the forest with a mild thermal habitat, are more vulnerable to heat than thermoregulators, which are more common in savannas where the habitat is warmer (*Huey et al., 2009*). Nonetheless, there is some evidence regarding thermoregulator species buffering their vulnerability to heating, for instance, a macroscale study of the thermal traits in different populations of *K. calcarata* across the Amazon showed higher values for CT_{max} to for populations close to the Cerrado ecotone (open areas) and lower values in the same species located in the core of the biome (*Pontes-da-Silva et al., 2018*). We found the same patterns for the same species, but on a local scale in which the CT_{max} reached 44.3 °C close to the savanna habitats; while *Pontes-da-Silva et al. (2018)* recorded values below 44 °C in the same ecotone.

We did not encounter a significant difference for the TTR of individuals between forest and savanna habitats or between the two main thermoregulation modes, thus reflecting the weak environmental filtering for thermal traits discussed previously. However, in line with expectations (*e.g.*, *Huey et al., 2012*; *Grigg & Buckley, 2013*), thermoregulator lizards showed a narrower pattern of the thermal range when compared to the thermoconformers, which is a difference that implies different community responses to global warming. Active thermoregulation can mitigate climate change effects at the local scale, which vary according to the environments' thermal heterogeneity, and is more limited in forest habitats than in open areas. Environments that are thermally more homogeneous, such as forests, represent fewer possibilities for variation in the lizards' activity period (*Fitzgerald, Shine & Lemckert, 2003*; *Kiefer, Van Sluys & Rocha, 2007*). Moreover, the warming tolerance (WT) is also known to be affected by the environment's thermal variability, whereby less heterogeneous environments have low WT. Consequently, thermoconformers should be more affected, as they are more frequent in the forest and have less tolerance capacity than open-habitat thermoregulators (*Deutsch et al., 2008*; *Huey et al., 2012*). Our results indicated this pattern, since we found a lower WT for thermoconformers, thus reiterating expectations of their greater vulnerability.

Although thermoconformers were the most common in the forest plots, there was no difference in lizard WT between the forest and savanna plots. This result indicates that assemblages in forest areas might be already suffering from the influence of assemblages from surrounding open habitats (*Brando et al., 2014*; *Sales, Galetti & Pires, 2020*). *Huey et al. (2012)* warned that in forest lizards heat stress would trigger another type of stress called biotic stress, whereby species from open areas will occupy niches to escape from warming and benefit from forest structure changes. Our observations of some species from open environments in forest plots, but not the reverse, apparently support Huey's warning. Further studies are needed in order to assess the impact of global warming on community dynamics and the likelihood of "savannization" of tropical lizard communities at broader scales (*Sales, Galetti & Pires, 2020*).

Finally, we conclude that lizard communities in Amazonian forest-savanna transitions tend to be ecologically structured by habitat heterogeneity. The species' thermal ecology traits are not dissimilar between the environmental filters of forest-savanna gradient and seem to be more associated with their evolutionary history. The same is not true when evaluating the thermoregulatory modes and their parameters of thermal and warming tolerance. However, all these findings proved to be connected when we consider the responses of lizard species to global warming. Firstly, the forest structure, which is very important for the taxonomic composition, may already be suffering from changes (*Algar, Morley & Boyd, 2018*; *Sales, Galetti & Pires, 2020*) and, thus, benefits species from open areas, which find more favorable conditions in these environments, such as a refuge from overheating. Secondly, the thermal tolerance range and the warming tolerance demonstrate an asymmetry between the thermoregulation modes and, consequently, in the vulnerability to climate change, which is greater for thermoconformers than thermoregulators. This pattern leads to biotic stress on forest habitats and their associated species which are mostly thermoconformers, and potentially increases their vulnerability and risk of extinction.

ACKNOWLEDGEMENTS

We are extremely grateful to Julio M. Alvarenga, Erik H.L. Choueri, Ivan J. Lima, Rafael N. Leite, João M. Capurucho, and Marina Maximiano for their assistance in the field expeditions. We thank the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) for all its crucial logistic support under very challenging field conditions, with special thanks to Bruno C. Cambraia and Wilhan Assunção. We also thank the Werneck Lab (Brazil) and the Amazon Research Team (UTU-Finland) for paper revisions and discussions, Gabriela F. Maia and Leandro J.C.L. Moraes for analytical support, and Ariane A. Silva for the support in depositing the specimens at the Herpetological Collection of the Instituto Nacional de Pesquisas da Amazônia (INPA-H). I am also grateful to Ana Maria de Souza Oliveira (*in memoriam*) for her support, love and trust throughout the process of this study and in all my life.

