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Hugo Enrique Cabral Beconi

Biogeography of snakes from the Gran Chaco

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Tese apresentada como parte dos requisitos para obtenção do título de Doutor em Biologia Animal, junto ao Programa de Pós-Graduação em Biologia Animal, do Instituto de Biociências, Letras e Ciências Exatas da Universidade Estadual Paulista "Júlio de Mesquita Filho", Câmpus de São José do Rio Preto.

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Comissão Examinadora

Prof. Dr. Diego José Santana Silva
Universidade Federal de Mato Grosso do Sul
Orientador

Profª. Drª. Paola Carrasco
Universidad Nacional de Córdoba

Prof. Dr. Francisco Brusquetti
Instituto de Investigación Biológica del Paraguay

Profª. Drª. Nicolas Pelegrin
Universidade Federal de Uberlândia

Drª. Karoline Ceron
Universidade Estadual de Campinas

Campo Grande
09 de janeiro de 2023

Dedico a meus pais, irmãos e sobrinhos,
sem eles nada disto seria possível

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I don't want to look back. I want to keep going forward, I still have something to say to people.

The future is unwritten.

(Joe Strummer)

RESUMO

Os estudos sobre a evolução e o padrão geográfico da biota Neotropical aumentaram rapidamente nas últimas décadas, com contribuições de quase todas as ecorregiões que abrangem uma variedade de organismos. No entanto, o conhecimento desses processos está centrado principalmente em florestas tropicais como a Amazônia e a Mata Atlântica, deixando de lado as áreas abertas da América do Sul, como Caatinga, Cerrado e Gran Chaco. No entanto, o Chaco é talvez o mais negligenciado desses três, com estudos que se concentram apenas na conservação, ou taxonomia de gêneros ou grupos específicos, ou não abrangendo toda a distribuição do Chaco, e só alguns tratando de processos evolutivos. Neste trabalho, usamos dados moleculares, ecológicos, morfológicos e de distribuição para estudar o processo evolutivo que moldou a distribuição de serpentes de áreas abertas, com ênfase principalmente no Chaco. Descobrimos que no Chaco, alguns caracteres evoluídos respondem a fatores bióticos e abióticos. Por exemplo, encontramos um padrão latitudinal, com uma acentuada verticalidade, na qual espécies fossoriais são impulsadas principalmente pelas condições do solo no Chaco. O padrão de distribuição das serpentes do Chaco também reflete sua história evolutiva, com uma marcada regionalização filogenética. Além disso, eventos no Mioceno/Plioceno como introgressões marinhas e oscilações climáticas, e a heterogeneidade da paisagem são importantes condutores da estrutura genética e história demográfica de *Erythrolamprus poecilogyrus caesius* no Chaco, do mesmo modo as introgressões marinhas e a formação da Bacia do Pantanal são importantes para explicar a diversificação e divisão de *Xenodon pulcher* e *X. matogrossensis*. Finalmente, espera-se que as assembleias de serpentes no Chaco mudem com os cenários climáticos no futuro próximo com uma clara tendência à homogeneização biótica da ecorregião, com consequente homogeneização da diversidade filogenética e funcional das assembleias locais. Essas mudanças negativas se refletiriam nas Unidades de Conservação do Chaco, das quais muitas UCs sofreriam homogeneização biótica e perda de riqueza de espécies.

Palavras–chave: Conservação. Distribuição. Ecologia. Evolução. Filogenia. Xenodontinae.

ABSTRACT

Studies on the evolution and geographical pattern of Neotropical biota has been increased rapidly in the last decades with contributions from almost all ecoregions covering a variety of organism. However, knowledge of these processes is mainly centered in tropical forests such Amazonia and Atlantic Forest, leaving aside the South American open areas, like the Caatinga, Cerrado and Gran Chaco. However, the Chaco is perhaps the most neglected of those three, with several studies that focus mainly on conservation, or taxonomy of specific genera or groups, or not covering the entire distribution of the Chaco, and just a few dealings with evolutionary processes. Here, we used molecular, ecological, morphological, and distributional to studies evolutionary process that shaped the distribution of snakes from open areas, with an emphasizing mainly on the Chaco. We found that in the Chaco, some characters evolved has a response to biotic and abiotic factors. For example, we found a latitudinal pattern, with a marked verticality, and fossoriality is mainly driven by soil conditions in the Chaco. The distribution pattern of Chacoan snakes also reflects their evolutionary history, with a marked phylogenetic regionalization. Also, events during Miocene/Pliocene like marine introgressions, climatic oscillations, and landscape heterogeneity are important drivers of the genetic structure and demographic history for *Erythrolamprus poecilogyrus caesius*, in the Chaco, and some marine introgresions and the formation of the Pantanal Basin are important in explain the diversification and split of *Xenodon pulcher* and *X. matogrossensis*. Finally, is expected that the snakes' assemblages in the Chaco change with climatic scenarios in a near future with clear trend to biotic homogenization of the ecoregion, with consequent homogenization of phylogenetic and functional diversity of local assemblages. These negative changes would be reflected in the Protected Areas of the Chaco, of which PAs would suffering biotic homogenization, and loss of species richness.

