Contrasting patterns of phylogenetic turnover in amphibians and reptiles are driven by environment and geography in Neotropical savannas

Article *in* Journal of Biogeography · May 2021

DOI: 10.1111/jbi.14131

CITATIONS
4

READS
367

4 authors:

Josué Anderson Azevedo
Instituto Nacional de Pesquisas da Amazônia
30 PUBLICATIONS **1,234** CITATIONS
SEE PROFILE

Cristiano de Campos Nogueira
University of São Paulo
122 PUBLICATIONS **4,971** CITATIONS
SEE PROFILE

Alexandre Antonelli
Royal Botanic Gardens, Kew
518 PUBLICATIONS **18,415** CITATIONS
SEE PROFILE

Søren Faurby
University of Gothenburg
161 PUBLICATIONS **4,831** CITATIONS
SEE PROFILE

Received: 18 May 2020 | Revised: 1 December 2020 | Accepted: 29 March 2021

DOI: 10.1111/jbi.14131

Journal of Biogeography WILEY

RESEARCH ARTICLE

Contrasting patterns of phylogenetic turnover in amphibians and reptiles are driven by environment and geography in Neotropical savannas

Josué A. R. Azevedo[1,2,3] | Cristiano de C. Nogueira[4] | Alexandre Antonelli[1,2,5,6] | Søren Faurby[1,2]

[1]Gothenburg Global Biodiversity Centre, Göteborg, Sweden

[2]Department of Biological and Environmental Sciences, University of Gothenburg, Göteborg, Sweden

[3]Programa de Coleções Científicas Biológicas, Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil

[4]Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil

[5]Royal Botanic Gardens, Kew, Surrey, UK

[6]Department of Plant Sciences, University of Oxford, Oxford, UK

Correspondence
Josué A. R. Azevedo, Gothenburg Global Biodiversity Centre, Box 461, SE-405 30 Göteborg, Sweden.
Email: josueanderson21@gmail.com

Funding information
Vetenskapsrådet; Stiftelsen för Strategisk Forskning; Instituto Serrapilheira; Fundação de Amparo à Pesquisa do Estado de São Paulo; Royal Botanical Gardens, Kew; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior

Handling editor: Camila Ribas

Abstract

Aim: Cross-taxonomic congruence in biodiversity patterns is key to understanding the main drivers of community structure, for biogeographical regionalization and to guide conservation. We aim to map the patterns of phylogenetic turnover and disentangle the geographical and environmental factors that drive the phylogenetic composition of distinct faunal assemblages.

Location: The Cerrado savannas of South America.

Taxa: Reptiles and amphibians.

Methods: We measured the proportion of phylogenetic branches shared among sites (i.e. phylogenetic turnover) using presence-absence matrices for all species in the Cerrado and for endemics only, including only well-sampled localities from previously compiled inventories. We then tested whether phylogenetic turnover is different from null expectations based on taxonomic turnover. We used generalized dissimilarity modelling (GDM) to test whether geography, topography, soil or climate best explain phylogenetic turnover. Finally, we mapped the observed and the GDM-predicted clustering of phylogenetic turnover to assess geographical congruence between reptiles and amphibians.

Results: For all reptiles, geographical distance is the most important factor explaining phylogenetic turnover, whereas for endemic reptiles and amphibians, in general, a set of climatic variables and relief roughness are more important. We did not find any significant correlation between the phylogenetic turnover of reptiles and amphibians, as evidenced by non-congruent phylogenetic clustering and by different responses to geographical and environmental gradients.

Main conclusions: The different relationships of phylogenetic turnover of reptiles and amphibians to geographical and environmental distances have ultimately shaped the phylogenetic regionalization of these two groups. This incongruence indicates the differential importance of niche filtering, dispersal limitation and the influence of neighbouring biomes in the regionalization of different groups of organisms. Therefore,

Alexandre Antonelli and Søren Faurby these authors contributed equally to this work.

diversity patterns of one group should ideally not be used as a surrogate to map general patterns or to understand the drivers of diversity of other co-occurring groups. Thus, conservation efforts need to be designed and implemented for each organismal group.

KEYWORDS
beta diversity, Cerrado, connectivity, generalized dissimilarity modelling, herpetofauna, regionalization

1 | INTRODUCTION

The influence of intrinsic characteristics of distinct organisms—such as ecophysiological requirements, habitat use, dispersal ability and degree of niche conservatism—on large-scale biodiversity patterns has been a long-standing point of discussion in biogeography (De Candolle, 1820; Nelson, 1978). With increasing knowledge on the geographical distribution of multiple species and their respective evolutionary relationships, this question can be more precisely tackled (Saladin et al., 2019). It is now possible to estimate changes in lineage composition across space by measuring the replacement of phylogenetic branches among sites (phylogenetic turnover; Rosauer et al., 2014). Phylogenetic turnover may highlight breaks in lineage distribution among sites, which is shown to be correlated with the borders of biogeographical regions (e.g. ecoregions, domains) (Daru et al., 2017). Although biogeographical regionalization is the classification of biotas and areas into distinct entities, it reflects processes that shape biotas, such as vicariance, dispersal and niche filtering (Daru et al., 2018; Vilhena & Antonelli, 2015), often correlating with climatic breaks, orographic barriers and tectonic history (Ficetola et al., 2017). Therefore, phylogenetic turnover can be used as a framework to assess how fine-scale changes in lineage composition can lead to large-scale differences in biogeographical patterns across different groups of organisms.

The importance of the evolutionary history of distinct organisms in shaping biodiversity patterns can be investigated by comparing how much phylogenetic turnover departs from taxonomic (species) turnover (Weinstein et al., 2014). For example, the rate of phylogenetic turnover is expected to be lower than the rate of taxonomic turnover when most taxa above species level are present in the majority of sites (Bryant et al., 2008). When both taxonomic and phylogenetic turnover are low, this may indicate high dispersal rates, weak historical isolation and a low degree of niche conservatism (Alexander Pyron & Burbrink, 2009; Guevara et al., 2016). Conversely, high phylogenetic turnover is thought to be related to ancient geographical barriers, dispersal limitation, a high degree of niche conservatism or high extinction rates (Graham & Fine, 2008). Higher phylogenetic turnover is also expected with increasing elevation, due to greater isolation and habitat heterogeneity in highlands, and along extreme and ancient environmental gradients (Bryant et al., 2008), whereas lowlands may facilitate faunal interchange (Nogueira et al., 2011), resulting in low phylogenetic turnover. If both the degree of phylogenetic turnover over evolutionary history and the responses to geography and environment are similar among taxa, the result is a common pattern of phylogenetic regionalization of the biota (Daru et al., 2017).

Squamate reptiles (lizards and snakes) and anuran amphibians (frogs and toads) generally present very distinctive habitat requirements (Vitt & Caldwell, 2013), which may influence dispersal and isolation. Amphibians generally show a lower vagility due to a stronger association to wet or humid environments (Marshall et al., 2018), which tend to be geographically more restricted in open biomes such as savannas. In contrast, reptiles occur not only in these areas but are also abundant in interfluves and drier habitats (Costa et al., 2007), with varying degrees of habitat specialization for different taxa (Nogueira et al., 2009). Consequently, water-related variables can be more critical for structuring the composition of communities and connectivity among sites for amphibians than for most reptiles, since species of several amphibian clades rely on standing water for breeding (Wells, 2007). Changes in faunal assemblage composition could therefore be more related to environmental distances for amphibians and to geographical distances for reptiles (Chen et al., 2011). Conversely, temperature is shown to be an important driver for reptile distribution due to thermoregulatory strategies (Huey & Stevenson, 1979), whereas interactions between minimum temperatures and precipitation might drive the distributions of nocturnal ectotherms, such as most amphibians (Hillman et al., 2009). Finally, ground characteristics can be critical to driving connectivity among sites for both groups due to habitat preferences of distinct taxa, from fossorial organisms (several reptile taxa) to rock-outcrop specialists—breeding sites for several amphibian species and also preferred habitat for saxicolous reptiles (Vitt, 1993). Thus, if local habitat influences connectivity and isolation among regions for long periods, this may result in contrasting rates of phylogenetic turnover (Daru et al., 2017) between reptiles and amphibians.

In the Cerrado savannas of South America, almost 200 species of squamate reptiles and anuran amphibians have narrowly distributed ranges coincident with several relief units (Fig. S1—Azevedo et al., 2016). This coincident distribution among Cerrado endemics suggests a similar biogeographical history for both groups (Nogueira et al., 2011), which could also indicate a coincident phylogenetic regionalization across the same highlands. The comparison of the distribution patterns between species endemic or not to the Cerrado has indicated a high importance of the proximity to nearby biomes in structuring amphibian faunal assemblages in general, and with lowlands acting as corridors for faunal interchange among biomes

mostly for non-endemic reptiles (Nogueira et al., 2011; Valdujo et al., 2012). Species of reptiles and amphibians endemic to the Cerrado are generally more associated with open savanna ecosystems, especially across the plateaus and highlands, better reflecting the history of the typical Cerrado biota than the non-endemic species, which generally are either more habitat-generalist, forest-dwelling and widely ranged (Nogueira et al., 2011). Therefore, a comparison of patterns between all species and Cerrado endemics only may provide relevant insights into the relative importance of topography, environment and nearby biomes in the patterns of phylogenetic turnover.

