



RESEARCH PAPER

Journal of
Biogeography

WILEY

Evolutionary history of Neotropical savannas geographically concentrates species, phylogenetic and functional diversity of lizards

Jessica Fenker¹ | Fabricius M. C. B. Domingos² | Leonardo G. Tedeschi¹ | Dan F. Rosauer¹ | Fernanda P. Werneck³ | Guarino R. Colli⁴ | Roger M. D. Ledo⁵ | Emanuel M. Fonseca⁶ | Adrian A. Garda⁷ | Derek Tucker⁸ | Jack W. Sites Jr.⁹ | Maria F. Breitman¹⁰ | Flávia Soares¹¹ | Lilian G. Giugliano¹¹ | Craig Moritz¹

¹Division of Ecology and Evolution, Australian National University, Canberra, Australia

²Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, PR, Brasil

³Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia, Manaus, AM, Brasil

⁴Departamento de Zoologia, Universidade de Brasília, Brasília, DF, Brasil

⁵Instituto Federal de Educação, Ciência e Tecnologia de Brasília, Samambaia, DF, Brasil

⁶Department of Evolution, Ecology and Organismal Biology, The Ohio State University, Columbus, OH, USA

⁷Departamento de Botânica e Zoologia, Universidade Federal do Rio Grande do Norte, Natal, RN, Brasil

⁸School of Life Sciences, Arizona State University, Tempe, AZ, USA

⁹Department of Biology and M.L. Bean Life Science Museum, Brigham Young University, Provo, UT, USA

¹⁰Department of Biology, University of Missouri, St. Louis, MO, USA

¹¹Departamento de Genética e Morfologia, Universidade de Brasília, Brasília, DF, Brasil

Correspondence

Jessica Fenker, Division of Ecology and Evolution, Australian National University, Canberra, Australia.
Email: jessica.fenker@anu.edu.au

Present address

Fernanda P. Werneck, Department of Organismic and Evolutionary Biology, Museum of Comparative Biology, Harvard University, Cambridge, MA, USA

Jack W. Sites, Department of Biology, Austin Peay State Univ., Clarksville, TN, USA

Abstract

Aim: Understanding where and why species diversity is geographically concentrated remains a challenge in biogeography and macroevolution. This is true for the Cerrado, the most biodiverse tropical savanna in the world, which has experienced profound biodiversity loss. Previous studies have focused on a single metric (species composition), neglecting the fact that 'species' within the biome are often composed of cryptic species. In order to identify biodiversity hotspots more robustly and across multiple dimensions we integrate functional, spatial and new phylogeographic data for the Cerrado lizard fauna by (a) mapping the spatial patterns of species and phylogenetic diversity; and (b) using endemism measures to identify areas of unique diversity. We then quantify the extent to which existing protected areas represent the diversity.

Location: Brazilian savanna (Cerrado).

Methods: We generated species distribution models using distribution records for all Cerrado lizard species. These, combined with mitochondrial DNA phylogenies and natural history data, allowed us to map species richness, phylogenetic and functional diversity and phylogenetic and weighted endemism. Phylogenetic endemism maps were then cross-referenced against protected areas to calculate the amount of evolutionary history preserved within these areas.

Results: The central region of the Cerrado, a vast and climatically stable plateau, stands out as important under all biodiversity metrics. Including evolutionary relationships in biodiversity assessment, we detected four regional hotspots with high concentration of spatially restricted evolutionary diversity. Protected areas cover only 10% of the Cerrado area and hold 11.64% of the summed phylogenetic endemism of all lizards in the biome.

Main Conclusions: We highlighted both stable (*Chapada dos Veadeiros* and *Serra do Espinhaço* plateaus) and environmentally heterogeneous regions (*Araguaia* and *Tocantins* valleys) as hotspots of evolutionary diversity. The creation and/or manipulation of

Funding information

Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Grant/Award Number: 88881.169862/2018-0; Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: 425571/2018-1, 305535/2017-0, (#310942/2018-7, 206958/2017-0 and 431433/2016-0; FAPEAM, Grant/Award Number: 062.00665/2015 and 062.01110/2017; PEER NAS; USAID, Grant/Award Number: AID-OAA-A-11-00012; L'Oréal-UNESCO For Women In Science Program

Handling Editor: David Chapple

areas for conservation are essential for the conservation and survival of the rich and endemic lizard fauna of the Cerrado.

KEYWORDS

biodiversity, Cerrado, conservation, diversity metrics, phyloendemism, richness

1 | INTRODUCTION

Describing patterns and explaining which processes shaped the unique South American tropical biodiversity have intrigued naturalists for centuries (Bates, 1862; Prance, 1982; Wallace, 1853). There are numerous ways to measure biodiversity, going from estimating the number of species in a determined area (species richness—Gaston, 2000) to looking for concentration of spatially restricted species or community assemblages (endemism—Myers, 2003; Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000). However, species are not independent units, and will share many biological attributes as the result of the evolutionary processes of diversification (Agapow, 2005; Mace, Gittleman, & Purvis, 2003; Vane-Wright, Humphries, & Williams, 1991). Thus, incorporating different sources of biological information such as species traits, phylogenetic relationships and natural history, can provide new insights on how biodiversity was shaped at the landscape scale. Phylogenetic diversity (PD; Faith, 1992) is a widely used measure to represent the evolutionary diversity of a given area, calculated from a phylogenetic tree (Carvalho et al., 2017; Pollock et al., 2015; Rosauer et al., 2016). PD has special importance for conservation when it is spatially restricted (phylogenetic endemism [PE]), indicating

geographic concentration of evolutionarily unique biodiversity (Rosauer, Laffan, Crisp, Donnellan, & Cook, 2009). Measuring PE at phylogeographic scales also provides more robust estimation when taxonomy is in flux (Rosauer et al., 2009). Finally, incorporating functional diversity (FD), a measure of the functional trait variation in a community, such as foraging mode and habitat-use traits, can provide insights on the community-wide diversity of adaptations, which is a proxy of how the organisms might interact with the ecosystem (Petchey & Gaston, 2002; Tilman, 2001).

The use of a wide range of methods to estimate important areas for the maintenance of biodiversity is especially important in complex environments. The Cerrado is the most biodiverse savanna in the world (da Silva & Bates, 2002). It originally spanned nearly 2,000,000 km², covering 22% of Brazil's territory (Oliveira & Marquis, 2002). It is distributed primarily across the Central Brazilian Plateau, a complex landscape of alternating ancient plateaus and younger inter-plateau depressions, reflecting different edaphic factors and plant physiognomies occurring together locally, usually given to explain the high levels of species richness and endemism (Figure 1a) (Colli, Bastos, & Araujo, 2002; Nogueira, Ribeiro, Costa, & Colli, 2011; Ratter, Bridgewater, & Ribeiro, 2003; Silva, 1995; Valdujo, Carnaval, & Graham, 2013). Plateaus reach up to

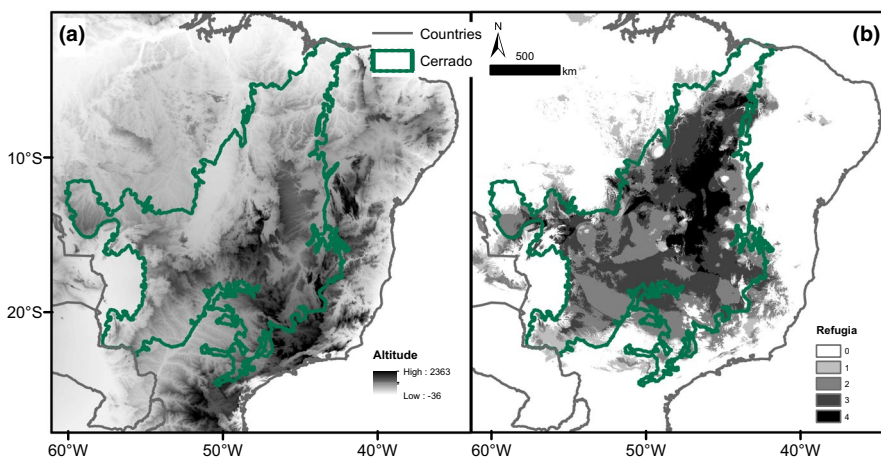


FIGURE 1 Introductory map with elevations and climatic stability surfaces estimated by overlapping predicted logistic outputs under current, 6 ka, 21 ka and 120 ka climatic scenarios (adapted from Werneck, Nogueira, et al., 2012) of the Cerrado



1,676m at Chapada dos Veadeiros National Park (de Carvalho Júnior, Guimarães, de Souza Martins, & Gomes, 2015), are largely covered by savanna vegetation, and are inferred to have experienced relatively high climatic stability at millennial time-scales (Figure 1b) (Burbridge, Mayle, & Killeen, 2004; Werneck, Nogueira, Colli, Sites, & Costa, 2012). Depressions were carved by the headwaters of three large river basins—Tocantins-Araguaia, São Francisco, and Paraná—and are covered by a mosaic of savannas and gallery forests which have shifted during Quaternary climatic cycles (Silva, 1995). Hypotheses about the mechanisms that have promoted high biodiversity in the Cerrado suggest that this hybrid geological history contributed to the assembly of older lineages on plateaus and younger lineages in depressions, called the 'plateau/depression hypothesis' (reviewed in Werneck, 2011).