Keywords: Conservation. Distribution. Ecology. Evolution. Phylogeny. Xenodontinae.

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CHAPTER 1

LIST OF ABBREVIATIONS

Mya	Millions of years ago
mtDNA	Mitochondrial Deoxyribonucleic Acid
bp	Base pair
ER	Equal rates
SYM	Symmetric rates
ARD	All rates different
MCMC	Markov chain Monte Carlo
pp	Posterior probability
HPD	Highest posterior density
ΔAICc	Delta Akaike Information Criteria with correction
wAICc	Weight Akaike Information Criteria
m.a.s.l	Meters above sea level
GARD	Global Assessment of Reptile Distributions
TT	Total length
TL	Tail length
SVL	Snout-vent length
mm	millimeters
VIF	Variance Influence Factor
AET	Annual actual evapotranspiration
NPP	Net primary productivity
NDVI	Normalized difference vegetation index
EVI	Enhaced Vegetation Index
TC	Tree cover
FRAG	Volumetric percentage of coarse fragments
SAND	Proportion of sand particles in the soil

km	Kilometers
PCA	Principal Component Analysis
SES	Standardized effect size
SAR	Spatial autoregressive models
ED	Evolutionary distinctness
NMDS	Non-metric multidimensional scaling
IIBP	Instituto de Investigación Biológica del Paraguay
LGE	Laboratorio de Genética Evolutiva
ZUFMS	Coleção Zoológica da Universidade Federal Mato Grosso do Sul
UFMS	Universidade Federal Mato Grosso do Sul
CA	California
USA	United States of America
PCR	Polymerase Chain Reaction
ASAP	Assemble species by automatic partitioning
GMYC	Generalized Mixed Yule Coalescent
BI	Bayesian Inference
IBD	Isolation by Distance
Hd	Haplotype diversity
AMOVA	Analysis of Molecular Variance
BSP	Bayesian Skyline Plots
FML	Fundación Miguel Lillo
MNHNP	Museo Nacional de Historia Natural del Paraguay
UNNEC	Universidad Nacional del Nordeste
IPCC	Intergovernmental Panel on Climate Change
SSP	Shared Socioeconomic Pathways
GCM	Generalized circulation models

ENM	Ecological niche models
RND	Random allocation of pseudo-absences
MXD	Maximum Entropy default
GLM	Generalized Linear Models
OBR	Occurrence-based restriction
PCoA	Principal Coordinate Analysis
UPGMA	Unweighted Pair Group Method with Arithmetic mean
PD	Phylogenetic diversity
PB	Phylogenetic beta diversity
SesMPD	Standardized effect size of mean pairwise distance
FRic	Functional richness
FEve	Functional evenness
FDis	Functional dispersion
PA	Protected Areas
WDPA	World Database Protected Areas

SUMMARY

1 INTRODUCTION

Studies on the evolution and geographical pattern of Neotropical biota have increased rapidly in the last decades with contributions from almost all ecoregions covering a variety of organism (BROWN et al., 2020; BRUSQUETTI et al., 2018; WERNECK, 2011; WERNECK et al., 2012). However, knowledge of these processes is mainly centered in tropical forests such Amazonia and Atlantic Forest, leaving aside the Dry Diagonal (VANZOLINI, 1963; WERNECK, 2011), which include the Caatinga, Cerrado and Gran Chaco (hereafter Chaco). Fortunately, in the last decade several studies aim to understand the evolutional and geographical pattern in open areas, with research on amphibians, mammals, fishes, and plants (AZEVEDO et al., 2021; CAMPS et al., 2018; DELSUC et al., 2012; FRANÇA et al., 2008; ROCHA et al., 2020; WERNECK et al., 2015).

The Chaco is perhaps the most neglected of those three, with several studies that focus mainly in conservation, or taxonomy of specific genera or groups, or not covering the entire distribution of the Chaco (ANDRADE-DÍAZ et al., 2019; NORI; GÓMEZ; LEYNAUD, 2011; SEMPER-PASCUAL et al., 2018), and just a few dealing with evolutionary process (BRUSQUETTI et al., 2019; CACCIALI et al., 2016a; DELSUC et al., 2012; NORI et al., 2016; ROMERO-MUÑOZ et al., 2020). In the case of reptiles, important works were published for the Cerrado (AZEVEDO; VALDUJO; NOGUEIRA, 2016; BARBO; NOGUEIRA; SAWAYA, 2021; NOGUEIRA et al., 2011) and Caatinga (CAMURUGI et al., 2022; GUEDES; SAWAYA; NOGUEIRA, 2014; WERNECK et al., 2015; XAVIER; GUEDES; NAPOLI, 2015).