Species composition and lineage diversification of the Cerrado herpetofauna are mostly related to major biogeographical events and changes in climate since the middle Miocene in the region (Azevedo et al., 2020; Domingos et al., 2014; Vasconcellos et al., 2020). From that time, global climate cooling led savanna ecosystems to become more widespread, as evidenced by some Cerrado lineages showing signals of range expansion (Machado et al., 2014; Prado et al., 2012). The Miocene to Pliocene uplift of the Central Brazilian Plateau, followed by its erosion by river drainages, compartmentalized the Cerrado into different mountain ranges (Ab'Sáber, 1998), which clearly delimit many ranges of numerous lineages (Guarnizo et al., 2016; Werneck et al., 2012), and is related to endemism patterns in the region (Azevedo et al., 2016; Nogueira et al., 2011). Topography also influences climate stability in the region, with plateaus and mountains harbouring a higher species richness of typical Cerrado species than in flat, lowland areas (Costa et al., 2007). More recently, Pleistocene climate fluctuations may have led to the expansion and retraction of forested biomes into the Cerrado core, fragmenting even more the ranges of some Cerrado lineages (Vasconcellos et al., 2019). These fluctuations may also explain the occurrence of lineages typical of Amazonian or Atlantic Forests, in enclaves and gallery forests of the Cerrado, and species that further specialized to living in savanna habitats (Fouquet et al., 2014; Valdujo et al., 2012). Altogether, climate, vegetational and topographic dynamics, and the proximity to other biomes have potentially shaped phylogenetic turnover, explaining breaks in lineage distributions, and finally, shaping regionalization patterns in the region.

In this study, we estimate phylogenetic turnover for amphibians and reptiles in the Cerrado, comparing analyses including all species with analyses including only Cerrado endemics, and addressing the following questions:

1. *How much does phylogenetic turnover differ from taxonomic turnover?* We expect to find a larger difference in amphibians than in reptiles due to their generally low vagility and higher association with nearby biomes (Valdujo, Silvano, et al., 2012). For amphibians, this difference will be related to the presence of more lineages typical of neighbouring biomes restricted to areas closer to the ecotones, including either species that occur only marginally in the Cerrado or endemic species derived from lineages that have diversified mostly in other biomes (Valdujo, Silvano, et al., 2012). For reptiles, as lineages typical of neighbouring biomes are more widespread within the Cerrado (Nogueira et al., 2011), the difference between taxonomic and phylogenetic turnover should be smaller.
2. *Which environmental variables are correlated to phylogenetic turnover?* Habitat-use differences between reptiles and amphibians should influence the rate of phylogenetic turnover along environmental gradients (Ferrier et al., 2007). Soil-related variables should be important for reptiles due to the large number of fossorial and semi-fossorial species in the Cerrado (Nogueira et al., 2011), and also for amphibians, as these variables may influence the formation and duration of breeding sites and shelter availability during the dry season (Vitt & Caldwell, 2013). The importance of each climatically related variable should differ between the two groups due to the differences in the thermal ecology of diurnal or active thermoregulators (mostly reptiles) and nocturnal ectotherms (most amphibians) (Huey & Stevenson, 1979).
3. *Does the clustering of phylogenetic turnover among sites result in geographically concordant breaks in lineage composition for reptiles and amphibians?* Considering their potentially different responses to geography and environment (*Question 2*), we expect a distinct pattern in the clustering of phylogenetic turnover for these groups. However, as in the case of endemism patterns, a congruent pattern should emerge between both groups, considering the importance of relief units to shape the distribution of organisms in the region.

2 | MATERIAL AND METHODS

2.1 | Study area

We used the delimitation of the Cerrado as an ecoregion (Olson et al., 2001), not including the complex ecotonal ecoregion Maranhão Babaçu forests (between Caatinga and Amazonia) due to its transitional nature and scarcity of herpetofaunal data. The Cerrado is a vast savanna occupying about 1.98 million square kilometres in central South America (IBGE, 2004). The topography is characterized by plateaus, generally above 500 m, and depressions eroded by major drainage systems (Fig. S1). Gallery forests are ubiquitous at most scales, along with typical interfluvial grasslands and savannas (Ratter et al., 1997). This high water availability differentiates the Cerrado savannas from most African savannas (Cole, 1988), and is possibly the reason for the high species richness and endemism of amphibians in the region (Valdujo, Carnaval, et al., 2012). On a large scale, the texture of soils in the region varies from rocky outcrops mostly on highlands and escarpments (Ribeiro & Walter, 2008), sandy soils especially across or nearby ancient sandstones (e.g. north-western Cerrado) or alluvial deposits (e.g. Tocantins-Araguaia Basins) (Villela & Nogueira, 2011) and weathered, deep, clay-rich soils found mostly across tablelands of the Central Brazilian Shield (Ribeiro & Walter, 2008). Mean annual temperature varies within a 10° range (18–28°C), with lower mean temperatures generally towards the south,

and with minimum temperatures mostly in high elevation areas (da Silva et al., 2008). Precipitation exhibits a large degree of variation in the region (~800–2400 mm per year; Bueno et al., 2018), with drier climates in the north-east and south-western Cerrado, and a mild east-to-west increase in annual precipitation.

2.2 | Distributional data

We used a previously compiled voucher-verified dataset of occurrence records for 265 species of squamate reptiles and 193 species of anuran amphibians occurring in the Cerrado (Azevedo et al., 2016; Nogueira et al., 2019; Valdujo, Silvano, et al., 2012). We then produced presence-absence matrices using a cylindrical equal-area Behrman projection grid where the width of each cell was 0.1 degrees. This choice reflects the finest resolution for a substantial part of our data (Valdujo, Silvano, et al., 2012). From this grid, we only included cells containing a minimal number of recorded species, from where we also sampled the environmental variables: (1) cells containing at least 10 recorded species for each group, as in Valdujo, Carnaval, et al., (2012); (2) sites with at least two species endemic to the Cerrado savannas; and (3) in the case of reptiles, sites with at least one species of lizard and one species of snake endemic to the Cerrado, as these two groups vary widely in detectability levels (snakes have much lower detectability; Vitt & Caldwell, 2013). Finally, we also produced a subset of the presence-absence matrices including only species endemic to the Cerrado (100 reptiles and 92 amphibians, as defined in Nogueira et al., 2010; Valdujo, Silvano, et al., 2012; Azevedo et al., 2016). We included all selected sites in the procedure above for each group, and as very few sites coincide between reptiles and amphibians, we checked whether they represent similar distributions of environmental conditions in the region (see *Modelling phylogenetic turnover*).

2.3 | Phylogenetic data

To calculate phylogenetic turnover, we followed the phylogenetic hypotheses proposed by Tonini et al., (2016) and Jetz and Pyron, (2018) for reptiles and amphibians respectively. As species without molecular data were assigned to the respective genus in a posterior distribution representing different combinations of within-genus evolutionary relationships, we repeated all phylogeny-dependent analyses for a sample of 100 of these phylogenies. We then used the median values in all subsequent analyses. In the resulting phylogenies, around 60% of all species were included through assignments to genus level. We recognize that our results should be carefully interpreted at the species level. Previous sensitivity analyses with similar phylogenies indicated good accuracy and low sensitivity for mapping phylogenetic patterns (Azevedo et al., 2019). Even so, we accounted for this uncertainty in our analyses by weighting phylogenetic turnover according to the proportions of species with molecular data in each site (see the subsection *Modelling phylogenetic turnover*).

2.4 | Phylogenetic turnover

2.4.1 | Phylogenetic beta diversity

Phylogenetic turnover is one of the two phylogenetic beta diversity components and accounts for the proportion of phylogenetic branches that are replaced from one site to another. We measured phylogenetic turnover between sites with the Simpson derived pairwise phylogenetic dissimilarity index (Leprieur et al., 2012), a metric less sensitive to the total species richness, which ranges from 0 (all branches are shared between sites) to 1 (no branches are shared). The second component is called nestedness and accounts for losses without replacement in phylogenetic branches (Baselga, 2010). We estimated the total multiple site phylogenetic beta diversity related to each of these components (Baselga, 2013). However, for the subsequent analyses, we only considered the turnover component to separate the potentially complex effects of differences in species richness among sites (Soininen et al., 2018). For the tests against the null distributions (see below), we also measured the taxonomic turnover as the Simpson pairwise dissimilarity (Koleff et al., 2003).