Lizards are good models for biogeographical studies, occurring in various types of environments, and representing fossorial, terrestrial, saxicolous, aquatic and arboreal lifestyles (Pianka & Vitt, 2003). Their sensitivity to climatic variation, short generation times and relatively limited mobility make lizards good models for ecological and evolutionary studies, including identifying areas with high endemism (Camargo, Sinervo, & Sites, 2010; Pianka & Vitt, 2003; Roll et al., 2017). The Cerrado lizard fauna is characterized by high diversity and many endemic species (Colli et al., 2002; Nogueira et al., 2011), and mapping of this diversity has focused on species composition (Costa, Nogueira, Machado, & Colli, 2007), and recovered coincident regional patterns with anurans and snakes (Azevedo, Valdujo, & Nogueira, 2016). These species-level analyses show that the central portion of the Cerrado (in the Central Brazilian plateau) concentrates the highest diversity, with additional biogeographic units over ancient plateaus. Nevertheless, these studies only measured one attribute of diversity, and have not considered other important elements. Recent studies of Cerrado lizards have shown that single 'species' often display strong phylogeographic structure; in fact, many represent species complexes, show high and unprecedented diversity unknown in previous studies (Domingos, Colli, Lemmon, Lemmon, & Beheregaray, 2017; Fonseca et al., 2018; Giugliano, Nogueira, Valdujo, Collevatti, & Colli, 2013; Guarnizo et al., 2016; Recoder et al., 2014; Werneck, Gamble, Colli, Rodrigues, & Sites, 2012). The high numbers of cryptic species in the Cerrado and the consequent taxonomic uncertainty potentially hide diversity patterns and hamper explanations about the main determinants of lizard diversity.

Previous studies that incorporated functional or phylogenetic diversity did not identify critical regions for the maintenance of this diversity (Batalha, Cianciaruso, & Motta-Junior, 2010; Carvalho, Cianciaruso, Trindade-Filho, Sagnori, & Loyola, 2010; Hidasi-Neto, Loyola, & Cianciaruso, 2013). The use of diversity metrics independent of named taxa, and combining these diversity measures to understand biodiversity distribution patterns is expected to subsidize conservation initiatives (Pollock et al., 2015; Tucker, Davies, Cadotte, & Pearse, 2018) when erosion of genetic diversity happens as a distinct segment of wide-ranging species complexes is lost in areas where the alpha taxonomy is unreliable or incomplete (Isaac, Mallet, & Mace, 2004). Cerrado has experienced dramatic biodiversity loss,

mainly from the fragmentation and conversion of natural areas for livestock and agriculture, introduction of exotic species and climate change (Butchart et al., 2010; Dirzo & Raven, 2003). Less than 47% of natural vegetation remains intact (Beuchle et al., 2015; Brannstrom et al., 2008), and projected plant extinction is extremely high (Strassburg et al., 2017). Although the Cerrado is considered a global biodiversity hotspot (Myers et al., 2000), Brazilian conservation policies often neglect non-forest ecosystems (Marris, 2005; Overbeck et al., 2015). Indeed, less than 8% of this biome is protected, compared with 46% of the Amazon rainforest (Soares-Filho et al., 2014). Therefore, mapping concentrations of diversity for Cerrado taxa, including intraspecific diversity, is particularly important for understanding the correlates of biodiversity patterns, and for prioritizing conservation efforts at local and regional scales (Faith, Reid, & Hunter, 2004; Moritz, 2002).

In this study we integrate functional, spatial and new phylogenetic and phylogeographic data, to provide a multidimensional perspective on Cerrado lizard diversity by: (a) mapping spatial patterns of species and phylogenetic diversity for the lizard communities; and (b) identifying areas with unique diversity using endemism measures. In accordance with findings in rainforest systems (Carnaval et al., 2014; Rosauer, Catullo, VanDerWal, Moussalli, & Moritz, 2015), and the 'plateau/depression' hypothesis, we expect lizard endemism in particular to be higher in older and more climatically stable areas, including the central Brazilian plateau, and depicting a stronger correlation with endemism than diversity since more widespread taxa could expand their range to relatively unstable areas. Moreover, we overlay areas of unique evolutionary biodiversity with the current protected areas network of the biome to identify potential areas that need urgent conservation.

2 | MATERIALS AND METHODS

2.1 | Data

Based on recent literature (see complete list on Data S1) and data published on the Redlist of Brazilian Reptiles (ICMBio, 2018), we updated Nogueira, Colli, Costa, and Machado (2010) Cerrado's lizard species list. Four new species (*Bachia didactyla* De Freitas, Strussmann, De Carvalho, Kawashita-Ribeiro, and Mott (2011); *Bachia geralista* Teixeira Jr et al. (2013); and *Vanzosaura multiscutata* and *V. savanicola* Recoder et al., 2014) were added based on the species list provided from the Brazilian Herpetological Society (Costa & Bérnils, 2018). Since the publication of Nogueira et al. (2010), new data available on literature (ICMBio, 2018 and reference list on Data S2) improved knowledge of species taxonomy and distribution areas, and we exclude questionable distribution points of some species from Cerrado's distribution. Details of the species excluded can be found on the Data S1. This selection resulted in a list of Cerrado lizard species including 66 taxa, used for the functional and species richness analyses. For the functional component, we compiled natural history information from

the literature, seeking traits known to be important in lizard ecology, such as body size, diel activity, habitat use and reproduction, to represent the functional differences among communities (see more details and the complete list in Data S1).

Since mitochondrial data are the most widely available molecular data for Cerrado species, we used different mitochondrial markers for phylogenetic analyses, obtained from phylogeography and population genetics papers where the species were widely distributed within the Cerrado. Previous studies based on multilocus Cerrado lizard datasets have shown overall congruency between mitochondrial and nuclear data (Domingos et al., 2014, 2017; Werneck, Gamble, et al., 2012). Because we aimed to represent the total distribution of every species, we excluded species for which genetic sampling was restricted to small parts of their geographic ranges. With this constraint, the data for our phylogenetic analyses (phylogenetic diversity and endemism) included 26 of the 66 Cerrado species with a well sampled geographic mtDNA dataset. Roughly half of this data were sequences downloaded from Genbank, while the other half were newly generated mtDNA data for many taxa (Table S2). These data were further supplemented by all available mtDNA data for congeneric species that occurred in adjacent areas (50 species), to avoid effects of the limited spatial coverage on endemism calculations (Rosauer et al., 2016, 2009). In some cases, these were Cerrado species with limited mtDNA data for the more inclusive analyses (as *Polychrus marmoratus*, *Salvator duseni* and a few species of *Tropidurus*); see Data S2 for the complete list.

2.2 | Species and lineage distribution models

We generated species distribution models (SDM) using the available records for the entire distribution of each species, values for 19 bioclimatic variables obtained from WorldClim version 1.4 (Hijmans, Cameron, & Parra, 2006) at 2.5 min resolution and a Python 2.7 script (available at github.com/DanRosauer/phylospatial) to automate data preparation and modelling in ArcGIS 10 (ESRI, 2011) and MaxEnt v3.3 predictive modelling approach (Phillips, Dudik, & Schapire, 2012). We retained all bioclimatic variables, even if correlated, following Elith et al. (2011), allowing MaxEnt to determine the required predictors for each model. Background points were limited to a 3-degree radius (Rosauer et al., 2015, 2016) around the location records to avoid overprediction to non-continuous areas but still gather enough information for the surrounding regions of the species' locations, improving the discrimination of suitable habitat within each species and emphasizing the extent of occurrence. Predicted distributions were clipped to the Cerrado biome (IBGE, 2004). For each SDM we took the median of 25 bootstrap replicates. In order to capture the spatial structure of intraspecific diversity, where genetic data revealed multiple lineages within a species (cryptic species), we fitted lineage distribution models (LDMs) following the method described in Rosauer et al. (2015, 2016). In locations where a SDM predicts the occurrence of a species, the LDM estimates the

relative probability that each of the known lineages occurs there, based on habitat connectivity to known locations of the lineage. We thus extrapolated the distribution of each lineage beyond locations of sequenced samples, partitioning the SDM into a separate model for each main lineage.

2.3 | Measures of diversity

We initially estimated metrics of the three main components of biodiversity, namely species richness, functional and phylogenetic diversity; and later focused on elements geographically restricted to small areas using endemism measures. Diversity and endemism layers were produced at the SDM grid resolution (2.5 min) and extent. SDMs are sometimes combined to map diversity by first thresholding models to translate suitability into predicted presence and absence, but this may introduce systematic biases (Calabrese, Certain, Kraan, & Dormann, 2014), and discards information about relative suitability. Instead, we summed the suitability scores directly (Bush, Nipperess, Theischinger, Turak, & Hughes, 2014; Calabrese et al., 2014) so that a low suitability score for a grid cell makes a small contribution, for example to richness or FD in the cell, or the range size of a species. We thus estimated species richness (SR) by summing the SDM values of all Cerrado lizard species. To infer FD, we generated a UPGMA distance dendrogram (cluster) with Gower distances, using the R package 'ade4' (Dray & Dufour, 2007). This was necessary because our traits include both categorical and continuous data (Pavoine, Gasc, Bonsall, & Mason, 2013), representing the functional relationships between species (see Data S1). With many distance measures and clustering techniques available, UPGMA is considered a robust method in a biogeographical framework (Kreft & Jetz, 2010; Petchey & Gaston, 2002). We then combined the UPGMA tree with the SDM predictions to visualize the spatial distribution of FD, summing the lengths of branches linking the species occurring in each cell, weighted by the species' SDM value. Finally, we calculated PD separately for each genus using its lineage tree and the corresponding LDM predictions. We then summed the PD scores across taxa (all genera). We assessed the residuals relating species richness and phylogenetic diversity, to evaluate the component of PD not explained by SR.