In southern South America, one ecoregion with semiarid, stressful environments and marked climatic seasonality is the Great American Chaco, covering Argentina, Bolivia, Paraguay and Brazil (CABRERA, 1994; PRADO, 1993), one of the most extensive continuous forested areas of South America (BUCHER, 1982). The Chaco is the result of

Andean uplift, marine introgressions, and several alluvial systems (GREGORY-WODZICKI, 2000; HERNÁNDEZ et al., 2005; IRIONDO, 1993). The most important characteristic of the Chaco is his geomorphology, which consist in an extensive sedimentary alluvial plain with soils derived from the massive accumulation of Quaternary sediments (PENNINGTON; PRADO; PENDRY, 2000; PRADO, 1993). This region is characterized by xerophytic vegetation formed by a mosaic of grasslands, savannas, open woodlands, and thorn forest (PRADO, 1993; WILLIG et al., 2000). This area shows an impressive monotony along his distributions, with scarce high elevation hills, the few elevations hills are located mostly in their western limit in Argentina and Bolivia (PRADO, 1993), resulting in a horizontal terrain, provoking that only four allochthonous rivers crossing the Chaco (PRADO, 1993). So, apparently no geographical barriers for organism dispersion are present in the Chaco (BUCHER, 1982) nevertheless, some barriers have been proposed, like the Sierras Pampeanas and Subandinas in Argentina, and the rivers mentions above (IRIONDO, 1993).

In the Chaco, the highest absolute temperature for South America has been registered (PRADO, 1993), this area with maxima temperature up to of 48.9°C is referred by (PROHASKA, 1959) as the South American Pole of Heat. This extreme hot summer is associated with frost winters, in almost the entire Chaco, in some area's temperature can reach -1.1°C in Corrientes or -7.2°C, an east-west pattern (PRADO, 1993). The precipitation in the Chaco also follows an east-west gradient with more than 1200 mm of annual precipitation in the east to 350mm in the west (PRADO, 1993). This climatic condition is reflected in a marked dry and rainy season, in some west areas the summer rains are the only ones of the year (PRADO, 1993).

Among the Chaco, two regions could be differentiated, the Humid and Dry Chaco (DINERSTEIN et al., 2017). The Humid Chaco is characterized by a mosaic of gallery forest with flooded savannas with *Copernicia alba*, which that extends from east Bolivia to northern

Argentina, following the course of the Paraguay and in some parts the Parana River (PRADO, 1993), On the other hand, the Dry Chaco is characterized by xerophytic vegetation with thorny forest, from southwest Bolivia, west of Paraguay and northern Argentina (PRADO, 1993).

The first work that deals with the snakes of the Chaco is LEYNAUD & BUCHER (1999), which provides distributions maps, and natural history notes of the species known for the Chaco at that time. Subsequent works deals with the distribution, biology, or conservation of snakes from the Chaco of Argentina (ANDRADE-DÍAZ et al., 2019; GIRAUDO; SCROCCHI, 2002; GIRAUDO, 2002; LEYNAUD; BUCHER, 2005), Paraguay (CACCIALI et al., 2016b; CACCIALI; CABRAL; YANOSKY, 2015; CACCIALI; UBILLA, 2016), Bolivia (EMBERT, 2007; HARVEY, 1999; HARVEY et al., 2008; HARVEY; APARICIO; GONZALES, 2005; JANSEN; KÖHLER, 2008), and Brazil (SOUZA et al., 2010). Therefore, understanding the historical and evolutionary processes that have shaped the geographic pattern of species distribution in this region becomes increasingly relevant.

This become more important because, Chaco has been suffering high deforestation rates (HANSEN et al., 2013) and landscape degradation, making it a priority area for conservation (DE LA SANCHA et al., 2021; FRATE et al., 2015; KUEMMERLE et al., 2017). Several studies have pointed out the importance of taking conservation actions in the Chaco, along with measuring their threats and identifying priority conservation areas (KUEMMERLE et al., 2017; NORI et al., 2016; ROMERO-MUÑOZ et al., 2020; SEMPER-PASCUAL et al., 2018). However, most of those works was focused on mammals, birds, or amphibians. Recently, ANDRADE-DÍAZ et al. (2019) identified priority conservation areas for 12 endemic snakes of the Dry Chaco in Argentina. showing that expansion of the agricultural frontier has potentially negative effects on the distribution of snakes in this region, with deforestation being the biggest threat (ANDRADE-DÍAZ et al., 2019).