2.4.2 | Decoupling of phylogenetic and taxonomic turnover (Question 1)

To test whether phylogenetic turnover is decoupled from taxonomic turnover, we regressed their scores against each other (site by site). We then compared this result (observed) to a null distribution of slope values of phylogenetic turnover against the taxonomic turnover. We generated this null distribution by randomly shuffling the tips of the phylogeny in 1,000 randomizations. We considered phylogenetic turnover to be decoupled from taxonomic turnover if the resulting slope was outside the interval between the 2.5 and 97.5% of the slopes resulting from the null distribution (Fig. S2).

2.5 | Environmental characterization

To characterize the climate of each site (*Question 2 - Which environmental variables are correlated to phylogenetic turnover?*), we downloaded 19 bioclimatic variables from the CHELSA project (http://chelsa-climate.org/; Karger et al., 2016). We also characterized soils in each site from layers of predicted values of the proportion of sand, clay and coarse fragments (median values for the first 15 cm of the soil surface) downloaded from soilgrids.org (Hengl et al., 2014). Additionally, we estimated the elevation, relief roughness and slope of each site with a digital elevation model (GTOPO30, 2015), and the distance to the nearest stream (derived from: Lehner et al., 2008). However, this last variable was not included as it does not show any variation within the grid resolution used here. We measured relief roughness as the largest difference in elevation of each site with its eight closest neighbours. This variable represents environmental heterogeneity and may account for the presence of a greater variety

of microhabitats within a site. We then retained only variables with no multicollinearity problems after calculating their variance inflation factor (VIF), using a threshold of 10 (Naimi et al., 2014). This selection resulted in five layers for precipitation and five for temperature, representing most of the climatic variation in the region (Table 1). Among the non-climatic variables, the slope was excluded due to high collinearity with relief roughness. Although we automatically removed variables with high VIF, we discussed all highly correlated variables (> 0.9; Dohoo et al., 1997) as groups (e.g. relief roughness and slope; Fig. S3). All groups of environmental predictors have biological justification for explaining lineage distributions (Table 1).

2.6 | Modelling phylogenetic turnover

2.6.1 | Correlates of phylogenetic turnover (Question 2)

To test which set of environmental variables best explain phylogenetic turnover, we used generalized dissimilarity modelling (GDM), a modelling technique based on regressions of nonlinear distance matrices (Ferrier et al., 2007). First, we produced GDM models with all possible combinations of variables with low VIF scores described above (five temperature, five precipitation, three soil, relief roughness, elevation and geographical distance). Then, starting from the full model, we successively eliminated the variable with the smallest contribution. In each round, we calculated the relative variable importance (percentage of explained deviance between a model with and without a variable) and significance (P-value <0.05) through matrix permutations for each variable (n = 1,000). Model selection using Akaike's Information Criterion (AIC) does not apply to techniques of regression matrices such as GDM (Wagner & Fortin, 2015). Therefore, we used an equivalent strategy by selecting the model with the highest value of explained deviance which retained only variables that were important in more than 160 rounds of permutation (following the 0.16 optimization level suggested in Heinze et al., 2018). We then visualized the most important variables using I-splines, which describe nonlinear monotonic relationships among variables and phylogenetic turnover (i.e. partial ecological distance). We calculated the unique contributions of geographical and environmental distances by partitioning the explained deviance of GDM models including only each set of distances (geography or environment) and the model including all sets (Fitzpatrick et al., 2013). All

TABLE 1 Environmental correlates of phylogenetic turnover for reptiles and amphibians selected in the best GDM model, and the respective biological interpretation

Selected variable (correlated variables)	Biological interpretation
Relief roughness (Slope)	Geographical barriers, environmental complexity.
Percentage of sand (Percentage of clay*)	Soil characteristics influence vegetation structure, locomotion strategies for reptiles and breeding sites for amphibians.
Temperature seasonality (Precipitation of driest month)	Climatic seasonality/stability in general. One of the main differences between Cerrado and the surrounding forested biomes.
Max. temp. of the warmest month (Elevation*, Mean temp. Wettest quarter, Mean temp. Driest quarter, Mean temp. Warmest quarter, Mean temp. Coldest quarter.)	Encompasses a broad range of temperature characteristics inversely correlated to elevation in the Cerrado region, with the highest temperatures occurring in lower elevation areas.
Precipitation of the wettest month (Precipitation of the wettest quarter)	The amount of precipitation in the rainy season influences booms of food availability and the reproduction season for both groups.
Precipitation seasonality (Precipitation of the driest quarter*)	Highly seasonal areas in the Cerrado demand ecophysiological and behavioural adaptations of organisms, influencing species ranges.
Precipitation of the Warmest Quarter (Min Temp. Coldest Month*, Mean Temp. of Coldest Quarter*)	These variables represent a climatic latitudinal gradient (within the Cerrado only), with coldest temperatures in the southern parts of the Cerrado. Minimum temperatures limit ranges of ectothermic organisms.

Highly correlated variables (>0.9) not included in the model selection but representing equivalent environmental gradients in the region are shown in parentheses (see also Fig. S3). Asterisks denote a negative correlation with the selected variables.

GDM models were produced with the R-package *gdm* (Ferrier et al., 2007). As sites selected for reptiles and amphibians are generally non-overlapping, we visually inspected whether they encompass the same environmental spaces to verify the influence of site selection on our GDM modelling.

To take into consideration the variation in the phylogenies used here, we weighted the contribution of each site to the GDM models by the standard deviation in the phylogenetic diversity of a site across the sample of 100 phylogenies divided by the respective number of species at each site (PD – Faith, 1992). In this way, sites with considerable PD variation per species due to the random taxonomic assignment will have a lower contribution to the final results.

2.6.2 | Observed and predicted clustering (Question 3)

To address *Question 3* (*Does the clustering of phylogenetic turnover among sites result in geographically concordant breaks in lineage composition for reptiles and amphibians?*), we compared the observed values of phylogenetic turnover between reptiles and amphibians as well as the GDM model predictions projected onto geographical space. We classified sites that are phylogenetically more similar to each other by clustering both the observed and the predicted phylogenetic turnover using UPGMA, a widely applied method for clustering dissimilarity matrices in bioregionalization analyses (Kreft & Jetz, 2010). As our intention is not to provide a definitive bioregionalization scheme, but rather assess whether breaks in the phylogenetic turnover are congruent between reptiles and amphibians, we mapped the first 12 clusters for each group in different colours. This number was chosen to be comparable to previous regionalization schemes using species-level analyses of endemism (Azevedo et al., 2016).

3 | RESULTS

3.1 | Phylogenetic beta diversity

The multiple site tests indicated that nearly all phylogenetic beta diversity for reptiles (turnover =0.94, nestedness =0.03) and amphibians (turnover =0.95, nestedness =0.02) was explained by the turnover component. This shows that the vast majority of differences in phylogenetic branches shared among sites are not related to losses in phylogenetic branches without replacement.

3.2 | Decoupling of phylogenetic and taxonomic turnover (Question 1)

For all datasets (both reptiles and amphibians with all species or only Cerrado endemics), there was a positive increase in phylogenetic turnover with increasing taxonomic turnover, which shows greater slope values for the datasets with all species compared to endemics, and with both turnover metrics more decoupled for amphibians in general (Table 2, Fig. S4 a-b).

3.3 | Correlates of phylogenetic turnover (Question 2)

In general, phylogenetic turnover was higher for amphibians than reptiles across the environmental gradient, except for precipitation seasonality (similar response) and precipitation of warmest quarter (collinear with minimum winter temperatures) with higher importance for endemic reptiles (Figure 1, Table 3). Relief roughness was significantly important for amphibians (both datasets), whereas the percentage of sand was only significant for endemic amphibians (Table 3, Figure 1). In general, the effects of geographical distance alone were more important for the dataset including all reptiles (32% of explained GDM deviance), whereas for all other datasets, purely environmental distances were more important (> 50%, Fig. S5). Sites selected for reptiles and amphibians represented a similar environmental space (Fig. S6), thus allowing comparison between both groups. Finally, we did not find any major differences in the results using our procedure to weight phylogenetic turnover according to the number of species with molecular data available, when compared to the analyses without the weighting procedure (all results shown are derived from the weighted procedure).

3.4 | Observed and predicted clustering (Question 3)

The clustering of phylogenetic turnover indicated spatial mismatches in the direction of phylogenetic turnover between reptiles and amphibians. For both amphibians and reptiles, there was a latitudinal and a longitudinal differentiation in the phylogenetic composition of sites (Figure 2a and b). However, this differentiation was not so abrupt for reptiles, with several sites classified in different clusters occurring side by side (Figure 2a). The clustering of predicted values of phylogenetic turnover indicated a more

TABLE 2 Rate of increase in phylogenetic turnover with taxonomic turnover

Dataset	Slope
Reptiles	1.39 (0.56)
Endemic reptiles	0.64 (0.70)
Amphibians	1.05 (0.04)
Endemic amphibians	0.48 (0.08)

The numbers indicate the rate of turnover (coefficient) estimated by linear regressions. Numbers in parentheses indicate the proportion of times phylogenetic turnover rates were lower than the null distribution. Rates of phylogenetic turnover departed more from taxonomic turnover for amphibians than for reptiles (numbers in parentheses and Fig. S4).