Funding

This work was funded through research projects for Fernanda P. Werneck by the Conselho Nacional de Desenvolvimento Científico e Tecnológico-CNPq (475559/2013-4, 305535/2017-0, and 311504/2020-5), the Serrapilheira Institute (Serra-1811-25857), the Fundação de Amparo à Pesquisa do Estado do Amazonas-FAPEAM (062.01110/2017 and 062.00665/2015), the Partnerships for Enhanced Engagement in Research from the U.S. National Academy of Sciences and U.S. Agency of International Development (PEER NAS/USAID AID-OAA-A-11-00012), and L'Oréal-UNESCO-ABC For Women In Science awards (Brazil-2016 and International Rising Talents-2017), and scholarships for AFSO by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior-CAPES. We also were supported by the Academy of Finland for grants to Hanna Tuomisto, and an Erasmus+ exchange grant for Alan F Souza-Oliveira and Fernanda P Werneck to visit Turku. The Graduate Program via the Coordination for the Improvement of Higher Education Personnel - Brazil (CAPES) - PROEX and the Amazonas State Research Support Foundation (FAPEAM) with EDITAL POSGRAD and EDITAL N. 038/2022 - PDPG-CAPES supported the APC for this article. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Grant Disclosures

The following grant information was disclosed by the authors:
The Conselho Nacional de Desenvolvimento Científico e Tecnológico-CNPq: 475559/2013-4, 305535/2017-0, and 311504/2020-5.
The Serrapilheira Institute: Serra-1811-25857.
The Fundação de Amparo à Pesquisa do Estado do Amazonas-FAPEAM: 062.01110/2017 and 062.00665/2015.
The U.S. National Academy of Sciences and U.S. Agency of International Development: PEER NAS/USAID AID-OAA-A-11-00012.

L'Oréal-UNESCO-ABC For Women.

AFSO by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior-CAPES.

The Academy of Finland.

The Graduate Program via the Coordination for the Improvement of Higher Education Personnel - Brazil (CAPES) - PROEX.

The Amazonas State Research Support Foundation (FAPEAM) with EDITAL POSGRAD and EDITAL N. 038/2022 - PDPG-CAPES.

Competing Interests

The authors declare there are no competing interests.

Author Contributions

- Alan F. Souza-Oliveira conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Gabriela Zuquim analyzed the data, authored or reviewed drafts of the article, and approved the final draft.
- Lidia F. Martins performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Lucas N. Bandeira performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Luisa Maria Diele-Viegas performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Victor H.G.L. Cavalcante performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Fabricio Baccaro analyzed the data, authored or reviewed drafts of the article, and approved the final draft.
- Guarino Rinaldi Colli conceived and designed the experiments, analyzed the data, authored or reviewed drafts of the article, and approved the final draft.
- Hanna Tuomisto analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Fernanda P. Werneck conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.

Animal Ethics

The following information was supplied relating to ethical approvals (i.e., approving body and any reference numbers):

The Commission of Ethics and Animal Use from the University of Brasília (33786/2016) and INPA (029/2014) provided full approval for this research.

Field Study Permissions

The following information was supplied relating to field study approvals (i.e., approving body and any reference numbers):

Field experiments were approved by the Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio (#57707).

Data Availability

The raw data are available in the Supplemental Files and at OSF: de Souza Oliveira, Alan F. "The Role of Environmental Gradients and Microclimates in Structuring Lizard's Community and Functional Groups at a Rainforest-savanna Transition." OSF, 3 Jan. 2023. Web. https://doi.org/10.17605/OSF.IO/2CERX.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.16986#supplemental-information.

REFERENCES

Ab'Sáber A. 2002. Base for the study of ecosystems in the Brazilian Amazon. *Studies Advances* **16**:7–30 (In Portuguese).

Adeney JM, Christensen NL, Vicentini A, Cohn-Haft M. 2016. White-sand ecosystems in Amazonia. *Biotropica* **48**:7–23.