Weighted Endemism (WE; Crisp, Laffan, Linder, & Monro, 2001) is the proportion of the range of each species lineages predicted to occur in each grid cell, summed for all species. It was calculated as species richness, but with the local occurrence (SDM prediction) divided by the sum of SDM predictions for all cells (the species total range) (Rosauer et al., 2015). PE (Rosauer et al., 2009, 2015) combines both WE and PD, highlighting the areas where a substantial component of phylogenetic variation is restricted to a small area. PE calculation is similar to WE, but multiplies the length of each branch on the tree by the proportion of its range occurring in a cell. We calculated PD and PE separately for each genus, and then summed across all genera. We also identified the genus that most contributed to our result in each grid cell and assessed the residuals relating WE and PE.

2.4 | Spatial patterns of diversity

We evaluated the spatial patterns revealed by the biodiversity measures by first looking for areas with high values of species richness, functional and phylogenetic diversity. Then, we explicitly assessed the relationship between PE and weighted endemism (WE) with climatic stable areas performing a linear regression with Cerrado climatic stable areas determined by Werneck, Nogueira et al. 2012. Secondly, to analyse how our results could inform conservation decisions, we focused on PE results, given that this measure, when applied to comparative phylogeographic data, is robust to taxonomic resolution (Rosauer et al., 2018). We intersected the combined PE map with shapes of protected areas in Brazil (MMA website, 2017) to calculate the amount of evolutionary history within currently protected areas. We followed the terminology adopted by the Brazilian government in relation to conservation status, adapted from IUCN categories (Figure S3.3 in Data S3), where Strict Use units do not allow human activities and Sustainable Use units allow restricted human interference while maintaining diversity. Indigenous lands (FUNAI, 2017) are not considered protected areas in Brazil, but we included them in our analysis to evaluate their importance for biodiversity conservation. We calculated the area of each protected unit, their PE values and how much of their areas were inside each PE hotspot.

3 | RESULTS

3.1 | Diversity measures across dimensions

The diversity analyses for richness, PD and FD found similar geographic patterns and all highlighted the central area of Cerrado as a region of high diversity (Figure 2). This area is characterized by a vast plateau (known as *chapada* and referred to here as the *Chapada dos Veadeiros* region); this feature resulted from the collision between the Congo and São Francisco cratons in the Neoproterozoic, in the core area of the Brazilian Shield (de Carvalho Júnior et al., 2015). The high values for PD (Figure 2-PD) are more scattered and also highlight as important other plateau region in the southwest (*Chapada dos Guimarães* region—highlighted with a star in Figure 2-PD), in the vicinity of the Pantanal, a large wetland area situated in the depression of the Paraguay River, on the southwestern border of the Cerrado.

The distribution of standardized residuals from the regression of SR with PD (Figure 3a) reveals greater PD in the south of the biome compared to species richness, in a west-to-east pattern, in contrast to a lower level of PD than SR in the north. This points to the species in the southern Cerrado being phylogenetically disparate, since this region is not detected with such emphasis in the PE results (see below). By contrast, in the north region, including the central plateau, species richness' greater value could potentially indicate that the species assemblages in that area come from a smaller subtree,

due to a more recent local radiation or selection for conserved traits that suit the local environment.

3.2 | FD diversity and endemism

We found three distinct areas with high endemism (Figure 2-WE): The Cerrado core area *Chapada dos Veadeiros*, again presented high values for FD and PD and appears to be important for endemism. The *Tocantins Valley* Region, situated in the northeast part of the biome, adjacent to Tocantins River Valley; and the *Serra do Espinhaço* region, an isolated mountain range located at the southeast boundary of the Cerrado, adjacent to the Atlantic Forest and Caatinga. These three regions were also highlighted for PE, indicating concentrations of spatially restricted evolutionary diversity, and are highlighted on the PE map (Figure 2-PE, where the *Tocantins valley* region is marked 1, *Chapada dos Veadeiros* region marked 3 and *Serra do Espinhaço* region marked 4), with the addition of another area, with more importance for PE than WE. The *Araguaia valley* region (marked 2 on Figure 2-PE) is characterized by a vegetation mosaic, incorporating elements from Cerrado and Amazon forest, and also includes the Caiapó mountain range and its contact with the *Araguaia valley*. The standardized residuals from the regression between PE versus WE, though small, relative to the range of the PE values, highlight excess PE scores in the southwestern region (Figure 3b), indicating a considerable number of unique evolutionary lineages in that area. The linear regression showed a positive and significant correlation between climatic stable areas in both PE and WE (adjusted R-squared 0.2072 and p value > .05).

The four PE hotspots together cover 5.52% of the Cerrado area, holding 11.29% of all range-weighted diversity (PE sum; Table 1). The *Tocantins valley* and *Serra do Espinhaço* regions showed the highest PE values, collectively representing 11% of the diversity in just 5.5% of the land area (Table 1). These patterns are driven by the same genera independent of the area: *Phyllopezus*, a phylogenetically diverse genus, and *Tropidurus*, with many described species (Table 1; Data S3).

3.3 | Protected areas

Protected areas, including strict protection and sustainable use, cover only 10% of the Cerrado area and contain 11.64% of the summed PE of all lizards in the biome (Data S3). When indigenous lands are included, protected areas cover 14% and 16.85% of the PE respectively (Data S3). By overlapping protected areas with the four hotspots highlighted by the PE analysis we note that much of this diversity is not protected; the PE value inside protected areas in the four hotspots represents 1.23% of the total Cerrado area (Table 2). *Chapada dos Veadeiros* region is the only exception, with a considerable proportion of its PE (72%) occurring within protected areas. Most of this area (68%) is composed of sustainable use lands, but an important strict

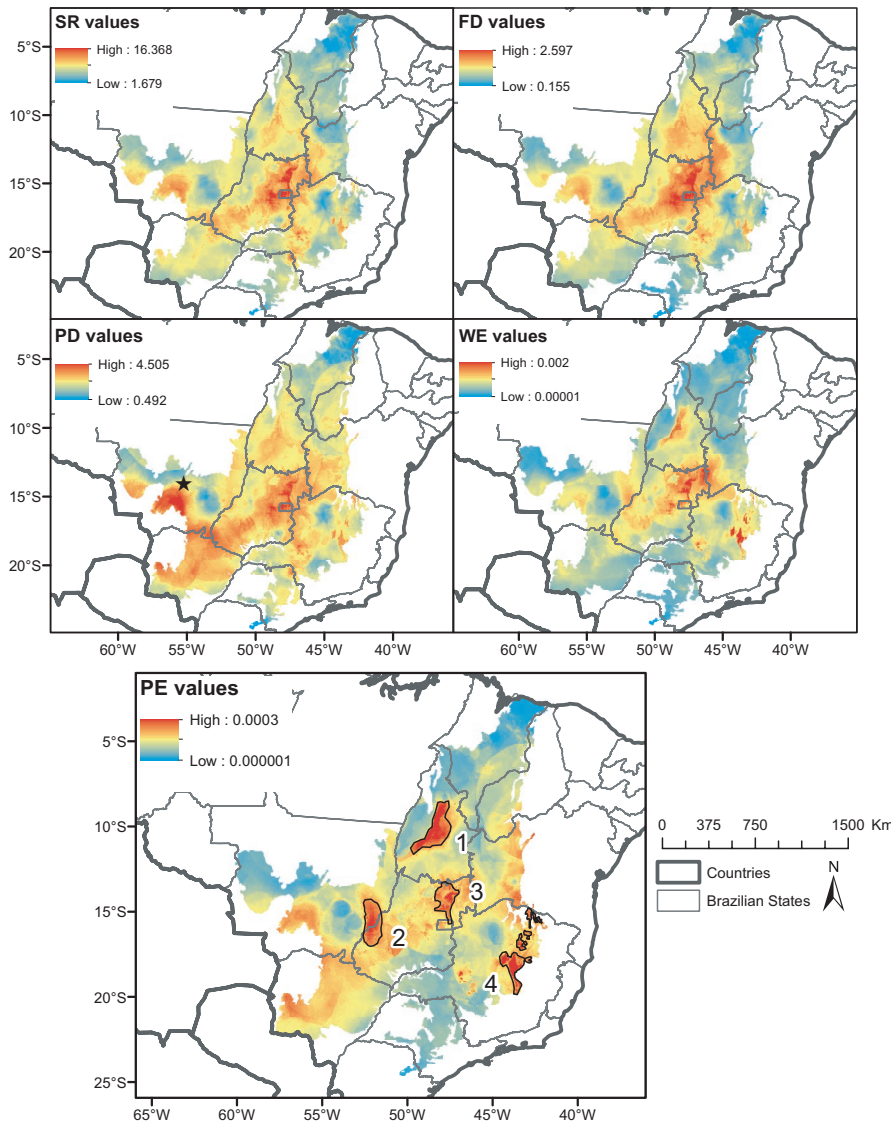


FIGURE 2 Diversity measures: richness (SR), functional diversity (FD) and phylogenetic diversity (PD) and endemism measures: phylogenetic endemism (PE) and weighted endemism (WE) for Cerrado lizards. Heat colours represent priority areas based on each measure. The star symbol on the PD map represents *Chapada dos Guimarães*. Numbers on the PE map represent the four areas considered priorities for conservation based on their high levels of evolutionary diversity: 1—*Tocantins valley*; 2—*Araguaia valley*; 3—*Chapada dos Veadeiros*; and 4—*Serra do Espinhaço*. Units represent values provided on the output of each analysis—summing the species distribution modelling values for SR, summing the lengths of branches linking the species occurring in each cell, weighted by the species/lineage distribution value for FD and PD and using the proportion of the range of each species/lineage in each grid cell for the endemism measures (see Methods for more details)