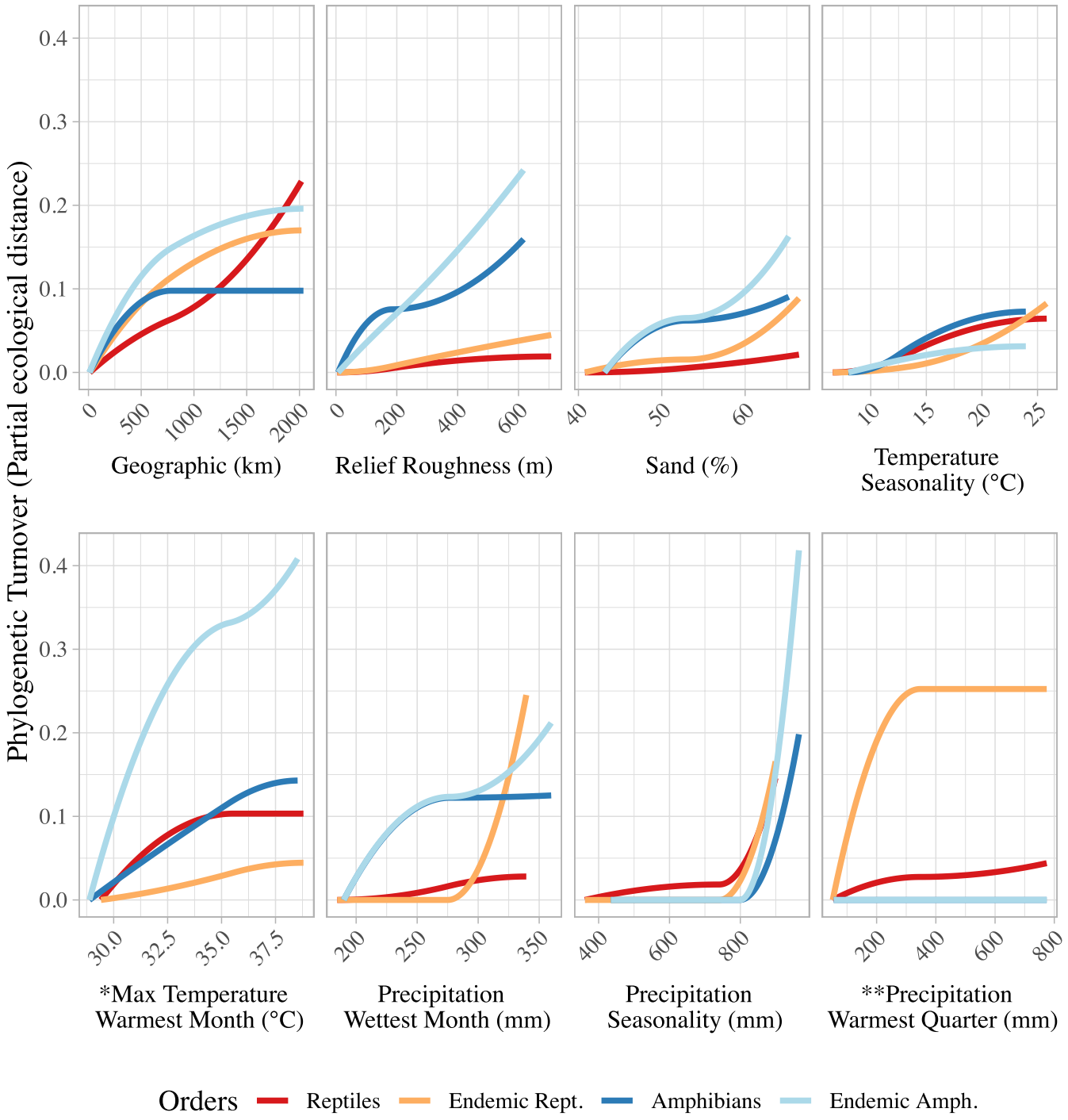

FIGURE 1 Geographical and environmental predictors of phylogenetic turnover. I-splines were estimated from GDM models. The height of each I-spline indicates the relative contribution of each variable to the phylogenetic turnover observed along each environmental gradient (i.e. the partial ecological distance). Asterisks highlight variables with variation in additional climatic/environmental classes: *Highly collinear with elevation; **Highly collinear with minimal winter temperatures (see Table 1 and Fig. S3). Precipitation seasonality is a key variable for both reptiles and amphibians, whereas the relationship of phylogenetic turnover to all other variables differs considerably between each group

phylogenetically uniform biota in the western part of the Cerrado for amphibians (Figure 2d) when compared to reptiles (Figure 2c). There was also a higher spatial mismatch between observed and predicted clusters for reptiles, indicating a lower tracking of environmental conditions for this group. Similar patterns were obtained for the endemics-only dataset (Fig. S7), with a less uniform structuring in the predicted clustering for endemic reptiles (as compared to all reptiles) and an even more extensive area with uniform lineage composition for endemic amphibians in the western part of the Cerrado (Fig. S7).

TABLE 3 Best GDM model for reptiles and amphibians and the respective subsets composed only of the species endemic to the Cerrado (End-)

	Reptiles	End-Reptiles	Amphibia	End-Amphibia
Best model				
Model deviation	206.3	405.7	154.3	457.5
Percentage of deviation explained	12.8	18.0	34.6	29.1
Variable importance				
Geographical distance	34.5***	9.0***	5.5***	7.0***
Relief roughness	–	–	5.3*	6.4**
Percentage of sand	–	–	1.8	3.1*
Temperature seasonality	–	–	2.8	–
Max. temp. (warmest month[a])	12.1	–	4.1*	5.8**
Precipitation (wettest month)	–	7.3	5.8**	2.9
Precipitation seasonality	19.2*	6.8	18***	24.4***
Precipitation (warmest quarter[b])	–	18.2**	–	–

All four models explain significantly more deviation than expected by random ($p < 0.001$). Asterisks indicate: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. Variable importance is the percentage of change of explained deviance calculated through matrix permutations for each variable (1000×). Except for geographical distance and precipitation seasonality, significant variables for reptiles are not the same as for amphibians.

[a]Highly correlated with Elevation.

[b]Highly correlated with Minimum winter temperatures.

4 | DISCUSSION

We found differences between reptiles and amphibians in relation to all three questions tackled here. Firstly, in the degree of decoupling between phylogenetic and taxonomic turnover (higher for amphibians, *Question 1*). Secondly, the importance of environmental and geographical distances in relation to phylogenetic turnover differs between the two taxonomic groups—this is also true for the respective datasets with Cerrado endemics only, with geography alone important only for all reptiles (*Question 2*). Thirdly, we found that the clustering of phylogenetic turnover is largely incongruent between reptiles and amphibians (including the endemic-only datasets) in the Cerrado savannas of South America (*Question 3*).

Our results contrast with the species-level geographical congruence in the distributions of reptiles and amphibians (Azevedo et al., 2016), reinforcing the importance of including information on the evolutionary relationships among species to understand biogeographical patterns (Fenker et al., 2014, 2020). These differences between major groups are likely to be the result of long-term evolutionary distinct responses to geography and environment, indicating that small-scale habitat preferences and ecophysiological differences may lead to detectable imprints in the geographical distribution of lineages.

The higher decoupling of phylogenetic and taxonomic turnover in amphibians (*Question 1*) is in accordance with our predictions and may indicate a combination of higher dispersal limitation, higher association with nearby biomes and higher niche conservatism for this group (Myers et al., 2013; Weinstein et al., 2014). This expectation holds true even when excluding species typical of other biomes that marginally occur in the Cerrado (endemic-only dataset). The coupling between both turnover estimations for reptiles could be related to the still incomplete molecular data in the phylogenies used here, which is known to decrease the power of analyses depending on branch length estimations (Title & Rabosky, 2016). However, the reasonably complete genus-level resolution of the phylogenies used here allowed us to infer that phylogenetic turnover is not driven mostly by species from the same genus (e.g. as in Amazonian white-sand forests; Guevara et al., 2016). Also, phylogenetic turnover for all reptiles and endemic reptiles and amphibians is not predominantly driven by species from distantly related lineages (above genus level), which is more common when comparing sites from two distinct biogeographical regions (e.g. Neotropics vs. Nearctic; Antonelli, 2017). Although we are not directly assessing the evolutionary processes that shaped phylogenetic turnover, our findings indicate distinct patterns for reptiles and amphibians and the underlying processes could potentially differ at different time scales.