In this work, we aim to study the evolutionary process that shaped the distribution of snakes of the Dry Diagonal, with an emphasis mainly on snakes from the Chaco. In addition to the

evolutionary process, we also are interested to fill the gap of knowledge of ecology, natural history, and conservation of the snakes inhabiting Chaco. Seen this, this contribution is divided into 4 chapters, the first one focus on the evolution of two discrete characters on the genus *Xenodon*, distributed along the forested and the dry diagonal of the Neotropics (Caatinga, Cerrado and Chaco). The second chapter is focused on the functional and evolutionary drivers that explain the geographic patterns of vertical stratification of snakes from the Chaco. Chapter three deals with the phylogeography of *E. poecilogyrus caesius*; and the diversification of *X. pulcher* and *X. matogrossensis* in the Chaco; finally, the fourth chapter focus on the conservation of snakes from the Chaco, in a future perspective.

2 OBJECTIVES

This research aims to investigate the historical events that have been contributing to the evolutionary process that has shaped the current distribution of the snakes in the Chaco, and the current factors that predict the distribution of species in the Dry Diagonal, emphasizing the snakes from Gran Chaco.

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3 CHAPTER 1: EVOLUTION OF ROSTRAL SCALE AND MIMICRY IN THE GENUS *XENODON* BOIE, 1826 (SERPENTES, DIPSADIDAE, XENODONTINAE)

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4 ABSTRACT

Snakes represent an interesting lifeform from an evolutionary perspective. Despite the basic morphological body shape (limbless, and tubular body), these animals are extremely diverse vertebrates. The Neotropical region is one of the most diverse regions for snakes in the world, with more than 650 known species. Within this great diversity, the genus *Xenodon* is comprised of 12 species, with interesting adaptations to terrestrial and semi-fossorial habitats. Members of this genus are mostly diurnal, terrestrial, feed mainly on anurans, and have Batesian mimicry with venomous snakes of the genera *Bothrops* or *Micrurus.* Here, through phylogenetic analysis and ancestral estimation, we explore the evolution of the rostral scale and mimicry within the genus *Xenodon*. Our results suggest that the ancestral lineage of *Xenodon* had a rounded rostral scale with *Bothrops* mimicry. The evolution of the rostral scale in *Xenodon* may be related to abiotic factors, as an adaptation for open and forested habitats, and mimicry are likely related to biotic factors, as a defensive strategy resembling those of venomous snakes.

Keywords: Batesian. *Bothrops.* Forest Habitats. *Micrurus.* Neotropical. South America. Snakes. Open Areas.

5 INTRODUCTION

Snakes are one of the most interesting lifeforms from an evolutionary perspective, with a basic morphological body shape (limbless and tubular body). This vertebrate group is extremely diverse, not only ecologically but also in the number of species (VITT; CALDWELL, 2009), and are one of the most neglected groups in conservation (GUEDES et al., 2018). Among squamates, snake-like body form has independently evolved at least 26 times (Wiens, Brandley, & Reeder, 2006), and snakes are the most successful of those lineages with more than 3900 species (UETZ et al., 2021). The diversity of morphology and how these changes or transitions occurred along with their evolution is one of the main goals of evolutionary biology (FUTUYMA, 2005). For example, if one morphological character evolves over multiple times, there is evidence that it is strongly favored by natural selection (HARVEY; PAGEL, 1991).

Numerous traits have evolved independently multiple times along their evolution in reptiles (e.g., loss of digits, ovoviviparity, body shape, fangs, venom, diet or size), but resulting with the same traits status or function (BRANDLEY, HUELSENBECK, & WIENS, 2008; PYRON & BURBRINK, 2014; FELDMAN et al., 2015; RABOSKY et al., 2016; NAIK, KGADITSE, & ALEXANDER, 2021). Furthermore, ecological opportunities can trigger divergent selection and lead to new adaptations to cover empty niches, which would promote and increase speciation and morphological diversification (NOSIL, 2012; SCHLUTER, 2001). These adaptations are especially diverse in regions with varied environments, such as the Neotropics (DA SILVA et al., 2017; GRUNDLER; RABOSKY, 2014; WIENS; BRANDLEY; REEDER, 2006).