Algar AC, Kerr JT, Currie DJ. 2011. Quantifying the importance of regional and local filters for community trait structure in tropical and temperate zones. *Ecology* **92**:903–914 DOI 10.1890/10-0606.1.

Algar AC, Morley K, Boyd DS. 2018. Remote sensing restores predictability of ectotherm body temperature in the world's forests. *Global Ecology and Biogeography* **27**:1412–1425 DOI 10.1111/geb.12811.

Alvarenga JM, Vieira CR, Godinho LB, Campelo PH, Pitts JP, Colli GR. 2017. Spatial–temporal dynamics of neotropical velvet ant (Hymenoptera: Mutillidae) communities along a forest-savanna gradient. *PLOS ONE* **12**:e0187142 DOI 10.1371/journal.pone.0187142.

Angilletta M. 2009. *Thermal adaptation: a theoretical and empirical synthesis.* Oxford: Oxford University press.

Anderson RO, Meiri S, Chapple DG. 2022. The biogeography of warming tolerance in lizards. *Journal of Biogeography* **49**:1274–1285 DOI 10.1111/jbi.14380.

Bodensteiner BL, Agudelo-Cantero GA, Arietta AZA, Gunderson AR, Muñoz MM, Refsnider JM, Gangloff EJ. 2020. Thermal adaptation revisited: how conserved are thermal traits of reptiles and amphibians? *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology* 1–22 DOI 10.1002/jez.2414.

Brando PM, Balch JK, Nepstad DC, Morton DC, Putz FE, Coe MT, Silvério D, Macedo MN, Davidson EA, Nóbrega CC, Alencar A, Soares-Filho BS. 2014. Abrupt increases in Amazonian tree mortality due to drought-fire interactions. *Proceedings of the National Academy of Sciences of the United States of America* **111**:6347–6352 DOI 10.1073/pnas.1305499111.

Caetano GHO, Santos JC, Godinho LB, Cavalcante VHGL, Diele-Viegas LM, Campelo PH, Martins LF, Oliveira AFS, Alvarenga JM, Wiederhecker HC, de Novaese Silva V, Werneck FP, Miles DB, Colli GR, Sinervo BR. 2020. Time of activity is a better predictor of the distribution of a tropical lizard than pure environmental temperatures. *Oikos* **129**:953–963 DOI 10.1111/oik.07123.

Cavender-Bares J, Kozak KH, Fine PVA, Kembel SW. 2009. The merging of community ecology and phylogenetic biology. *Ecology Letters* **12**:693–715 DOI 10.1111/j.1461-0248.2009.01314.x.

Chevin LM, Lande R, Mace GM. 2010. Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLOS Biology* **8** DOI 10.1371/journal.pbio.1000357.

Clusella-Trullas S, Chown SL. 2014. Lizard thermal trait variation at multiple scales: a review. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* **184**:5–21 DOI 10.1007/s00360-013-0776-x.

Colli GR, Bastos RP, Araujo AFB. 2002. The character and dynamics of the Cerrado herpetofauna. In: Oliveira PS, Marquis RJ, eds. *The Cerrados of Brazil: ecology and Natural History of a Neotropical Savanna.* New York: Columbia University Press, 223–241.

De'ath G. 1999. Extended Dissimilarity: a method of robust estimation of ecological distances from high beta diversity data. *Plant Ecology* **144**:191–199.

Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR. 2008. Impacts of climate warming on terrestrial ectotherms across latitude Thermal Safety margin. *Proceedings of the National Academy of Sciences of the United States of America* **105**:6668–6672.

Dias-Terceiro RG, Kaefer IL, de Fraga R, de Araújo MC, Simões PI, Lima AP. 2015. A Matter of Scale: historical and environmental factors structure Anuran assemblages from the Upper Madeira River, Amazonia. *Biotropica* **47**:259–266 DOI 10.1111/btp.12197.

Diele-Viegas LM, Figueroa RT, Vilela B, Rocha CFD. 2020. Are reptiles toast? A worldwide evaluation of Lepidosauria vulnerability to climate change. *Climatic Change* **159**:581–599 DOI 10.1007/s10584-020-02687-5.