Our results indicate that environmental filtering is more important in explaining phylogenetic turnover for amphibians (both datasets), whereas geographical distance is more important for all reptiles (*Question 2*). For amphibians in general, the presence of breeding sites (e.g. relief roughness and soil texture) and the effects of temperature on metabolism (warmer temperatures and high precipitation) (Hillman et al., 2009) are the main correlates of phylogenetic turnover, potentially indicating niche-filtering processes.

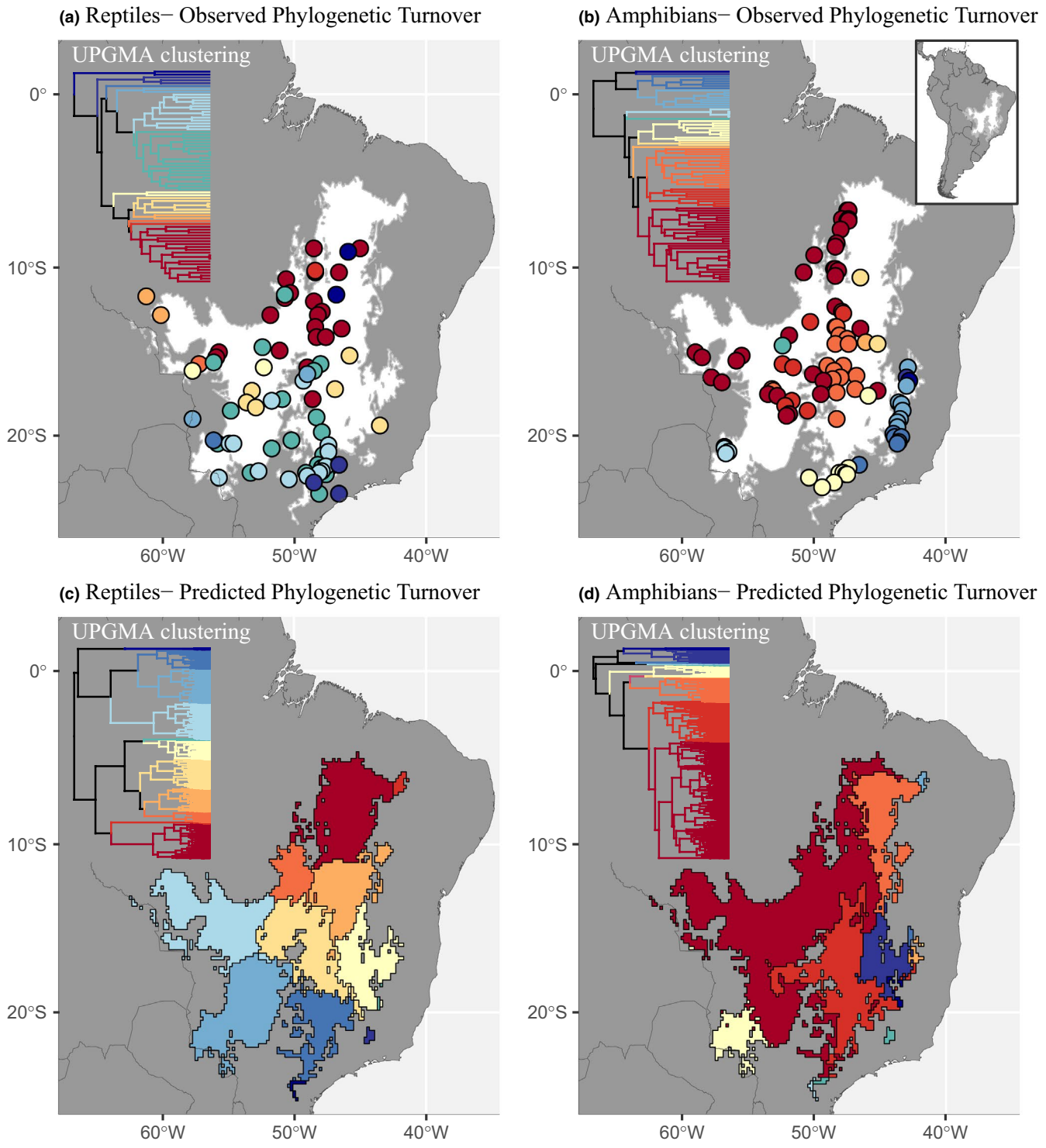

FIGURE 2 Clustering of phylogenetic turnover for reptiles and amphibians of the Cerrado savannas. Sites with the same colour share more phylogenetic branches (= less turnover). Each terminal of the UPGMA dendrograms indicates a distinct site. (a and b) Clustering of the observed pairwise phylogenetic turnover for well-sampled sites (at least 10 species, and two Cerrado endemics). (c and d) Clustering of the GDM predictions of phylogenetic turnover with geographical distance, precipitation and temperature variables for reptiles (Table 2), plus soil and elevation variables for amphibians. This figure demonstrates strikingly contrasting patterns of phylogenetic turnover between reptiles and amphibians in both the observed and in the predicted patterns. Maps are displayed on an equal-area Behrman projection

This combination of climatic variables is related to the fact that in amphibians, the permeability of the skin constrains responses to temperature, as most amphibians do not actively thermoregulate (Wells, 2007). Therefore, extremes of (especially lower) temperature in highly seasonal areas may demand additional physiological and behavioural adaptations in amphibians (Cunningham et al., 2016),

as most Cerrado species spend most of their time outside water as adults. The same variables are also important for the presence of breeding sites, as the formation and duration of temporary ponds/streams (breeding sites for most Cerrado amphibians; Valdujo, Silvano, et al., 2012) are related to relief roughness or soil texture and climatic conditions respectively.

The greater phylogenetic turnover with geographical distance for all reptiles indicates the importance of the four biomes surrounding the Cerrado in the assemblage of reptiles (i.e. sites at opposite borders will present higher phylogenetic turnover). Potential geographical barriers in the Cerrado have possibly limited dispersal of most non-endemics across the entire region (Nogueira et al., 2011). These barriers include tabletop mountains and highlands separated by peripheral depressions and river valleys (Silva, 1997), which were also suggested to have a strong impact on Cerrado endemic reptiles and amphibians by fragmenting ancestral ranges (Azevedo et al., 2016). However, for the dataset with the endemics only, temperature and precipitation variables were more important (Figure 1, *Question 2*), and the importance of geographical distance alone was minor (Fig. S5). In general, temperature is considered one of the most important determinants of the distribution of reptile species (Huey, 1982). Distinct thermoregulatory strategies and temperature optima can vary across different phylogenetic levels in this group (Diele-Viegas et al., 2018). This may explain the importance of minimum winter temperatures for endemic reptiles (collinear with precipitation of warmest quarter, Figure 1), although this pattern could also be the result of the concentration of endemic reptiles across the larger plateaus in the south and south-east Cerrado (Nogueira et al., 2011), generally more prone to lower temperatures (da Silva et al., 2008). Such differences in the importance of geography and environment between the two reptile datasets highlight the importance of intrinsic environmental conditions within the region for Cerrado endemics (Costa et al., 2007), when compared to the more generalist or widely ranged non-endemics.

In contrast to the pattern found for all reptiles, phylogenetic turnover does not increase considerably with distance for amphibians in the Cerrado (Figure 1, *Question 2*). This pattern may be related to the presence of species typical of forested biomes in areas of high relief roughness in the ecotone with the Atlantic Forest (higher phylogenetic differentiation, see UPGMA clustering, Figure 2d), and the lower phylogenetic clustering across the more extensive Amazonian-Cerrado ecotone. The entire Amazonian-Cerrado ecotone is represented by a single large cluster mostly across lowland areas, which indicates a higher connectivity of these amphibian faunas in the region. Also, amphibians typical of lowland forests in this ecotone may have experienced higher extinction rates during past climate changes (i.e. lower climate buffering, Araújo et al., 2008), resulting in a lower phylogenetic turnover.

For endemic amphibians, the even greater importance of relief roughness in relation to all amphibians may be related to the fact that in the Cerrado, small streams in open savannas or grasslands are the primary habitat for most endemic species of this group (Valdujo, Silvano, et al., 2012). This environment is mostly restricted to highlands, which are not uniformly distributed in the Cerrado, but concentrated on the central and south-eastern areas (Simon & Proença, 2000; see Fig. S1). The proximity with drier regions (Caatinga and Chaco, north-eastern and south-western borders respectively) further indicates the importance of nearby biomes in structuring amphibian assemblages. In fact, the clustering of phylogenetic turnover in amphibians was much closer to these borders than in reptiles, suggesting that the environmental similarity with neighbouring biomes is of greater importance in driving these patterns, as proposed by Valdujo, Carnaval, et al., (2012).