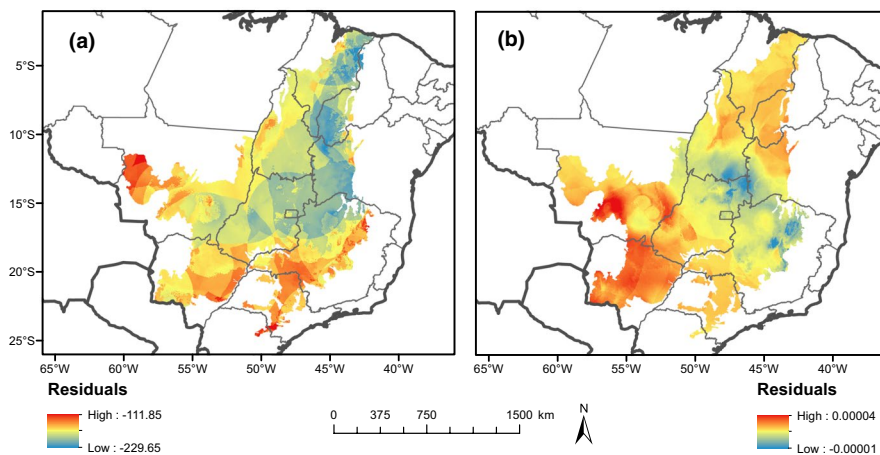


FIGURE 3 Standardized residuals from linear regression of (a) phylogenetic diversity (PD) versus richness (SR) and (b) phylogenetic endemism (PE) versus species endemism (WE) for lizards of the Cerrado

protection area, the Chapada dos Veadeiros National Park (Data S3), is also located here. For the other PE hotspots, the scenario changes: on the *Serra do Espinhaço* region only 28% is within protected areas

(Table 2). Indigenous lands gain importance in the *Tocantins valley* and *Araguaia valley* region, representing 14% and 12% of PE respectively (Table 2).

TABLE 1 Phylogenetic endemism hotspots: a) area in thousands of km² and as a percentage of the Cerrado region; b) summed PE across the region and percentage of the Cerrado; c) Protected areas (including Strict and Sustainable Use) inside the hotspot region; and d) genus with the highest summed PE in each hotspot. Numbers refer to areas marked on Figure 2

Hotspot name	Area		PE		Protected area		Principal taxa	
	km ²	%	Sum	%	Sum	%	Genus	Sum
1 Tocantins valley	34,994.10	1.716	0.24573	3.665	1867.41755	0.092	<i>Phyllopezus</i>	0.184
							<i>Tropidurus</i>	0.027
							<i>Norops</i>	0.012
							Others	0.023
2 Araguaia valley	28,648.39	1.405	0.17773	2.651	281.84651	0.014	<i>Phyllopezus</i>	0.111
							<i>Tropidurus</i>	0.031
							<i>Norops</i>	0.009
							Others	0.026
3 Chapada dos Veadeiros	20,985.42	1.029	0.12555	1.872	15,070.6141	0.739	<i>Tropidurus</i>	0.049
							<i>Phyllopezus</i>	0.036
							<i>Norops</i>	0.015
							Others	0.024
4 Serra do Espinhaço	27,913.56	1.369	0.20822	3.105	7,890.34064	0.387	<i>Phyllopezus</i>	0.108
							<i>Tropidurus</i>	0.080
							<i>Cercosaura</i>	0.005
							Others	0.014
TOTAL % for Cerrado		5.52		11.29		1.23		

Abbreviation: PE, phylogenetic endemism.

TABLE 2 Area (km²) and percentage of different conservation areas (Strict [St] and Sustainable Use [Su], and Indigenous lands [Indg]) inside the PE hotspot region for the Cerrado

Hotspot name	Strict use		Sustainable use		St + Su		Indigenous land		St + Su + Indg	
	Area	%	Area	%	Area	%	Area	%	Area	%
Tocantins valley	107.50	0.31	1759.92	5.03	1867.42	5.34	4,931.64	14.09	6,799.05	19.43
Araguaia valley	110.49	0.39	171.35	0.60	281.85	0.98	3,533.14	12.33	3,814.98	13.32
Chapada dos Veadeiros	743.72	3.54	14,326.90	68.27	15,070.61	71.81	347.62	1.66	15,418.23	73.47
Serra do Espinhaço	3,838.44	13.75	4,051.90	14.52	7,890.34	28.27	0.00	0.00	7,890.34	28.27

Abbreviation: PE, phylogenetic endemism.

4 | DISCUSSION

4.1 | Biodiversity patterns

All dimensions of lizard diversity in the Cerrado coincide on the Brazilian Central plateau (Colli, 2005), an ancient and stable area highlighted as important for biodiversity conservation in other analyses and taxa (Nogueira et al., 2011; Simon & Proença, 2000). Ab'Sáber (1983) hypothesized that this spatially continuous plateau has formed a single large Cerrado refugium during the Late Pleistocene. This is related to the positive relationship between the area with higher PE

values and climatic stable regions. Stable areas are known to act as biotic refugia during climatic fluctuations and are associated with high species richness and endemism (Carnaval et al., 2014; Gamble, Colli, Rodrigues, Werneck, & Simons, 2012; Keppel et al., 2012), even for organisms with such different ecological requirements as anurans and squamates (Azevedo et al., 2016). A previous study which observed the general squamate richness showed a slightly different pattern from this study, with high diversity in the southwest portion of the biome (Costa et al., 2007). This difference could be related to the inclusion of snakes and amphisbaenians in the study by Costa et al. (2007). For Cerrado endemic terrestrial vertebrates as a group, the richness pattern is similar to our result (Diniz-Filho et al., 2008).

It is expected that similar geographic patterns for the three diversity measures are observed as some correlation between these metrics (Pavoine et al., 2013). However, by adding each measure we add multidimensionality of ecological diversity among species, related to the performance and accumulation of temporal niches changes, and supporting the maintenance of ecosystem services (Cadotte, Carscadden, & Mirotnick, 2011; Carvalho et al., 2010; Tucker et al., 2018). The emphasis given in the PD results in the *Chapada dos Guimarães* region, located on the edge of the central plateau (Ab'Sáber, 2006), and reveals new areas with high diversity values that would not be evident without the inclusion of phylogenetic history (Faith, 1992; Rosauer et al., 2016), when based on dense intraspecific sampling and species/population delimitation methods. This region seems to be important not only for the diversification of Cerrado lizard lineages, but also for amphibians (Prado, Haddad, & Zamudio, 2012).

The observed high values of not just the stable areas, but also of the more heterogeneous valley regions in our PE results, emphasize again the importance of including evolutionary relationships—which alone identify extensive cryptic diversity—when visualizing fine-scale species distribution patterns (Barratt et al., 2017; Carnaval et al., 2014; Rosauer et al., 2016). This is not the first time that a dynamic relationship between the Cerrados' plateaus and valleys have been considered as key processes in lizard community diversification (Fonseca et al., 2018; Nogueira et al., 2011; Santos, Nogueira, Giugliano, & Colli, 2014). Such landscape dynamics results in a variety of vegetation mosaics as well as geographical, ecological and physiological barriers and filters (Brown Jr. & Gifford, 2002; Silva, 1997), and have influenced the patterns of diversity we observe today, and the many shared patterns among organisms with different requirements. This is the case, for example, for the Central Plateau area, Serra do Espinhaço, a region already known as a centre of endemism for many taxa (Azevedo et al., 2016; Echternacht, Trovó, Oliveira, & Pirani, 2011; Giulietti & Pirani, 1987; Silva, 1997; da Silva & Bates, 2002; Simon & Proença, 2000; Valdujo, Silvano, Colli, & Martins, 2012), and the Araguaia river valley for birds (Silva, 1997; da Silva & Bates, 2002). However, additional analyses are necessary to relate stability to the diversity patterns in order to make more informed conclusions.