The Neotropical region is one of the most diverse regions in the world in terms of habitat diversity, like rainforest, montane forest, savannas, montane savannas, steppes, with a great diversity of species, many of which are endemics (AZEVEDO et al., 2020;

DINERSTEIN et al., 2017; NOGUEIRA et al., 2019; OLSON et al., 2006). Among this great diversity, the genus *Xenodon* currently contains 12 species and is one of most widespread snake groups in South America (NOGUEIRA et al., 2019). Those species was previously classified in the genus *Waglerophis* (characterized mainly by a short maxillary bone), and several others were in the genus *Lystrophis* (identified by the presence of a shovel-shaped rostral scale with a central keel) (CEI, 1993; SCROCCHI; CRUZ, 1993). The synonymization of these two genera with *Xenodon* was proposed to maintain the monophyly based on molecular analyses (GRAZZIOTIN et al., 2012; ZAHER et al., 2009). Species of this genus are mostly diurnal, terrestrial, feed mainly on anurans, and all species have Batesian mimicry with venomous snakes of the genera *Bothrops* or *Micrurus* (SAZIMA & ABE, 1991; CEI, 1993; CARREIRA, MENEGHEL, & ACHAVAL, 2005; CACCIALI, 2009; RABOSKY et al., 2016).

Xenodon is distributed from southern Mexico to northern Argentina (CEI, 1993; CARREIRA et al., 2005; UETZ et al., 2021). Within the genus, two morphological, non-monophyletic, groups can be easily distinguished: species with a rounded rostral scale and species with keeled rostral scale (Table 1). This first group contains *Xenodon guentheri* Boulenger 1984, *X. merremii* (Wagler, 1824), *X. neuwiedii* Günther, 1863, *X. rabdocephalus* (Wied-Neuwied, 1824), *X. severus* (Linnaeus, 1758) and *X. werneri* (Eiselt, 1963). These species are associated with forested areas and terrestrial habits, except for *X. merremii*, which is distributed mainly in open areas with records in adjacent forested areas (MARTINS & OLIVEIRA, 1998; MARQUES, ETEROVIC, & SAZIMA, 2001; GIRAUDO, 2002) (Fig. S1-3).

Table 1. Species of *Xenodon* with the type of rostral scale, mimicry, and habitat information. Semi-fossorial species are marked with *.

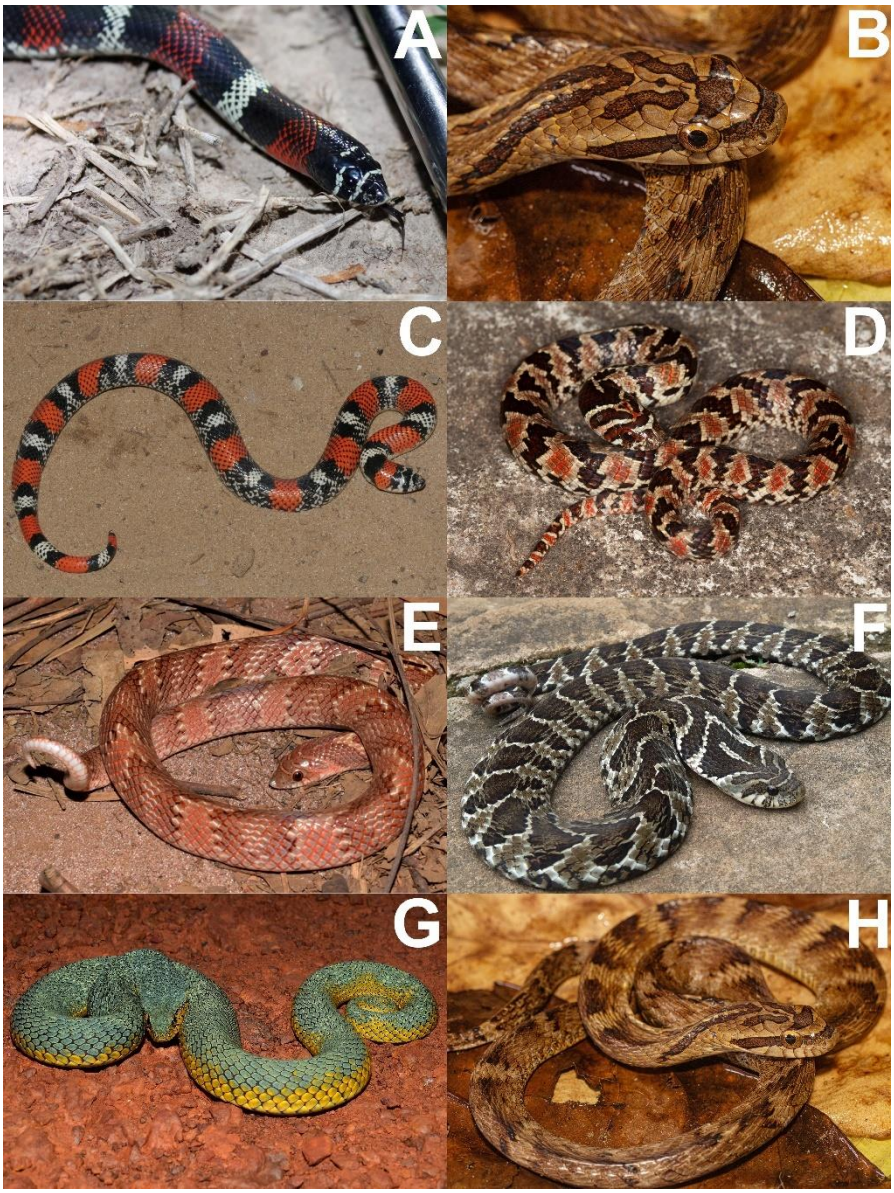
Species	Rostral Scale	Mimicry	Habitat	References
Xenodon merremii	rounded	*Bothrops*	Open and Forest	(CACCIALI, 2010; CEI, 1993; PIZZATTO; JORDÃO; MARQUES, 2008)
Xenodon werneri	rounded	*Bothrops*	Forest	(CHIPPAUX, 1986; HOOGMOED, 1985)
Xenodon severus	rounded	*Bothrops*	Forest	(CHIPPAUX, 1986; KAHN, 2010; SILVA; SOUZA; BERNARDE, 2010)
*Xenodon matogrossensis**	keeled	*Micrurus*	Open	(CABRAL et al., 2020)
*Xenodon pulcher**	keeled	*Micrurus*	Open	(CEI, 1993; NENDA; CACIVIO, 2007; SCROCCHI; CRUZ, 1993)
*Xenodon semicinctus**	keeled	*Micrurus*	Open	(CEI, 1993; NENDA; CACIVIO, 2007; SCROCCHI; CRUZ, 1993)
Xenodon guentheri	rounded	*Bothrops*	Forest	(ABEGG et al., 2016; BÉRNILS; BATISTA; BERTELLI, 2001)
*Xenodon nattereri**	keeled	*Bothrops*	Open	(CEI, 1993; MARQUES et al., 2015; FIORILLO, MACIEL, & MARTINS, 2021)
*Xenodon histricus**	keeled	*Micrurus*	Open	(CARREIRA, 2002; CARREIRA; MENEGHEL; ACHAVAL, 2005; CEI, 1993)