Contrary to our expectations, soil variables were not important in explaining phylogenetic turnover for all reptiles (*Question 2*), although they were slightly more important for endemics, and significantly important for endemic amphibians. As discussed earlier, this pattern is potentially due to the formation and duration of breeding sites, and also because some amphibians hide in the soil during the dry season (e.g. Nomura et al., 2009). One possible explanation is that soil variables, such as the proportion of sand and clay, vary and drive phylogenetic turnover at an even finer geographical scale than that of the available data (Figueiredo et al., 2018). It is also possible that these variables only drive phylogenetic turnover at shallow phylogenetic levels, which could be masked when analysing phylogenetic turnover in groups with such a deep evolutionary history as reptiles and amphibians (Rosauer et al., 2014). For example, several of the endemic lizard and snake species adapted to sand soils (e.g. in the Jalapão region) have closely related species occurring in other Cerrado environments (e.g. *Kentropyx*, *Cnemidophorus*, *Apostolepis* and *Bachia*) (Nogueira et al., 2010). The low level of niche conservatism and high lability of traits related to the use of soil in reptiles are patterns observed worldwide, with convergent adaptations of lizards and snakes to specific sandy or rocky substrates (Rodrigues, 1993).

At broader geographical scales, phylogenetic and taxonomic turnover are consistently congruent for most ectothermic tetrapods, especially in areas with steep relief or in biome transitions (Buckley & Jetz, 2008; Saladin et al., 2019). In contrast to the Atlantic Forest or Amazonia, proposals for regionalization on continental scales generally result in one continuous terrestrial unit for the Cerrado (Olson et al., 2001; Dinerstein et al., 2017; but see Colli-Silva et al., 2019). Within the Cerrado, a recent study shows that phytogeographical regions for trees are uniformly structured across the region (Françoso et al., 2020), similar to what we found for the predicted clustering for reptiles, although the observed phylogenetic turnover indicates that sites from different clusters occur side by side without sharp breaks (*Question 3*). For amphibians, a previous study indicated the clustering of taxonomic beta diversity (turnover and nestedness not separated) in six equally distributed regions (Valdujo, Carnaval, et al., 2012). In contrast, our results, based on phylogenetic turnover, indicate a more homogenous phylogenetic composition of amphibian assemblages with breaks in the phylogenetic composition concentrated in the east. Once again, our results reinforce the importance of adding phylogenetic information when mapping biogeographical

patterns. Historical events since the middle Miocene (climate, topographic and vegetational dynamics) are correlated to species-level patterns of richness and endemism (Azevedo et al., 2016; Costa et al., 2007), and the diversification at genus and species levels for many Cerrado lineages (e.g. Giugliano et al., 2013; Prado et al., 2012; Vasconcellos et al., 2020). In contrast, more ancient, large-scale distributional patterns of reptiles and amphibians in the continent—for example, larger diversity of frogs in tropical forests (Buckley & Jetz, 2007; Roll et al., 2017) —may have ultimately shaped their contrasting patterns of regionalization within the Cerrado, when considering the deep phylogenetic relationships among lineages as we found here.

Phylogenetic turnover among biological communities is driven by the history of speciation and extinction and by intrinsic clade characteristics related to dispersal limitation and niche conservatism (Daru et al., 2017). In contrast to predictions based on species diversity (Azevedo et al., 2016), our results indicate that diversity is unevenly distributed for different groups of organisms when considering their phylogenetic relationships (*Question 3*). These differences hamper cross-taxonomic generalizations on how biodiversity evolved in the region and highlight the phylogenetic uniqueness of different portions of the Cerrado savannas. The complexity of the biogeographical patterns in one of the most endangered biomes in the world indicates that irreplaceable areas for conservation of distinct lineages of organisms are not always coincident, even if species-level diversity patterns are congruent. This suggests that conservation efforts need to be designed and implemented taking into consideration as many organismal groups as possible.

ACKNOWLEDGEMENTS

We thank Alexander Zizka, Camila Ritter, Gabriel Costa, Harith Farooq, Johan Nylander, Paula H. Valdujo, Rhian Smith, Associate Editor Camila Ribas and three anonymous reviewers for providing insightful comments on previous versions of this manuscript. JARA thanks Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for providing a doctoral fellowship (99999.001292/2015-03), and Instituto Serrapilheira for a post-doctoral fellowship. CN is funded by FAPESP (2015/20215-7). SF is funded by the Swedish Research Council (#2017-03862). AA is funded by Swedish Research Council (B0569601), the Swedish Foundation for Strategic Research and the Royal Botanic Gardens, Kew. No collecting permits were needed for this research.

DATA AVAILABILITY STATEMENT

The raw distribution data used in this work were published in Azevedo et al., 2016. All tables for phylogenetic turnover measures and environmental variables are available in the Dryad repository (https://doi.org/10.5061/dryad.rr4xgxd7z). Scripts necessary for reproducing all analyses are available on https://github.com/Josh212325/p_turnover_cerrado.

ORCID

Josué A. R. Azevedo https://orcid.org/0000-0001-7394-2670
Cristiano de C. Nogueira https://orcid.org/0000-0003-1835-6761
Søren Faurby https://orcid.org/0000-0002-2974-2628

REFERENCES

Ab'Sáber, A. N. (1998). Participação das depressões periféricas e superfícies aplainadas na compartimentação do Planalto Brasileiro - considerações finais e conclusões. *Revista do Instituto Geológico*, *19*, 51–69.

Alexander Pyron, R., & Burbrink, F. T. (2009). Lineage diversification in a widespread species: Roles for niche divergence and conservatism in the common kingsnake, *Lampropeltis getula*. *Molecular Ecology*, *18*, 3443–3457.

Antonelli, A. (2017). Drivers of bioregionalization. *Nature Ecology and Evolution*, *1*, 1–2.

Araújo, M. B., Nogués-Bravo, D., Diniz-Filho, J. A. F., Haywood, A. M., Valdes, P. J., & Rahbek, C. (2008). Quaternary climate changes explain diversity among reptiles and amphibians. *Ecography*, *31*, 8–15.

Azevedo, J. A. R., Collevatti, R. G., Jaramillo, C. A., Strömberg, C. A. E., Guedes, T. B., Matos-Maraví, P., Bacon, C. D., Carillo, J. D., Faurby, S., & Antonelli, A. (2020) On the young savannas in the land of ancient forests. R. Valentí, & C. Ana (Eds.), *Neotropical Diversification: Patterns and Processes* (pp. 271–298). Cham.

Azevedo, J. A. R., Guedes, T. B., de Nogueira, C. C., Passos, P., Sawaya, R. J., Prudente, A. L. C., Barbo, F. E., Strüssmann, C., Franco, F. L., Arzamendia, V., Giraudo, A. R., Argôlo, A. J. S., Jansen, M., Zaher, H., Tonini, J. F. R., Faurby, S., & Antonelli, A. (2019). Museums and cradles of diversity are geographically coincident for narrowly distributed Neotropical snakes. *Ecography*, *42*, 1–12.

Azevedo, J. A. R., Valdujo, P. H., & Nogueira, C. (2016). Biogeography of anurans and squamates in the Cerrado hotspot: coincident endemism patterns in the richest and most impacted savanna on the globe. *Journal of Biogeography*, *43*, 2454–2464.

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *19*, 134–143.

Baselga, A. (2013). Multiple site dissimilarity quantifies compositional heterogeneity among several sites, while average pairwise dissimilarity may be misleading. *Ecography*, *36*, 124–128.

Bryant, J. A., Lamanna, C., Morlon, H., Kerkhoff, A. J., Enquist, B. J., & Green, J. L. (2008). Microbes on mountainsides: contrasting elevational patterns of bacterial and plant diversity. *Proceedings of the National Academy of Sciences*, *105*, 11505–11511.

Buckley, L. B., & Jetz, W. (2007). Environmental and historical constraints on global patterns of amphibian richness. *Proceedings of the Royal Society B: Biological Sciences*, *274*, 1167–1173.

Buckley, L. B., & Jetz, W. (2008). Linking global turnover of species and environments. *Proceedings of the National Academy of Sciences*, *105*, 17836–17841.

Bueno, M. L., Dexter, K. G., Pennington, R. T., Pontara, V., Neves, D. M., Ratter, J. A., & de Oliveira-Filho, A. T. (2018). The environmental triangle of the Cerrado Domain: Ecological factors driving shifts in tree species composition between forests and savannas. *Journal of Ecology*, *106*, 2109–2120.

Chen, S., Jiang, G., Zhang, J., Li, Y., & Qian, H. (2011). Species turnover of amphibians and reptiles in eastern China: disentangling the relative effects of geographic distance and environmental difference. *Ecological Research*, *26*, 949–956.

Colli-Silva, M., Vasconcelos, T. N. C., & Pirani, J. R. (2019). Outstanding plant endemism levels strongly support the recognition of campo rupestre provinces in mountaintops of eastern South America. *Journal of Biogeography*, 1723–1733.

Costa, G. C., Nogueira, C., Machado, R. B., & Colli, G. R. (2007). Squamate richness in the Brazilian Cerrado and its environmental-climatic associations. *Diversity and Distributions*, *13*, 714–724.