The strong influence of two genera on the PE values across all hotspots is related to their overall high diversity, but at different taxonomic scales. *Tropidurus* represents a species-rich radiation in the Cerrado and adjacent Neotropical biomes (de Carvalho, de Britto, & Fernandes, 2013). In contrast, the low-vagility *Phyllopezus pollicaris* gecko well known for its deep and spatially fine-grained phylogeographic diversity which, coupled with a conservative morphology, indicates that current taxonomy does not adequately reflect phylogenetic diversity (Gamble et al., 2012; Werneck, Gamble, et al., 2012). These features make these genera excellent systems for further investigating historical biogeographic processes, and how they shaped the current distribution of biodiversity in the Cerrado.

Careful examination of the maps (Figure 2) reveals some areas with extremely low values for all metrics. The extreme north and south regions may represent sampling gaps, where the number of studies is still low. However, we adopted SDMs to minimize the effect of sampling gaps and our methods for WE and PE also incorporate uncertainty in occurrences of species and lineages (Rosauer et al., 2016). The north area borders with Caatinga, a dry forest biome, and the south with Campos Sulinos, an open grassland biome. Both are known for low number of synthesis studies when compared to Cerrado, Amazonia and Atlantic Forest (this scenario is starting to change—Guedes, Sawaya, & Nogueira, 2014; Mesquita, Costa, Garda, & Delfim, 2017) and could be influencing the low values on these regions, but further investigation is necessary. Hence, we believe that the areas highlighted on the map are very conservative. For example, our modelling approaches cannot represent small-ranged species or genetic lineages, many of which have not yet been discovered; thus, further surveys targeting poorly sampled regions and based on dense geographic sampling and molecular phylogeographic analyses are important for science-based conservation planning in these regions.

4.2 | Conservation of phyloendemic diversity

Although a low percentage of Strict Protection areas compared to Sustainable Use areas are located inside the four PE hotspots, few studies have compared their effectiveness for biodiversity conservation (Carranza, Balmford, Kapos, & Manica, 2014; Fonseca et al., 2018; Françaço et al., 2015; Oliveira et al., 2017). However, given that Sustainable Use allows local land-use changes, Strict Protection areas are the only regions that fully protect all biodiversity. Strict Protection areas comprise 13% of *Serra do Espinhaço* region, but less than 5% of the other high-PE areas. After years of successive size reductions, in 2017, the *Chapada dos Veadeiros* National Park, was expanded to 240,000 hectares (Brazil federal Decree 05/06, 2017), representing an improvement for the conservation of this region.

In the regions of *Tocantins* and *Araguaia* valleys, Strict Protection areas cover 6% and 1% respectively, so that the creation of new protected areas (especially in the Strict Protection category) is necessary to maintain the high phylo-endemism values of both hotspots. Indigenous lands cover important areas of these valleys and should help maintain species diversity, since they often experience low deforestation rates (Carranza et al., 2014; Soares-Filho et al., 2010). Around 37% of the human-dominated land in the world is estimated to be of Indigenous Peoples' territories, mostly in intact places (Garnett et al., 2018). In Brazil, 13.8% of the entire territory is designated as indigenous lands, but 98% of this is concentrated in Amazonia, leaving 2% for the rest of Brazil (SocioAmbiental, 2014). The maintenance of these regions, in addition to its undeniable importance for the languages, culture, traditions and heritage of the Indigenous Peoples, is also essential for



biodiversity conservation (Altman & Kerins, 2012; Schwartzman & Zimmerman, 2005).

Programmes that combine conservation and sustainable land use to enhance cultural and economic benefits for local communities are a good alternative for the creation of new protected areas. The Extractive Reserves (*Reservas Extrativistas*) and Sustainable Development Reserves (*Reservas de Desenvolvimento Sustentável*) are part of the sustainable use protected areas system and follow this premise, and are considered innovative in protected area systems in general, but only one such reserve is inside our hotspots (*Reserva de Desenvolvimento Sustentável Nascentes Geraizeiras*, on the *Serra do Espinhaço* hotspot—see Data S3). Another example is the indigenous protected areas program (Department of the Environment, 2013), implemented by the Australian Government, where Indigenous People use their knowledge of the environment and partnerships with conservation and commercial organizations, to conserve and recognize the biodiversity of indigenous lands, and foster interactions between Indigenous owners, government and scientists (Altman & Kerins, 2012; Moritz, Ens, Potter, & Catullo, 2013).

4.3 | What to do now?

Our study has highlighted both stable areas (plateaus) as well as heterogeneous environments (valleys) as concentrations of lizards' evolutionary diversity, thus serving as important areas of conservation. Studies of genetic diversity in response to current and paleo-environmental factors will increase our understanding of the processes that drive patterns of lizard diversity, and why certain areas were identified as high in PE, as demonstrated here. Likewise, further studies could encompass more taxonomic groups to confirm our findings, and/or add new insights for species with different requirements.

The creation of new areas or/and manipulation of current areas for conservation is essential for the survival of the Cerrado, and given high deforestation rates, these additions should be adopted as soon as possible. While agriculture and livestock farming in the Cerrado generate undeniable socioeconomic benefits, the challenge is to show the importance that biodiversity plays in the functioning of ecosystems (Klink & Machado, 2005; Overbeck et al., 2015). In this way, areas with high values of diversity underlined in our paper could help in the selection of priority areas to focus conservation efforts. However, there is a big gap between science and public agencies, and an urgent need of better mechanisms to integrate academic research with policy/management is necessary.

This is the first study that integrates species, functional and phylogenetic diversity measures focused on the lizard fauna in the Cerrado biome, which is a global biodiversity hotspot (Myers et al., 2000). Our main contributions to the knowledge on Cerrado biodiversity and conservation are 1) the use of a refined population-level and phylogeographic datasets to improve phylogenetic diversity estimates, and 2) the mapping of the distribution of this diversity in order to assess conservation priorities. This is especially true for the rich herpetofauna, where the high cryptic diversity can impede

robust macroecological inferences. We highlight that the use of population-level datasets, mostly generated for other purposes, can be important conservation tools by helping to refine species limits and overcome taxonomic shortfalls that preclude large-scale inferences.

ACKNOWLEDGEMENTS

JF, EMF and RMDL thank Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – CAPES for their PhD scholarships. FPW thanks support from the Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq (project 425571/2018-1; productivity fellowship 305535/2017-0), CAPES (visiting professor fellowship 88881.169862/2018-0), Fundação de Amparo à Pesquisa do Amazonas-FAPEAM (projects 062.00665/2015 and 062.01110/2017); Partnerships for Enhanced Engagement in Research from the U.S. National Academy of Sciences and U.S. Agency of International Development-PEER NAS/USAID (project AID-OAA-A-11-00012 to GRC and FPW); and the L'Oréal-UNESCO For Women In Science Program (Brazil 2016 and IRT 2017). JWS, Jr. received support from NSF award EF 1241885, and a BYU Jessie Knight Award. AAG thanks CNPq for financial support (#310942/2018-7, 206958/2017-0, and 431433/2016-0). GRC thanks CAPES, CNPq, Fundação de Apoio à Pesquisa do Distrito Federal – FAPDF, and USAID's PEER program under cooperative agreement AID-OAA-A-11-00012 for financial support.

DATA AVAILABILITY STATEMENT

Supporting data is available at Data S1, S2 and S3. Scripts to compute the diversity and endemism indices are made available by Dan Rosauer (<https://github.com/DanRosauer/phylospatial>), <https://doi.org/10.5061/dryad.m0cfxpp05>.

ORCID

Jessica Fenker  <https://orcid.org/0000-0002-7430-3886>

Fabricius M. C. B. Domingos  <https://orcid.org/0000-0003-2069-9317>

Leonardo G. Tedeschi  <https://orcid.org/0000-0003-4211-5570>

Dan F. Rosauer  <https://orcid.org/0000-0002-2371-1767>

Fernanda P. Werneck  <https://orcid.org/0000-0002-8779-2607>

Guarino R. Colli  <https://orcid.org/0000-0002-2628-5652>

Roger M. D. Ledo  <https://orcid.org/0000-0003-0593-2037>

Emanuel M. Fonseca  <https://orcid.org/0000-0002-2952-8816>

Adrian A. Garda  <https://orcid.org/0000-0002-1178-1207>

Maria F. Breitman  <https://orcid.org/0000-0001-6964-841X>

Lilian G. Giugliano  <https://orcid.org/0000-0003-3165-9644>

Craig Moritz  <https://orcid.org/0000-0001-5313-7279>

REFERENCES

- Ab'Sáber, A. N. (1983). O domínio dos cerrados: introdução ao conhecimento. *Revista do Serviço Público*, 40(4), 41–55.
- Ab'Sáber, A. N. (2006). *Brasil, Paisagens de Exceção: O litoral e o Pantanal Mato-Grossense, Patrimônios Básicos* (2nd ed.). São Paulo, Brasil: Ateliê Editorial.
- Agapow, P. M. (2005). Species: demarcation and diversity. In A. Purvis, J. L. Gittleman, & T. Brooks (Eds.), *Phylogeny and conservation* (pp. 57–75). Cambridge, UK: Cambridge University Press.