			Open	(CARREIRA; MENEGHEL; ACHAVAL, 2005; CEI, 1993; NENDA; CACIVIO, 2007; TOZETTI; OLIVEIRA; PONTES, 2009; YANOSKY; CHANI, 1988)
*Xenodon dorbignyi****	keeled	Both		
Xenodon neuwiedii	rounded	*Bothrops*	Forest	(CEI, 1993; PEDROZO; MOROTI; MUSCAT, 2020)
Xenodon rabdocephalus	rounded	*Bothrops*	Forest	(AGUILAR-LÓPEZ et al., 2021; CHIPPAUX, 1986; MARQUES et al., 2015)

The other group is composed by species with a keeled rostral scale resembling a shovel (the former genus *Lystrophis*), composed by *X. dorbignyi* (Bibron, 1854), *X. histricus* (Jan, 1863), *X. matogrossensis* (Scrocchi & Cruz, 1993), *X. nattereri* (Steindachner, 1867), *X. pulcher* (Jan, 1863), and *X. semicinctus* (Duméril, Bibron & Duméril, 1854), which are distributed mainly in open areas, with semi-fossorial habits (CABRAL et al., 2015; CARREIRA; MENEGHEL; ACHAVAL, 2005; CEI, 1993; NOGUEIRA et al., 2019; SCROCCHI; CRUZ, 1993) (Fig. S4). Among the 12 species within *Xenodon*, seven are mimic of pitvipers (*Bothrops*), four species are mimics of coral snakes (*Micrurus*), and one species (*X. dorbignyi*) has a double mimicry with both *Bothrops* and *Micrurus* (YANOSKY & CHANI, 1988; CEI, 1993; TOZETTI, OLIVEIRA, & PONTES, 2009; ALVES et al., 2013) (Table 1) (Fig. 1).

The seven species with *Bothrops* mimics have a rounded rostral scale with terrestrial habits, except for *X. dorbignyi* and *X. nattereri* which have keeled rostral scale with semi-fossorial habits (CEI, 1993). On the other hand, the entire species with *Micrurus* mimics have keeled rostral scale with semi-fossorial habits, this keeled scale serves as a shovel for digging and help the species with their semi-fossorial habits (CEI, 1993; OREJAS-MIRANDA, 1966; SCROCCHI; CRUZ, 1993). The same member of the genus has different adaptations, a half are adapted to a terrestrial habit in forested environments (CEI, 1993; GIRAUDO, 2002), and the other half adapted to a semi-fossorial habitat strongly associated with open areas (CABRAL et al., 2015, 2020; CEI, 1993).