Diele-Viegas LM, Vitt LJ, Sinervo B, Colli GR, Werneck FP, Miles DB, Magnusson WE, Santos JC, Sette CM, Caetano GHO, Pontes E, Ávila-Pires TCS. 2018. Thermal physiology of Amazonian lizards (Reptilia: Squamata). *PLOS ONE* **13**:1–23 DOI 10.1371/journal.pone.0192834.

Fitzgerald M, Shine R, Lemckert F. 2003. A reluctant heliotherm: thermal ecology of the arboreal snake *Hoplocephalus stephensii* (Elapidae) in dense forest. *Journal of Thermal Biology* **28**:515–524 DOI 10.1016/S0306-4565(03)00052-4.

Gainsbury AM, Colli GR. 2003. Lizard assemblages from natural cerrado enclaves in southwestern Amazonia: the role of stochastic extinctions and isolation. *Biotropica* **35**:503–519 DOI 10.1646/03078.

García-Villacorta R, Dexter KG, Pennington T. 2016. Amazonian white sand forest show strong floristic links with surrouding oligotrophic habitats and the Guiana shield. *Biotropica* **48**:47–57 DOI 10.1111/btp.12302.

Garda AA, Wiederhecker HC, Gainsbury AM, Costa GC, Pyron RA, Vieira GHC, Werneck FP, Colli GR. 2013. Microhabitat variation explains local-scale distribution of terrestrial amazonian lizards in Rondônia, western Brazil. *Biotropica* **45**:245–252 DOI 10.1111/j.1744-7429.2012.00906.x.

Grigg JW, Buckley LB. 2013. Conservatism of lizard thermal tolerances and body temperatures across evolutionary history and geography. *Biology Letters* **9**:2013–2016 DOI 10.1098/rsbl.2012.1056.

Huey RB, Deutsch CA, Tewksbury JJ, Vitt LJ, Hertz PE, Pérez HJÁ, Garland T. 2009. Why tropical forest lizards are vulnerable to climate warming. *Proceedings of the Royal Society B: Biological Sciences* **276**:1939–1948 DOI 10.1098/rspb.2008.1957.

Huey RB, Kearney MR, Krockenberger A, Holtum JAM, Jess M, Williams SE. 2012. Predicting organismal vulnerability to climate warming: Roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal Society B: Biological Sciences* **367**:1665–1679 DOI 10.1098/rstb.2012.0005.

Huey RB, Slatkin M. 1976. Cost and benefits of lizard thermoregulation. *The Quarterly Review of Biology* **51**:363–384 DOI 10.1086/409470.

Huston MA. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos* **86**:393–401 DOI 10.2307/3546645.

ICMbio. 2009. Management Plan for the Campos Amazônico National Park. *Available at https://www.gov.br/icmbio/pt-br/assuntos/biodiversidade/unidade-de-conservacao/unidades-de-biomas/amazonia/lista-de-ucs/parna-campos-amazonicos*.

Jellineck S, Driscoll DA, Kirkpatrick JB. 2004. Environmental and vegetation variables have a greater influence than habitat fragmentation in structuring lizard communities in remnant urban bushland. *Austral Ecology* **29**:294–304.

Josué Azevedo AR, Collevatti RG CAJ, Strömberg CAE, Guedes TB PM-M, Bacon CD, Juan David Carillo SF, Antonelli A. 2020. On the young savannas in the land of ancient forests. In: Rull V, Carnaval AC, eds. *Neotropical diversification: patterns and processes*. Cham: Springer, 271–298.

Kearney RM. 2013. Activity restriction and the mechanistic basis for extinctions under climate warming. *Ecology Letters* **16**:1470–1479 DOI 10.1111/ele.12192.

Kiefer MC, Van Sluys M, Rocha CFD. 2007. Thermoregulatory behaviour in *Tropidurus torquatus* (Squamata, Tropiduridae) from brazilian coastal populations: an estimate of passive and active thermoregulation in lizards. *Acta Zoologica* **88**:81–87 DOI 10.1111/j.1463-6395.2007.00254.x.

Kraft NJB, Adler PB, Godoy O, James EC, Fuller S, Levine JM. 2015. Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology* **76629**:592–599 DOI 10.1111/1365-2435.12345.

Laliberté E, Legendre P, Shipley B. 2015. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R Package: version 1.0-12.