- Altman, J. C., & Kerins, S. (2012). *People on country: Vital landscapes, indigenous futures*. Sydney, Australia: Federation Press.
- Azevedo, J. A., Valdujo, P. H., & Nogueira, C. 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(12), 2454–2464. <https://doi.org/10.1111/jbi.12803>
- Barratt, C. D., Bwong, B. A., Onstein, R. E., Rosauer, D. F., Menegon, M., Doggart, N., ... Loader, S. P. (2017). Environmental correlates of phylogenetic endemism in amphibians and the conservation of refugia in the Coastal Forests of Eastern Africa. *Diversity and Distributions*, 23(8), 875–887. <https://doi.org/10.1111/ddi.12582>
- Batalha, M. A., Cianciaruso, M. V., & Motta-Junior, J. C. (2010). Consequences of simulated loss of open Cerrado areas to bird functional diversity. *Natureza & Conservação*, 8(1), 1–5. <https://doi.org/10.4322/natcon.00801005>
- Bates, H. W. (1862). Contributions to an insect fauna of the Amazon Valley: Lepidoptera: Heliconidae. *Transactions of the Linnean Society (London)*, 23, 495–566.
- Beuchle, R., Grecchi, R. C., Shimabukuro, Y. E., Seliger, R., Eva, H. D., Sano, E., & Achard, F. (2015). Land cover changes in the Brazilian Cerrado and Caatinga biomes from 1990 to 2010 based on a systematic remote sensing sampling approach. *Applied Geography*, 58, 116–127. <https://doi.org/10.1016/j.apgeog.2015.01.017>
- Brannstrom, C., Jepson, W., Filippi, A. M., Redo, D., Xu, Z., & Ganesh, S. (2008). Land change in the Brazilian Savanna (Cerrado), 1986–2002: Comparative analysis and implications for land-use policy. *Land Use Policy*, 25(4), 579–595. <https://doi.org/10.1016/j.landusepol.2007.11.008>
- Brown, K. S. Jr., & Gifford, D. R. (2002). Lepidoptera in the Cerrado Landscape and the Conservation of Vegetation, Soil and Topographical Mosaics. In P. S. Oliveira, & R. J. Marquis (Eds.), *The Cerrados of Brazil: Ecology and natural history of a neotropical savanna* (pp. 201–222). New York, NY: Columbia University Press.
- Burbridge, R. E., Mayle, F. E., & Killeen, T. J. (2004). Fifty-thousand-year vegetation and climate history of Noel Kempff Mercado National Park, Bolivian Amazon. *Quaternary Research*, 61, 215–230. <https://doi.org/10.1016/j.yqres.2003.12.004>
- Bush, A., Nipperess, D. A., Theischinger, G., Turak, E., & Hughes, L. (2014). Testing for taxonomic bias in the future diversity of Australian Odonata. *Diversity and Distributions*, 20(9), 1016–1028. <https://doi.org/10.1111/ddi.12196>
- Butchart, S. H., Walpole, M., Collen, B., Van Strien, A., Scharlemann, J. P., Almond, R. E., ... Watson, R. (2010). Global biodiversity: Indicators of recent declines. *Science*, 328(5982), 1164–1168. <https://doi.org/10.1126/science.1187512>
- Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, 48(5), 1079–1087. <https://doi.org/10.1111/j.1365-2664.2011.02048.x>
- Calabrese, J. M., Certain, G., Kraan, C., & Dormann, C. F. (2014). Stacking species distribution models and adjusting bias by linking them to macroecological models. *Global Ecology and Biogeography*, 23(1), 99–112. <https://doi.org/10.1111/geb.12102>
- Camargo, A., Sinervo, B., & Sites, J. W. Jr (2010). Lizards as model organisms for linking phylogeographic and speciation studies. *Molecular Ecology*, 19(16), 3250–3270. <https://doi.org/10.1111/j.1365-294X.2010.04722.x>
- Carnaval, A. C., Waltari, E., Rodrigues, M. T., Rosauer, D., VanDerWal, J., Damasceno, R., ... Moritz, C. (2014). Prediction of phylogeographic endemism in an environmentally complex biome. *Proceedings of the Royal Society B: Biological Sciences*, 281(1792), 1–8. <https://doi.org/10.1098/rspb.2014.1461>
- Carranza, T., Balmford, A., Kapos, V., & Manica, A. (2014). Protected area effectiveness in reducing conversion in a rapidly vanishing ecosystem: The Brazilian Cerrado. *Conservation Letters*, 7(3), 216–223. <https://doi.org/10.1111/conl.12049>
- Carvalho, R. D., Cianciaruso, M. V., Trindade-Filho, J., Sagnori, M. D., & Loyola, R. D. (2010). Drafting a blueprint for functional and phylogenetic diversity conservation in the Brazilian Cerrado. *Natureza & Conservação*, 8(2), 171–176. <https://doi.org/10.4322/natcon.00802011>
- Carvalho, S. B., Velo-Antón, G., Tarroso, P., Portela, A. P., Barata, M., Carranza, S., ... Possingham, H. P. (2017). Spatial conservation prioritization of biodiversity spanning the evolutionary continuum. *Nature Ecology & Evolution*, 1(6), 0151. <https://doi.org/10.1038/s41559-017-0151>
- Colli, G. R. (2005). As origens e a diversificação da herpetofauna do Cerrado. In A. Scariot, J. Sousa-Silva, & J. Felfili (Eds.), *Cerrado: Ecologia, Biodiversidade e Conservação* (pp. 247–264). Brasília, Brasil: Ministério do Meio Ambiente.
- Colli, G. R., Bastos, R. R. P., & Araujo, A. F. B. (2002). The character and dynamics of the Cerrado Herpetofauna. In P. S. Oliveira, & R. J. Marquis (Eds.), *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna* (pp. 201–222). New York, NY: Columbia University Press.
- 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(6), 714–724. <https://doi.org/10.1111/j.1472-4642.2007.00369.x>
- Costa, H., & Bérnils, R. (2018). Répteis do Brasil e suas Unidades Federativas: Lista de espécies. *Herpetologia Brasileira*, 7(1), 11–57.
- Crisp, M., Laffan, S., Linder, H. P., & Monro, A. (2001). Endemism in the Australian flora. *Journal of Biogeography*, 28(2), 183–198. <https://doi.org/10.1046/j.1365-2699.2001.00524.x>
- da Silva, J. M. C., & Bates, J. M. (2002). Biogeographic patterns and conservation in the South American Cerrado: A tropical savanna hotspot. *BioScience*, 52(3), 225–234. [https://doi.org/10.1641/0006-3568\(2002\)052\[0225:BPACIT\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2002)052[0225:BPACIT]2.0.CO;2)
- de Carvalho, A. L. G., de Britto, M. R., & Fernandes, D. S. (2013). Biogeography of the lizard genus *Tropidurus* Wied-Neuwied, 1825 (Squamata: Tropiduridae): Distribution, endemism, and area relationships in South America. *PlosOne*, 8(3), e59736. <https://doi.org/10.1371/journal.pone.0059736>
- de Carvalho Júnior, O. A., Guimarães, R. F., de Souza Martins, É., & Gomes, R. A. T. (2015). Chapada dos Veadeiros: The Highest Landscapes in the Brazilian Central Plateau. In B. C. Vieira, A. A. R. Salgado & L. J. C. Santos (Eds.), *Landscapes and Landforms of Brazil* (Vol. 1, pp. 221–230). Dordrecht, The Netherlands: Springer.
- De Freitas, J. L., Strussmann, C., De Carvalho, M. A., Kawashita-Ribeiro, R. A., & Mott, T. (2011). A new species of *Bachia* Gray, 1845 (Squamata: Gymnophthalmidae) from the Cerrado of Midwestern Brazil. *Zootaxa*, 2737, 61–68.
- Department of the Environment. (2013). Indigenous Protected Areas. Retrieved from <http://www.environment.gov.au/land/indigenous-protected-areas>.
- Diniz-Filho, J. A. F., Bini, L. M., Pinto, M. P., Terribile, L. C., de Oliveira, G., Vieira, C. M., ... Bastos, R. P. (2008). Conservation planning: A macroecological approach using the endemic terrestrial vertebrates of the Brazilian Cerrado. *Oryx*, 42(4), 567–577. <https://doi.org/10.1017/S0030605308001129>
- Dirzo, R., & Raven, P. H. (2003). Global state of biodiversity and Loss. *Annual Review of Environmental Resources*, 28, 137–167. <https://doi.org/10.1146/annurev.energy.28.050302.105532>
- Domingos, F. M., 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. <https://doi.org/10.1016/j.ympev.2014.07.022>