Cunningham, H. R., Rissler, L. J., Buckley, L. B., & Urban, M. C. (2016). Abiotic and biotic constraints across reptile and amphibian ranges. *Ecography*, *39*, 1–8.

da Silva, F. A. M., Assad, E. D., Steinke, E. T., & Müller, A. G. (2008). Clima do bioma Cerrado. In A. C. S. Albuquerque, & A. G. da Silva (Eds.), *Agricultura tropical: quatro décadas de inovações tecnológicas, institucionais e políticas* (pp. 93–148). Embrapa Informações Tecnológicas.

Daru, B. H., Elliott, T. L., Park, D. S., & Davies, T. J. (2017). Understanding the processes underpinning patterns of phylogenetic regionalization. *Trends in Ecology and Evolution*, *32*, 845–860.

Daru, B. H., van der Bank, M., & Davies, T. J. (2018). Unravelling the evolutionary origins of biogeographic assemblages. *Diversity and Distributions*, *24*, 313–324.

De Candolle, A. P. (1820). Essai élémentaire de géographie botanique. F.G. Levrault, Strasbourg.

Diele-Viegas, L. M., Vitt, L. J., Sinervo, B., Colli, G. R., Werneck, F. P., Miles, D. B., Magnusson, W. E., Santos, J. C., Sette, C. M., Caetano, G. H. O., Pontes, E., & Ávila-Pires, T. C. S. (2018). Thermal physiology of Amazonian lizards (reptilia: Squamata). *PLoS One*, *13*, e0192834.others

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N. D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E. C., Jones, B., Barber, C. V., Hayes, R., Kormos, C., Martin, V., Crist, E., … Saleem, M. (2017). An ecoregion-based approach to protecting half the terrestrial realm. *BioScience*, *67*, 534–545.

Dohoo, I. R., Ducrot, C., Fourichon, C., Donald, A., & Hurnik, D. (1997). An overview of techniques for dealing with large numbers of independent variables in epidemiologic studies. *Preventive Veterinary Medicine*, *29*, 221–239.

Domingos, F. M. C. B., Bosque, R. J., Cassimiro, J., Colli, G. R., Rodrigues, M. T., Santos, M. G., & Beheregaray, L. B. (2014). Out of the deep: Cryptic speciation in a Neotropical gecko (Squamata, Phyllodactylidae) revealed by species delimitation methods. *Molecular Phylogenetics and Evolution*, *80*, 113–124.

Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity. *Biological Conservation*, *61*, 1–10.

Fenker, J., Domingos, F. M. C. B., Tedeschi, L. G., Rosauer, D. F., Werneck, F. P., Colli, G. R., Ledo, R. M. D., Fonseca, E. M., Garda, A. A., Tucker, D., Sites, J. W., Breitman, M. F., Soares, F., Giugliano, L. G., & Moritz, C. (2020). Evolutionary history of Neotropical savannas geographically concentrates species, phylogenetic and functional diversity of lizards. *Journal of Biogeography*, *47*, 1130–1142.

Fenker, J., Tedeschi, L. G., Pyron, R. A., & de Nogueira, C. C. (2014). Phylogenetic diversity, habitat loss and conservation in South American pitvipers (Crotalinae: Bothrops and Bothrocophias). *Diversity and Distributions*, *20*, 1108–1119.

Ferrier, S., Manion, G., Elith, J., & Richardson, K. (2007). Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity. *Diversity and Distributions*, *13*, 252–264.

Ficetola, G. F., Mazel, F., & Thuiller, W. (2017). Global determinants of zoogeographical boundaries. *Nature Ecology and Evolution*, *1*, 1–7.

Figueiredo, F. O. G., Zuquim, G., Tuomisto, H., Moulatlet, G. M., Balslev, H., & Costa, F. R. C. (2018). Beyond climate control on species range: The importance of soil data to predict distribution of Amazonian plant species. *Journal of Biogeography*, *45*, 190–200.

Fitzpatrick, M. C., Sanders, N. J., Normand, S., Svenning, J. C., Ferrier, S., Gove, A. D., & Dunn, R. R. (2013). Environmental and historical imprints on beta diversity: insights from variation in rates of species turnover along gradients. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20131201.

Fouquet, A., Cassini, C. S., Haddad, C. F. B., Pech, N., & Rodrigues, M. T. (2014). Species delimitation, patterns of diversification and historical biogeography of the Neotropical frog genus Adenomera (Anura, Leptodactylidae). *Journal of Biogeography*, *41*, 855–870.

Françoso, R. D., Dexter, K. G., Machado, R. B., Pennington, R. T., Pinto, J. R. R., Brandão, R. A., & Ratter, J. A. (2020). Delimiting floristic biogeographic districts in the Cerrado and assessing their conservation status. *Biodiversity and Conservation*, *29*, 1477–1500.

Giugliano, L. G., Nogueira, C., Valdujo, P. H., Collevatti, R. G., & Colli, G. R. (2013). Cryptic diversity in South American Teiinae (Squamata, Teiidae) lizards. *Zoologica Scripta*, *42*, 473–487.

Graham, C. H., & Fine, P. V. A. (2008). Phylogenetic beta diversity: Linking ecological and evolutionary processes across space in time. *Ecology Letters*, *11*, 1265–1277.

GTOPO30 (2015) USGS Available online https://lta.cr.usgs.gov/GTOPO30, Accessed on Jan 2018.

Guarnizo, C. E., Werneck, F. P., Giugliano, L. G., Santos, M. G., Fenker, J., Sousa, L., D'Angiolella, A. B., dos Santos, A. R., Strüssmann, C., Rodrigues, M. T., Dorado-Rodrigues, T. F., Gamble, T., & Colli, G. R. (2016). Cryptic lineages and diversification of an endemic anole lizard (Squamata, Dactyloidae) of the Cerrado hotspot. *Molecular Phylogenetics and Evolution*, *94*, 279–289.

Guevara, J. E., Damasco, G., Baraloto, C. (2016). Low phylogenetic beta diversity and geographic neo-endemism in Amazonian white-sand forests. *Biotropica*, *48*, 34–46.

Heinze, G., Wallisch, C., & Dunkler, D. (2018). Variable selection – A review and recommendations for the practicing statistician. *Biometrical Journal*, *60*, 431–449.

Hengl, T., de Jesus, J. M., MacMillan, R. A., Batjes, N. H., Heuvelink, G. B. M., Ribeiro, E., Samuel-Rosa, A., Kempen, B., Leenaars, J. G. B., Walsh, M. G., & Gonzalez, M. R. (2014). SoilGrids1km-global soil information based on automated mapping. *PLoS One*, *9*, e105992.

Hillman, S. S., Withers, P. C., Drewes, R. C., & Hillyard, S. D. (2009). *Ecological and environmental physiology of amphibians*. Oxford University Press.

Huey, R. B. (1982). Temperature, physiology, and the ecology of reptiles. In C. Gans & F. H. Pough (Eds.), *Biology of the reptilia* (pp. 25–91). Academic Press.

Huey, R. B., & Stevenson, R. D. (1979). Integrating thermal physiology and ecology of ectotherms: A discussion of approaches. *Integrative and Comparative Biology*, *19*, 357–366.

IBGE (2004). Mapa de biomas do Brasil. Escala 1:5.000.000. Disponível em: http://mapas.ibge.gov.br/biomas2/viewer.htm.

Jetz, W., & Pyron, R. A. (2018). The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. *Nature Ecology and Evolution*, *2*, 850–858.

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N., Linder, H. P., & Kessler, M. (2016). Climatologies at high resolution for the Earth land surface areas. *Nature Scientific Data*, *4*, 1–19.

Koleff, P., Gaston, K. J., & Lennon, J. J. (2003). Measuring beta diversity for presence-absence data. *Journal of Animal Ecology*, *72*, 367–382.

Kreft, H., & Jetz, W. (2010). A framework for delineating biogeographical regions based on species distributions. *Journal of Biogeography*, *37*, 2029–2053.

Lehner, B., Verdin, K., & Jarvis, A. (2008). New global hydrography derived from spaceborne elevation data. *Eos*, *89*, 93–94.

Leprieur, F., Albouy, C., de Bortoli, J., Cowman, P. F., Bellwood, D. R., & Mouillot, D. (2012). Quantifying phylogenetic beta diversity: distinguishing between "true" turnover of lineages and phylogenetic diversity gradients. *PLoS One*, *7*, e42760.

Machado, T., Silva, V. X., & Silva, M. J. J. (2014). Phylogenetic relationships within Bothrops neuwiedi group (Serpentes, Squamata): geographically highly-structured lineages, evidence of introgressive hybridization and Neogene/Quaternary diversification. *Molecular Phylogenetics and Evolution*, *71*, 1–14.