Lewthwaite JMM, Debinski DM, Kerr JT. 2017. High community turnover and dispersal limitation relative to rapid climate change. *Global Ecology and Biogeography* **26**:459–471 DOI 10.1111/geb.12553.

Liautaud K, Barbier M, Loreau M. 2020. Ecotone formation through ecological niche construction: the role of biodiversity and species interactions. *Ecography* 714–723 DOI 10.1111/ecog.04902.

Masseli GS, Bruce AD, Dos Santos JG, Vincent T, Kaefer IL. 2019. Composition and ecology of a snake assemblage in an upland forest from central amazonia. *Anais Da Academia Brasileira de Ciencias* **91**:1–8 DOI 10.1590/0001-3765201920190080.

Maximiano MF de A, d'Horta FM, Tuomisto H, Zuquim G, Van doninck J, Ribas CC. 2020. The relative role of rivers, environmental heterogeneity and species traits in driving compositional changes in southeastern Amazonian bird assemblages. *Biotropica* 1–17 DOI 10.1111/btp.12793.

Menger J, Magnusson WE, Anderson MJ, Schlegel M, Pe'er G, Henle K. 2017. Environmental characteristics drive variation in Amazonian understorey bird assemblages. *PLOS ONE* **12**:1–20 DOI 10.1371/journal.pone.0171540.

Mesquita DO, Colli GR, Pantoja DL, Shepard DBC, Vieira GH, Vitt LJ. 2015. Juxtaposition and disturbance: disentangling the determinants of lizard community structure. *Biotropica* **47**:595–605 DOI 10.1111/btp.12236.

Milling CR, Rachlow JL, Olsoy PJ, Chappell MA, Johnson TR, Forbey JS, Shipley LA, Thornton DH. 2018. Habitat structure modifies microclimate: an approach for mapping fine-scale thermal refuge. *Methods in Ecology and Evolution* **9**:1648–1657 DOI 10.1111/2041-210X.13008.

Mouillot D, Villéger S, Scherer-Lorenzen M, Mason NWH. 2011. Functional structure of biological communities predicts ecosystem multifunctionality. *PLOS ONE* **6** DOI 10.1371/journal.pone.0017476.

Nogueira C, Valdujo PH, França FGR. 2005. Habitat variation and lizard diversity in a Cerrado area of Central Brazil. *Studies on Neotropical Fauna and Environment* **40**:105–112.

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, Mcglinn D, Minchin PR, O'hara RB, Simpson GL, Solymos P, Henry M, Stevens H, Szoecs E, Maintainer HW. 2019. Package vegan title community ecology package. *Community Ecology Package* **2**:1–297.

Peixoto GM, de Fraga R, Araújo MC, Kaefer IL, Lima AP. 2020. Hierarchical effects of historical and environmental factors on lizard assemblages in the upper Madeira River, Brazilian Amazonia. *PLOS ONE* **15**:1–19 DOI 10.1371/journal.pone.0233881.

Pepper M, Keogh JS. 2021. Life in the dead heart of Australia: the geohistory of the Australian deserts and its impact on genetic diversity of arid zone lizards. *Journal of Biogeography* **48**:716–746 DOI 10.1111/jbi.14063.

Petchey OL, Gaston KJ. 2002. Functional diversity (FD), species richness and community composition. *Ecology Letters* **5**:402–411 DOI 10.1046/j.1461-0248.2002.00339.x.

Pianka ER, Vitt LJ. 2003. *Lizards: windows to the evolution of diversity.* California: University of California Press.

Piantoni C, Curcio FF, Ibargüengoytía NR, Navas CA. 2019. Implications of climate change on the habitat shifts of tropical lizards. *Austral Ecology* **44**:1174–1186 DOI 10.1111/aec.12795.

Pomara LY, Ruokolainen K, Young KR. 2014. Avian species composition across the Amazon River: the roles of dispersal limitation and environmental heterogeneity. *Journal of Biogeography* **41**:784–796 DOI 10.1111/jbi.12247.

Pringle RM, Webb JK, Shine R. 2003. Canopy structure, microclimate, and habitat selection by a nocturnal snake, *Hoplocephalus bungaroides*. *Ecology* **84**:2668–2679 DOI 10.1890/02-0482.