Figure 1. Mimicry and the shape of rostral scale in the genus *Xenodon*. A) Lateral view of *X. pulcher* showing the keeled rostral scale and B) Lateral view of *X. neuwiedii* showing the rounded rostral scale. *Micrurus* (C-D) and *Bothrops* (E-H) mimicry in several species of *Xenodon*, C) *Xenodon matogrossensis* D) *X. histricus*, E) *X. nattereri*, F) *X. guentheri* G) *X. werneri*, H) *X. neuwiedii*, I) *X. neuwiedii*. Photograph credits: Henrique Nogueira (B, H), Marcio Martins (C), Santiago Carreira (D), Diego Cavalheri (E), Karoline Ceron (F), © Sébastien Sant /Parc Amazonien de Guyane (G).



Batesian mimicry involves the resemblance between two species, one of which implies potential danger or has some other unpleasant characteristics, and the other (the mimic), which is essentially harmless (MALLET; JORON, 1999; WICKLER, 1968). This mimicry often involves bright warning coloration, which a predator recognizes as unpleasant or dangerous and learns to avoid it (GREENE; MCDIARMID, 1981). Through the resemblance to the potentially dangerous species, the mimic deceives a third species (a predator) which results in less predation, treating non-dangerous prey as dangerous. (GREENE & MCDIARMID, 1981; MALLET & JORON, 1999; PFENNIG, HARCOMBE, & PFENNIG, 2001). Mimics and models coevolve in the classic sense of exerting reciprocal selection on one another through their respective effects on the receiver's response to signals (BRODIE; BRODIE JR., 2004; RABOSKY et al., 2016). In coral snakes and vipers, mimicry (coloration) has evolved independently, as an important defense system to avoid predation (BRODIE; BRODIE JR., 2004; RABOSKY et al., 2016; SAVAGE; SLOWINSKI, 1992) nonetheless, little is known about the evolutionary process of mimicry in snakes (BRODIE; BRODIE JR., 2004).

The evolution of mimicry is related to the sympatric presence of both, venomous and non-venomous species, in this case the model to be imitated (BRODIE; BRODIE JR., 2004; KIKUCHI; PFENNIG, 2010; PFENNIG; HARCOMBE; PFENNIG, 2001), which is an important prediction of the Batesian mimicry theory (RABOSKY et al., 2016; ROZE, 1983). Based on the dual morphology of the rostral scale, and the Batesian mimicry presented by *Xenodon* species, in this study we used ancestral character reconstruction to investigate the patterns of rostral scale and mimicry evolution. This genus is ideal to test evolutionary adaptations, once its species exhibit different adaptations, behavior, and habitat preferences. How evolved those characters or functional traits along the evolutionary timeline in relation to species ecology, would help us understand if such characters have evolved as an adaptation

to new habitats or environment (convergent evolution), or whether it occur randomly (DA SILVA et al., 2017; RAMM et al., 2018). Such characters can have multiple or independent origins, usually favored by natural selection (HARVEY; PAGEL, 1991), and often those origins are used as evidence for adaptative evolution (LOSOS et al., 2002; RAMM, ROYCROFT, & MÜLLER, 2020).

Since, the defensive behavior or strategies have evolved as a response to predation (LOSOS ET AL., 2002; YOUNG, EDMUND, & BRODIE III, 2004; STANKOWICH & CAMPBELL, 2016; Ramm et al., 2020), and mimicry is found in species in different neotropical environments associated with the presence of venomous or dangerous species (BRODIE III, 1993; BUASSO, LEYNAUD, & CRUZ, 2006; KIKUCHI & PFENNIG, 2010; RABOSKY et al., 2016; FRANÇA, BRAZ, & ARAÚJO, 2017), we would like to understand how the pattern of mimicry in the genus evolved.

Herein, we used a time-calibrated phylogeny to understand how the evolution of the rostral scale and mimicry in the genus *Xenodon* arose. We predict that the:

(1) Ancestral state in the genus was the presence of a rounded rostral scale (as in the remaining Xenodontini), and that the evolution of the rostral scale is related to environment adaptations, and that these conditions were favored by environmental pressure. The modified scale in *Xenodon* (formerly *Lystrophis*) serves as a shovel for digging in areas with sandy soils in open areas with that type of soil condition (CACCIALI, 2009; CARREIRA; MENEGHEL; ACHAVAL, 2005; CEI, 1993). On the other hand, the remaining species of *Xenodon* have a rounded rostral scale, and apparently it does not have a special function as a modified rostral scale.