- Domingos, F. M., Colli, G. R., Lemmon, A., Lemmon, E. M., & Beheregaray, L. B. (2017). In the shadows: Phylogenomics and coalescent species delimitation unveil cryptic diversity in a Cerrado endemic lizard (Squamata: *Tropidurus*). *Molecular Phylogenetics and Evolution*, 107, 455–465. <https://doi.org/10.1016/j.ympev.2016.12.009>
- Dray, S., & Dufour, A. B. (2007). The ade4 Package: Implementing the duality diagram for ecologists. *Journal of Statistical Software*, 22, 1–20. <https://doi.org/10.18637/jss.v022.i04>
- Echternacht, L., Trovó, M., Oliveira, C. T., & Pirani, J. R. (2011). Areas of endemism in the Espinhaço range in Minas Gerais, Brazil. *Flora - Morphology, Distribution, Functional Ecology of Plants*, 206(9), 782–791. <https://doi.org/10.1016/j.flora.2011.04.003>
- Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, 17(1), 43–57. <https://doi.org/10.1111/j.1472-4642.2010.00725.x>
- Environmental Systems Research Institute- ESRI. (2011). *ArcGIS desktop: release 10*. Redlands, CA: Environmental Systems Research Institute.
- Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity. *Biological Conservation*, 61(1), 1–10. [https://doi.org/10.1016/0006-3207\(92\)91201-3](https://doi.org/10.1016/0006-3207(92)91201-3)
- Faith, D. P., Reid, C. A. M., & Hunter, J. (2004). Integrating phylogenetic diversity, complementarity, and endemism for conservation assessment. *Conservation Biology*, 18(1), 255–261. <https://doi.org/10.1111/j.1523-1739.2004.00330.x>
- Fonseca, E. M., Gehara, M., Werneck, F. P., Lanna, F. M., Colli, G. R., Sites, J. W., ... Garda, A. A. (2018). Diversification with gene flow and niche divergence in a lizard species along the South American “diagonal of open formations”. *Journal of Biogeography*, 45, 1688–1700. <https://doi.org/10.1111/jbi.13356>
- Françoso, R. D., Brandão, R., Nogueira, C. C., Salmons, Y. B., Machado, R. B., & Colli, G. R. (2015). Habitat loss and the effectiveness of protected areas in the Cerrado Biodiversity Hotspot. *Natureza & Conservação*, 13(1), 35–40. <https://doi.org/10.1016/j.ncon.2015.04.001>
- FUNAI. (2017). Terras Indígenas do Brasil. Retrieved from <http://www.funai.gov.br/index.php/servicos/geoprocessamento>.
- Gamble, T., Colli, G. R., Rodrigues, M. T., Werneck, F. P., & Simons, A. M. (2012). Phylogeny and cryptic diversity in geckos (*Phyllopezus*; Phyllodactylidae; Gekkota) from South America's open biomes. *Molecular Phylogenetics and Evolution*, 62(3), 943–953. <https://doi.org/10.1016/j.ympev.2011.11.033>
- Garnett, S. T., Burgess, N. D., Fa, J. E., Fernández-Llamazares, Á., Molnár, Z., Robinson, C. J., ... Leiper, I. (2018). A spatial overview of the global importance of Indigenous lands for conservation. *Nature Sustainability*, 1(7), 369. <https://doi.org/10.1038/s41893-018-0100-6>
- Gaston, K. J. (2000). Biodiversity: Higher taxon richness. *Progress in Physical Geography*, 24, 117–127. <https://doi.org/10.1177/030913330002400108>
- Giugliano, L. G., de Campos Nogueira, C., Valdujo, P. H., Collevatti, R. G., & Colli, G. R. (2013). Cryptic diversity in South American Teiinae (Squamata, Teiidae) lizards. *Zoologica Scripta*, 42(5), 473–487. <https://doi.org/10.1111/zsc.12017>
- Giulietti, A. M., & Pirani, J. R. (1987). Patterns of geographic distribution of some plant species from the Espinhaço Range, Minas Gerais and Bahia. In P. Vanzolini, & W. Heyer (Eds.), *Proceedings of a Workshop on Neotropical Distribution Patterns* (pp. 39–69). Rio de Janeiro, Brazil: Academia Brasileira de Ciências.
- Guarnizo, C. E., Werneck, F. P., Giugliano, L. G., Santos, M. G., Fenker, J., Sousa, L., ... 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. <https://doi.org/10.1016/j.ympev.2015.09.005>
- Guedes, T. B., Sawaya, R. J., & Nogueira, C. N. (2014). Biogeography, vicariance and conservation of snakes of the neglected and endangered Caatinga region, north-eastern Brazil. *Journal of Biogeography*, 41, 919–931. <https://doi.org/10.1111/jbi.12272>
- Hidasi-Neto, J., Loyola, R. D., & Cianciaruso, M. V. (2013). Conservation actions based on red lists do not capture the functional and phylogenetic diversity of birds in Brazil. *PLoS ONE*, 8(9), e73431. <https://doi.org/10.1371/journal.pone.0073431>
- Hijmans, R., Cameron, S., & Parra, J. (2006). Worldclim global climate layers Version 1.4. Retrieved from WorldClim database <http://www.worldclim.org>.
- Instituto Brasileiro de Geografia e Estatística (IBGE) (2004). Mapa de biomas do Brasil. Escala 1:5.000.000. Retrieved from <http://mapas.ibge.gov.br/biomas2/viewer.htm>
- Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio). (2018). *Livro Vermelho da Fauna Brasileira Ameaçada de Extinção* (p. 4162). Brasília, Brazil: ICMBio.
- Isaac, N. J., Mallet, J., & Mace, G. M. (2004). Taxonomic inflation: Its influence on macroecology and conservation. *Trends in Ecology & Evolution*, 19(9), 464–469. <https://doi.org/10.1016/j.tree.2004.06.004>
- Keppel, G., Van Niel, K. P., Wardell-Johnson, G. W., Yates, C. J., Byrne, M., Mucina, L., ... Franklin, S. E. (2012). Refugia: Identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography*, 21(4), 393–404. <https://doi.org/10.1111/j.1466-8238.2011.00686.x>
- Klink, C. A., & Machado, R. B. (2005). Conservation of the Brazilian Cerrado. *Conservation Biology*, 19(3), 707–713. <https://doi.org/10.1111/j.1523-1739.2005.00702.x>
- Kreft, H., & Jetz, W. (2010). A framework for delineating biogeographical regions based on species distributions. *Journal of Biogeography*, 37, 2029–2053. <https://doi.org/10.1111/j.1365-2699.2010.02375.x>
- Mace, G. M., Gittleman, J. L., & Purvis, A. (2003). Preserving the tree of life. *Science*, 300, 1707–1709. <https://doi.org/10.1126/science.1085510>
- Marris, E. (2005). Conservation in Brazil: The forgotten ecosystem. *Nature*, 437, 944–945. <https://doi.org/10.1038/437944a>
- Mesquita, D. O., Costa, G. C., Garda, A. A., & Delfim, F. R. (2017). Species composition, biogeography, and conservation of the caatinga lizards. In J. M. C. Silva, I. Leal, & M. Tabarelli (Eds.), *Biodiversity, ecosystems services and sustainable development in Caatinga: The largest tropical dry forest region in South America* (pp. 151–180). Cham, Germany: Springer.
- MMA website. (2017). Cadastro Nacional de Unidades de Conservação. Retrieved from <http://www.mma.gov.br/areas-protetidas/cadastro-nacional-de-ucs/dados-georreferenciados.html>.
- Moritz, C. (2002). Strategies to protect biological diversity and the evolutionary processes that sustain it. *Systematic Biology*, 51(2), 238–254. <https://doi.org/10.1080/10635150252899752>
- Moritz, C., Ens, E. J., Potter, S., & Catullo, R. (2013). The Australian monsoonal tropics: An opportunity to protect unique biodiversity and secure benefits for Aboriginal communities. *Pacific Conservation Biology*, 19(4), 343–355. <https://doi.org/10.1071/PC130343>
- Myers, N. (2003). Biodiversity hotspots revisited. *BioScience*, 53, 916–917. [https://doi.org/10.1641/0006-3568\(2003\)053\[0916:BHR\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2003)053[0916:BHR]2.0.CO;2)
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403(6772), 853. <https://doi.org/10.1038/35002501>
- Nogueira, C., Colli, G. R., Costa, G. C., & Machado, R. B. (2010). Diversidade de répteis Squamata e evolução do conhecimento faunístico no Cerrado. In J. M.-F. I. R. Diniz, R. B. Machado, & R. B. Cavalcanti (Eds.), *Cerrado: Conhecimento Científico Quantitativo como Subsídio para Ações de Conservação* (pp. 333–375). Brasília, Brazil: Universidade de Brasília.
- Nogueira, C., Ribeiro, S., 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(10), 1907–1922. <https://doi.org/10.1111/j.1365-2699.2011.02538.x>
- Oliveira, P. S., & Marquis, R. J. (2002). *The Cerrados of Brazil: Ecology and natural history of a neotropical savanna*. New York, NY: Columbia University Press.
- Oliveira, U., Soares-Filho, B. S., Paglia, A. P., Brescovit, A. D., de Carvalho, C. J. B., Silva, D. P., ... Santos, A. J. (2017). Biodiversity conservation gaps in the Brazilian protected areas. *Scientific Reports*, 7(1), 9141. <https://doi.org/10.1038/s41598-017-08707-2>
- Overbeck, G. E., Vélez-Martin, E., Scarano, F. R., Lewinsohn, T. M., Fonseca, C. R., Meyer, S. T., ... Pillar, V. D. (2015). Conservation in Brazil needs to include non-forest ecosystems. *Diversity and Distributions*, 21(12), 1455–1460. <https://doi.org/10.1111/ddi.12380>
- Pavoine, S., Gasc, A., Bonsall, M. B., & Mason, N. W. (2013). Correlations between phylogenetic and functional diversity: Mathematical artefacts or true ecological and evolutionary processes? *Journal of Vegetation Science*, 24(5), 781–793. <https://doi.org/10.1111/jvs.12051>
- Petchey, O. L., & Gaston, K. J. (2002). Functional diversity (FD), species richness and community composition. *Ecology Letters*, 5, 402–411. <https://doi.org/10.1046/j.1461-0248.2002.00339.x>
- Phillips, S., Dudik, M., & Schapire, R. (2012). *MaxEnt 3.3*. Princeton, NJ: AT & T Labs-Research, Princeton University.
- Pianka, E. R., & Vitt, L. J. (2003). *Lizards: Windows to the evolution of diversity* (Vol. 5). Berkeley, CA: University of California Press.
- Pollock, L. J., Rosauer, D. F., Thornhill, A. H., Kujala, H., Crisp, M. D., Miller, J. T., & McCarthy, M. A. (2015). Phylogenetic diversity meets conservation policy: Small areas are key to preserving eucalypt lineages. *Philosophical Transactions of the Royal Society London B Biological Sciences*, 370(1662), 20140007. <https://doi.org/10.1098/rstb.2014.0007>
- Prado, C. P., Haddad, C. F., & Zamudio, K. R. (2012). Cryptic lineages and Pleistocene population expansion in a Brazilian Cerrado frog. *Molecular Ecology*, 21(4), 921–941. <https://doi.org/10.1111/j.1365-294X.2011.05409.x>
- Prance, G. T. I. (1982). *Biological diversification in the tropics*. New York, NY: Columbia, Univ. Press.
- Ratter, J. A., Bridgewater, S., & Ribeiro, J. F. (2003). Analysis of the floristic composition of the Brazilian Cerrado vegetation III: Comparison of the woody vegetation of 376 areas. *Edinburgh Journal of Botany*, 60(1), 57–109. <https://doi.org/10.1017/S0960428603000064>
- Recoder, R. S., Werneck, F. P., Teixeira, M. Jr, Colli, G. R., Sites, J. W. Jr, & Rodrigues, M. T. (2014). Geographic variation and systematic review of the lizard genus *Vanzosaura* (Squamata, Gymnophthalmidae), with the description of a new species. *Zoological Journal of the Linnean Society*, 171(1), 206–225.
- Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A. M., Bernard, R., ... Meiri, S. (2017). The global distribution of tetrapods reveals a need for targeted reptile conservation. *Nature Ecology and Evolution*, 1(11), 1677–1682. <https://doi.org/10.1038/s41559-017-0332-2>
- Rosauer, D., Laffan, S. W., Crisp, M. D., Donnellan, S. C., & Cook, L. G. (2009). Phylogenetic endemism: A new approach for identifying geographical concentrations of evolutionary history. *Molecular Ecology*, 18(19), 4061–4072. <https://doi.org/10.1111/j.1365-294X.2009.04311.x>
- Rosauer, D. F., Blom, M., Bourke, G., Catalano, S., Donnellan, S., Gillespie, G., ... Moritz, C. (2016). Phylogeography, hotspots and conservation priorities: An example from the Top End of Australia. *Biological Conservation*, 204, 83–93. <https://doi.org/10.1016/j.biocon.2016.05.002>
- Rosauer, D. F., Byrne, M., Blom, M. P. K., Coates, D. J., Donnellan, S., Doughty, P., ... Moritz, C. (2018). Real-world conservation planning for evolutionary diversity in the Kimberley, Australia, sidesteps uncertain taxonomy. *Conservation Letters*, 11, e12438. <https://doi.org/10.1111/conl.12438>
- Rosauer, D. F., Catullo, R. A., VanDerWal, J., Moussalli, A., Hoskin, C. J., & Moritz, C. (2015). Lineage range estimation method reveals fine-scale endemism linked to Pleistocene stability in Australian rainforest Herpetofauna. *PLoS ONE*, 10(5), e0126274. <https://doi.org/10.1371/journal.pone.0126274>
- Santos, M. G., Nogueira, C., Giugliano, L. G., & Colli, G. R. (2014). Landscape evolution and phylogeography of *Micrablepharus atticolus* (Squamata, Gymnophthalmidae), an endemic lizard of the Brazilian Cerrado. *Journal of Biogeography*, 41(8), 1506–1519. <https://doi.org/10.1111/jbi.12291>
- Schwartzman, S., & Zimmerman, B. (2005). Conservation alliances with indigenous peoples of the Amazon. *Conservation Biology*, 19(3), 721–727. <https://doi.org/10.1111/j.1523-1739.2005.00695.x>
- Silva, J. D. (1995). Birds of the cerrado region, South America. *Steenstrupia*, 21(1), 69–92.
- Silva, J. M. C. (1997). Endemic bird species and conservation in the Cerrado Region, South America. *Biodiversity & Conservation*, 6, 435–450.
- Simon, M., & Proença, C. (2000). Phylogeographic patterns of *Mimosa* (Mimosoideae, Leguminosae) in the Cerrado biome of Brazil: An indicator genus of high-altitude centers of endemism? *Biological Conservation*, 96(3), 279–296. [https://doi.org/10.1016/S0006-3207\(00\)00085-9](https://doi.org/10.1016/S0006-3207(00)00085-9)
- Soares-Filho, B., Moutinho, P., Nepstad, D., Anderson, A., Rodrigues, H., Garcia, R., ... Maretti, C. (2010). Role of Brazilian Amazon protected areas in climate change mitigation. *Proceedings of the National Academy of Sciences*, 107(24), 10821–10826. <https://doi.org/10.1073/pnas.0913048107>
- Soares-Filho, B., Rajao, R., Macedo, M., Carneiro, A., Costa, W., Coe, M., ... Alencar, A. (2014). Cracking Brazil's forest code. *Science*, 344, 363–364. <https://doi.org/10.1126/science.1246663>
- SocioAmbiental, I. I. (2014). *Povos Indígenas do Brasil* (S. P. Portuguese) (Ed.). Brasília, Brasil: Instituto SocioAmbiental.
- Strassburg, B. B. N., Brooks, T., Feltran-Barbieri, R., Iribarrem, A., Crouzeilles, R., Loyola, R., ... Balmford, A. (2017). Moment of truth for the Cerrado hotspot. *Nature Ecology & Evolution*, 1, 1–3. <https://doi.org/10.1038/s41559-017-0099>
- Teixeira, M. Jr, Recoder, R. S., Camacho, A., De Sena, M. A., Navas, C. A., & Rodrigues, M. T. (2013). A new species of *Bachia* Gray, 1845 (Squamata: Gymnophthalmidae) from the Eastern Brazilian Cerrado, and data on its ecology, physiology and behavior. *Zootaxa*, 3616(2), 173–189.
- Tilman, D. (2001). Functional diversity. *Encyclopedia of Biodiversity*, 3(1), 109–120.
- Tucker, C. M., Davies, T. J., Cadotte, M. W., & Pearse, W. D. (2018). On the relationship between phylogenetic diversity and trait diversity. *Ecology*, 99(6), 1473–1479. <https://doi.org/10.1002/ecy.2349>
- Valdujo, P. H., Carnaval, A. C. O., & Graham, C. H. (2013). Environmental correlates of anuran beta diversity in the Brazilian Cerrado. *Ecography*, 36(6), 708–717. <https://doi.org/10.1111/j.1600-0587.2012.07374.x>
- Valdujo, P. H., Silvano, 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(2), 63–78. <https://doi.org/10.2994/057.007.0209>
- Vane-Wright, R. I., Humphries, C. J., & Williams, P. H. (1991). What to protect?—Systematics and the agony of choice. *Biological Conservation*, 55(3), 235–254. [https://doi.org/10.1016/0006-3207\(91\)90030-D](https://doi.org/10.1016/0006-3207(91)90030-D)
- Wallace, A. R. (1853). *A narrative of travels on the Amazon and Rio Negro, with an account of the native tribes, and observations on the climate, geology, and natural history of the Amazon valley*. London, UK: Reeve and Co.
- Werneck, F. P. (2011). The diversification of eastern South American open vegetation biomes: Historical biogeography and