Marshall, J., Bastiaans, E., Caccone, A., Camargo, A., Morando, M., Niemiller, M., Pabijan, M., Russello, M., Sinervo, B., Sites, J. Jr., Vences, M., Werneck, F., Wollenberg Valero, K., & Steinfartz, S. (2018) Mechanisms of speciation in reptiles and amphibians: A synopsis. *PeerJ*, *6*, e27279v1.

Myers, J. A., Chase, J. M., Jiménez, I., Jørgensen, P. M., Araujo-Murakami, A., Paniagua-Zambrana, N., & Seidel, R. (2013). Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. *Ecology Letters*, *16*, 151–157.

Naimi, B., Hamm, N. A. S., Groen, T. A., Skidmore, A. K., & Toxopeus, A. G. (2014). Where is positional uncertainty a problem for species distribution modelling? *Ecography*, *37*, 191–203.

Nelson, G. (1978). From Candolle to Croizat: comments on the history of biogeography. *Journal of the History of Biology*, *11*, 269–305.

Nogueira, C. 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.

Nogueira, C., Colli, G. R., Costa, G., & Machado, R. B. (2010). Diversidade de répteis Squamata e evolução do conhecimento faunístico no Cerrado. In I. R. Diniz, & J. Marinho-Filho (Eds.), *Cerrado: conhecimento científico quantitativo como subsídio para ações de conservação* (pp. 331–371). Brasília.

Nogueira, C., Colli, G. R., & Martins, M. (2009). Local richness and distribution of the lizard fauna in natural habitat mosaics of the Brazilian Cerrado. *Austral Ecology*, *34*, 83–96.

Nogueira, C., Ribeiro, S. R., Costa, G. C., & Colli, G. R. (2011). Vicariance and endemism in a Neotropical savanna hotspot: distribution patterns of Cerrado squamate reptiles. *Journal of Biogeography*, *38*, 1907–1922.

Nomura, F., Rossa-Feres, D. C., & Langeani, F. (2009). Burrowing behavior of Dermatonotus muelleri (Anura, Microhylidae) with reference to the origin of the burrowing behavior of Anura. *Journal of Ethology*, *27*, 195–201.

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., & Kassem, K. R. (2001). Terrestrial ecoregions of the world: a new map of life on earth. A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience*, *51*, 933–938.

Prado, C. P. A., Haddad, C. F. B., & Zamudio, K. R. (2012). Cryptic lineages and Pleistocene population expansion in a Brazilian Cerrado frog. *Molecular Ecology*, *21*, 921–941.

Ratter, J. A., Ribeiro, J. F., & Bridgewater, S. (1997). The Brazilian Cerrado vegetation and threats to its biodiversity. *Annals of Botany*, *80*, 223–230.

Ribeiro, J. F., & Walter, B. M. T. (2008). As principais fitofisionomias do bioma Cerrado. In S. M. Sano, S. P. de Almeida, & J. F. Ribeiro (Eds.), *Cerrado: Ecologia e flora* (pp. 151–212). Embrapa Cerrados.

Rodrigues, M. (1993). Herpetofauna das dunas interiores do Rio São Francisco: Bahia: Brasil. V. Duas novas espécies de Apostolepis (Ophidia, Colubridae). *Memorias do Instituto Butantan*, *54*, 53–59.

Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A. M., Bernard, R., Böhm, M., Castro-Herrera, F., Chirio, L., Collen, B., Colli, G. R., Dabool, L., Das, I., Doan, T. M., Grismer, L. L., Hoogmoed, M., Itescu, Y., Kraus, F., LeBreton, M., … Meiri, S. (2017). The global distribution of tetrapods reveals a need for targeted reptile conservation. *Nature Ecology and Evolution*, *1*, 1677–1682.

Rosauer, D. F., Ferrier, S., Williams, K. J., Manion, G., Keogh, J. S., & Laffan, S. W. (2014). Phylogenetic generalised dissimilarity modelling: a new approach to analysing and predicting spatial turnover in the phylogenetic composition of communities. *Ecography*, *37*, 21–32.

Saladin, B., Thuiller, W., Graham, C. H., Lavergne, S., Maiorano, L., Salamin, N., & Zimmermann, N. E. (2019). Environment and evolutionary history shape phylogenetic turnover in European tetrapods. *Nature Communications*, *10*, 1–9.

Silva, J. M. C. (1997). Endemic bird species and conservation in the Cerrado Region, South America. *Biodiversity and Conservation*, *6*, 435–450.

Simon, M. F., & Proença, C. (2000). Phytogeographic patterns of Mimosa (Mimosoideae, Leguminosae) in the Cerrado biome of Brazil: An indicator genus of high-altitude centers of endemism? *Biological Conservation*, *96*, 279–296.

Soininen, J., Heino, J., & Wang, J. (2018). A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. *Global Ecology and Biogeography*, *27*, 96–109.

Title, P. O., & Rabosky, D. L. (2016). Do macrophylogenies yield stable macroevolutionary inferences? An example from squamate reptiles. *Systematic Biology*, *66*, 843–856.

Tonini, J. F. R., Beard, K. H., Ferreira, R. B., Jetz, W., & Pyron, R. A. (2016). Fully-sampled phylogenies of squamates reveal evolutionary patterns in threat status. *Biological Conservation*, *204*, 23–31.

Tyrrell, J. G., & Cole, M. M. (1988). The savannas: Biogeography and geobotany. *Geographical Review*, *78*, 462–464.

Valdujo, P. H., Carnaval, A. C. O. Q., & Graham, C. H. (2012). Environmental correlates of anuran beta diversity in the Brazilian Cerrado. *Ecography*, *35*, 1–10.

Valdujo, P. P. H., Silvano, D. D. L., Colli, G., & Martins, M. (2012). Anuran species composition and distribution patterns in Brazilian Cerrado, a Neotropical hotspot. *South American Journal of Herpetology*, *7*, 63–78.

Vasconcellos, M. M., Colli, G. R., & Cannatella, D. C. (2020). Paleotemperatures and recurrent habitat shifts drive diversification of treefrogs across distinct biodiversity hotspots in sub-Amazonian South America. *Journal of Biogeography*, *48*, 305–320.

Vasconcellos, M. M., Colli, G. R., Weber, J. N., Ortiz, E. M., Rodrigues, M. T., & Cannatella, D. C. (2019). Isolation by instability: historical climate change shapes population structure and genomic divergence of treefrogs in the Neotropical Cerrado savanna. *Molecular Ecology*, *28*, 1748–1764.

Vilhena, D. A., & Antonelli, A. (2015). A network approach for identifying and delimiting biogeographical regions. *Nature Communications*, *6*, 1–9.

Villela, F. N. J., & Nogueira, C. (2011). Geologia e geomorfologia da estação ecológica Serra Geral do Tocantins. *Biota Neotropica*, *11*, 217–229.

Vitt, L. J., & Caldwell, J. P. (1993). Ecological observations on cerrado lizards in rondonia, Brazil. *Journal of Herpetology*, *27*, 46–52.

Vitt, L. J., & Caldwell, J. P. (2013). *Herpetology: an introductory biology of amphibians and reptiles*. Academic press.

Wagner, H. H., & Fortin, M.-J. (2015) Basics of spatial data analysis: linking landscape and genetic data for landscape genetic studies. In N. Balkenhol, S. A. Cushman, A. T. Storfer, & L. P. Waits (Eds.), *Landscape genetics* (pp. 77–98). Wiley Online Library, West Sussex.

Weinstein, B. G., Tinoco, B., Parra, J. L., Brown, L. M., McGuire, J. A., Stiles, F. G., & Graham, C. H. (2014). Taxonomic, phylogenetic, and trait beta diversity in south american hummingbirds. *The American Naturalist*, *184*, 211–224.

Wells, K. D. (2007). *The ecology and behavior of amphibians*. University of Chicago Press.

Werneck, F. P., Gamble, T., Colli, G. R., Rodrigues, M. T., & Sites, J. W. Jr (2012). Deep diversification and long-term persistence in the South American 'Dry Diagonal': Integrating continent-wide phylogeography and distribution modeling of geckos. *Evolution*, *66*(10), 3014–3034.

BIOSKETCH

Josué A. R. Azevedo is broadly interested in the biogeography and evolution of terrestrial vertebrates. This work is the continuation of his Masters project on the Cerrado herpetofauna and part of his Ph.D. thesis in Gothenburg, Sweden. He collaborates in the Antonelli lab (https://antonelli-lab.net/) and on the Atlas of Brazilian snakes (https://www.cnbiogeo.com/atlas).

Author contributions: JARA and CCN provided species distribution data. JARA, CCN, AA and SF planned the project. JARA conducted the analyses, produced the figures, tables and led the writing. All authors contributed to the interpretation and discussion of the results and approved the final version of this manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Azevedo JA, de C. Nogueira C, Antonelli A, Faurby S. Contrasting patterns of phylogenetic turnover in amphibians and reptiles are driven by environment and geography in Neotropical savannas. *J Biogeogr*. 2021;00:1–14. https://doi.org/10.1111/jbi.14131