R Core Team. 2020. R: a language and environment for statistical computing. Vienna, Austria. *Available at http://www.r-project.org/index.html*.

Rapacciuolo G, Blois JL. 2019. Understanding ecological change across large spatial, temporal and taxonomic scales: integrating data and methods in light of theory. *Ecography* **42**:1247–1266 DOI 10.1111/ecog.04616.

Ricklefs RE. 1987. Community diversity: relative roles of local and regional processes. *Science* **235**:167–171 DOI 10.1126/science.235.4785.167.

Rocchini D, Luque S, Pettorelli N, Bastin L, Doktor D, Faedi N, Feilhauer H, Féret JB, Foody GM, Gavish Y, Godinho S, Kunin WE, Lausch A, Leitão PJ, Marcantonio M, Neteler M, Ricotta C, Schmidtlein S, Vihervaara P, Wegmann M, Nagendra H. 2018. Measuring β-diversity by remote sensing: a challenge for biodiversity monitoring. *Methods in Ecology and Evolution* **9**:1787–1798 DOI 10.1111/2041-210X.12941.

Rossetti D de F, Gribel R, Cohen MCL, Valeriano M de M, Tatumi SH, Yee M. 2019. The role of Late Pleistocene-Holocene tectono-sedimentary history on the origin of patches of savanna vegetation in the middle Madeira River, southwest of the Amazonian lowlands. *Palaeogeography, Palaeoclimatology, Palaeoecology* **526**:136–156 DOI 10.1016/j.palaeo.2019.04.017.

Ruokolainen K, Moulatlet GM, Zuquim G, Hoorn C, Tuomisto H. 2019. Geologically recent rearrangements in central Amazonian river network and their importance for the riverine barrier hypothesis. *Frontiers of Biogeography* **11**(**3**):e45046 DOI 10.21425/F5FBG45046.

Sales LP, Galetti M, Pires MM. 2020. Climate and land-use change will lead to a faunal savannization on tropical rainforests. *Global Change Biology* **26**:7036–7044 DOI 10.1111/gcb.15374.

Salovaara KJ, Thessler S, Malik RN, Tuomisto H. 2005. Classification of Amazonian primary rain forest vegetation using Landsat ETM+ satellite imagery. *Remote Sensing of Environment* **97**:39–51 DOI 10.1016/j.rse.2005.04.013.

Savage VM, Gillooly JF, Brown JH, West GB, Charnov EL. 2004. Effects of body size and temperature on population growth. *American Naturalist* **163**:E429–E441 DOI 10.1086/381872.

Schwieder M, Leitão PJ, da Cunha Bustamante MM, Ferreira LG, Rabe A, Hostert P. 2016. Mapping Brazilian savanna vegetation gradients with Landsat time series. *International Journal of Applied Earth Observation and Geoinformation* **52**:361–370 DOI 10.1016/j.jag.2016.06.019.

Seebacher F, White CR, Franklin CE. 2015. Physiological plasticity increases resilience of ectothermic animals to climate change. *Nature Climate Change* **5**:61–66 DOI 10.1038/nclimate2457.

Serbin SP, Philip TA. 2020. *Scaling functional traits from leaves to canopies.* Cham: Springer International Publishing DOI 10.1007/978-3-030-33157-3.

Pontes-da Silva E, Magnusson WE, Sinervo B, Caetano GH, Miles DB, Colli GR, Diele-Viegas LM, Fenker J, Santos JC, Werneck FP. 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 DOI 10.1016/j.jtherbio.2018.01.013.

Silva-Souza KJP, Souza AF. 2020. Woody plant subregions of the Amazon forest. *Journal of Ecology* 1–15 DOI 10.1111/1365-2745.13406.

Sinervo B, Méndez-de-la Cruz F, Miles DB, Heulin B, Bastiaans E, Cruz MVS, Lara-Resendiz R, Martínez-Méndez N, Calderón-Espinosa ML, Meza-Lázaro RN, Gadsden H, Avila LJ, Morando M, De La Riva IJ, Sepúlveda PV, Rocha CFD, Ibargüengoytía N, Puntriano CA, Massot M, Lepetz V, Oksanen TA, Chappie DG, Bauer AM, Branch WR, Clobert J, Sites JW. 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science* **328**:894–899 DOI 10.1126/science.1184695.