perspectives. *Quaternary Science Reviews*, 30, 1630–1648. <https://doi.org/10.1016/j.quascirev.2011.03.009>

Werneck, F. P., Nogueira, C., Colli, G. R., Sites, J. W., & Costa, G. C. (2012). Climatic stability in the Brazilian Cerrado: Implications for biogeographical connections of South American savannas, species richness and conservation in a biodiversity hotspot. *Journal of Biogeography*, 39(9), 1695–1706. <https://doi.org/10.1111/j.1365-2699.2012.02715.x>

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. <https://doi.org/10.1111/j.1558-5646.2012.01682.x>

BIOSKETCH

Jéssica Fenker is a PhD candidate at Australian National University (ANU), Canberra, Australia. She received her M.S. in Animal Biology at the Universidade de Brasília (UnB), Brasília-DF, Brazil. Her interests include integrative ecological, biogeographical and evolutionary approaches to investigate patterns of diversity of Squamates, with a special focus on savanna environments of Brazil and Australia.

SUPPORTING INFORMATION

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

How to cite this article: Fenker J, Domingos FMCB, Tedeschi LG, et al. Evolutionary history of Neotropical savannas geographically concentrates species, phylogenetic and functional diversity of lizards. *J Biogeogr.* 2020;00:1–13. <https://doi.org/10.1111/jbi.13800>