Taylor EN, Diele-Viegas LM, Gangloff EJ, Hall JM, Halpern B, Massey MD, Rödder D, Rollinson N, Spears S, Sun B jun, Telemeco RS. 2020. The thermal ecology and physiology of reptiles and amphibians: a user's guide. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology* **335**:13–44 DOI 10.1002/jez.2396.

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* **31**.

Tuomisto H, Poulsen AD, Ruokolainen K, Moran RC, Quintana C, Celi J, Cañas G. 2003a. Linking floristic patterns with soil heterogeneity and satellite imagery in Ecuadorian Amazonia. *Ecological Applications* **13**:352–371 DOI 10.1890/1051-0761(2003)013[0352:LFPWSH]2.0.CO;2.

Tuomisto H, Ruokolainen K, Aguilar M, Sarmiento A. 2003b. Floristic patterns along a 43-km long transect in an Amazonian rain forest. *Journal of Ecology* **91**:743–756 DOI 10.1046/j.1365-2745.2003.00802.x.

Tuomisto H, Ruokolainen K, Yli-Halla M. 2003. Dispersal, environment, and floristic variation of western Amazonian forests. *Science* **299**:241–244.

Tuomisto H, Ruokolainen L, Ruokolainen K. 2012. Modelling niche and neutral dynamics: on the ecological interpretation of variation partitioning results. *Ecography* **35**:961–971.

Tuomisto H, Van doninck J, Ruokolainen K, Moulatlet GM, Figueiredo FOG, Sirén A, Cárdenas G, Lehtonen S, Zuquim G. 2019. Discovering floristic and geoecological gradients across Amazonia. *Journal of Biogeography* **46(8)**:1734–1748 DOI 10.1111/jbi.13627.

Turner W, Spector S, Gardiner N, Fladeland M, Sterling E, Steininger M. 2003. Remote sensing for biodiversity science and conservation. *Trends in Ecology and Evolution* **18**:306–314 DOI 10.1016/S0169-5347(03)00070-3.

Van doninck J, Jones MM, Zuquim G, Ruokolainen K, Moulatlet GM, Sirén A, Cárdenas G, Lehtonen S, Tuomisto H. 2020. Multispectral canopy reflectance improves spatial distribution models of Amazonian understory species. *Ecography* **43**:128–137 DOI 10.1111/ecog.04729.

Van doninck J, Tuomisto H. 2018. A Landsat composite covering all Amazonia for applications in ecology and conservation. *Remote Sensing in Ecology and Conservation* **4**:197–210 DOI 10.1002/rse2.77.

Vitt LJ, Colli GR, Caldwell JP, Mesquita OD, Garda AA, França FGR. 2007. Detecting variation in microhabitat use in low-diversity lizard assemblages across small-scale habitat gradients. *Journal of Herpetology* **41**:654–663.

Vitt LJ, de Carvalho CM. 1995. Niche partitioning in a tropical wet season: lizards in the lavrado area of northern Brazil. *Copeia* **1995**:305–329.

Vitt LJ, Zani PA. 1998. Ecological relationships among sympatric lizards in a transitional forest in the northern Amazon of Brazil. *Journal of Tropical Ecology* **14**:63–86 DOI 10.1017/S0266467498000066.

Waldock C, Dornelas M, Bates AE. 2018. Temperature-driven biodiversity change: disentangling space and time. *BioScience* **68**:873–884 DOI 10.1093/biosci/biy096.

Werneck FP, Colli GR, Vitt LJ. 2009. Determinants of assemblage structure in Neotropical dry forest lizards. *Austral Ecology* **34**:97–115.

Whitney BM, Alonso JA. 1998. A new *Herpsilochmus* antwren (Aves: Thamnophilidae) from Northern Amazonian Peru and adjacent Ecuador: the role of edaphic heterogeneity of terra firme forest. *Auk* **115**:559–576 DOI 10.2307/4089406.

Zuquim G, Tuomisto H, Chaves PP, Emilio T, Moulatlet GM, Ruokolainen K, Van Doninck J, Balslev H. 2021. Revealing floristic variation and map uncertainties for different plant groups in western Amazonia. *Journal of Vegetation Science* **32**:e13081 DOI 10.1111/jvs.13081.