(2) The ancestral condition of the genus was the *Bothrops* mimicry, because the *Bothrops* ancestor was widely distributed in South America, which diversified during the Middle Miocene, around 11–12Mya (Parkinson, Campbell, & Chippindale, 2002; HAMDAN

et al., 2020). Moreover, at least two species of *Xenodon* with *Bothrops* mimics are distributed in the north of South America (Fig. S1), whereas the *Xenodon* with *Micrurus* mimics are distributed in open areas in southern South America (Fig. S4). In this sense, only one's species of *Xenodon* reach Central America (*X. rabdocephalus*) (NOGUEIRA et al., 2019), besides, *B. asper* is the only species of *Bothrops* that reach Central America, also distributed in northern South America (HAMDAN et al., 2020) associated with Amazon forest, which may support the idea of an ancestor with *Bothrops* mimic, is worth to known that *X. rabdocephalus* mimics *B. asper* and *B. atrox* (MYERS; MCDOWELL, 2014). Since all the *Xenodon* with *Micrurus* mimics are restricted to southern South America, and species of *Xenodon* with *Bothrops* mimics are more widely distributed, and these are the only species that reach Central America (*X. rabdocephalus*) and following the northern Plio-Pleistocene diversification (around 2.2 Mya) of *B. asper* we believe there is enough evidence to hypothesized that the ancestor of *Xenodon* have *Bothrops* mimic with terrestrial habits. Most *Bothrops* species tend to be more terrestrial (ALENCAR et al., 2017), as in *Xenodon* with *Bothrops* mimic, whereas *Micrurus* are usually cryptozoic (ROZE, 1996), similar to *Xenodon* with *Micrurus* mimic, which are semi-fossorial.

6 MATERIALS AND METHODS

The study area included the Neotropics, from southern Mexico to northern Argentina. We classified the species in two groups: rounded and keeled rostral scale (Fig 1A-B). To clarify the concepts, we referred to a rounded rostral scale as a smooth structure without keels, not projected horizontally or vertically (Fig. 1B), and a keeled rostral scale a structure heavily keeled with a horizontal or vertical projection (Fig. 1A). Information on the shape of the rostral scale was gathered from photographs and literature (ALVES et al., 2013; CARREIRA; MENEGHEL; ACHAVAL, 2005; CEI, 1993; GIRAUDO, 2002; SCROCCHI; CRUZ, 1993).

For the mimicry classification, we used various literature information (ALVES et al., 2013; CACCIALI, 2009; CAETANO et al., 2016; CARREIRA; MENEGHEL; ACHAVAL, 2005; CEI, 1993; DA SILVA, 2016; GIRAUDO, 2002; GREENE; MCDIARMID, 1981; YANOSKY; CHANI, 1988), especially for those species with *Bothrops* mimicry to avoid ambiguities or wrong interpretations. Species with coral snake patterns are easier to classify as *Micrurus* mimicry (Fig. 1C-D), however for some species, like *X. dorbignyi* and *X. histricus*, we gathered information from recent papers (ALVES et al., 2013; TOZETTI; OLIVEIRA; PONTES, 2009). For mimicry classification, we classified the species in *Bothrops* and *Micrurus* coloration, using only adult dorsal coloration (Fig. 1C-H). The typical coloration of *X. merremii* consists of a pattern with semicircular brownish lateral marks with wavy edges and skirted by thin white margins (CACCIALI, 2010; CEI, 1993; GIRAUDO, 2002). The typical coloration resembles that of several *Bothrops* species and the defensive mechanism of the species also imitates those of *Bothrops* by triangulating the head and with intimidating attacks (CEI, 1993), therefore, we classify *X. merremii* as *Bothrops* mimics.

We used the latest Brazilian snake checklist and complemented with recent papers and our own data (CACCIALI et al., 2016; NOGUEIRA et al., 2019; FRANÇA et al., 2020; PEREIRA FILHO et al., 2021; WILLIAMS, VERA, & DI PIETRO, 2021), to elaborate distributions maps of each species. Habitat preferences of *Xenodon* species were obtained using natural history information of the various species. Those that are usually found in the forest (forest-dwelling, forest specialists) were classified as forest species, and species found in open areas (Pampas, dry and humid Chaco, Pantanal) were associated with open areas. The natural history references are provided in Table 1. *Xenodon merremii*, were considered as both forest and open areas since this species is found in both types of habitats. In addition, we gathered information about the distribution of each species from several literature sources (CEI, 1993; CARREIRA et al., 2005; CACCIALI, 2009; TOZETTI et al., 2009; ALVES et

al., 2013; CABRAL et al., 2015; NOGUEIRA et al., 2019; PEDROZO, MOROTI, & MUSCAT, 2020). Additional information was also used to determine whether species were present in open or in forested areas.

6.1 Phylogenetic hypotheses

The latest snake phylogeny from (ZAHER et al., 2019) lists 11 of the 12 species of *Xenodon*. Nevertheless, we constructed our own calibrated tree to include all the species within the genus. We downloaded 12S and 16S mtDNA sequences of the 12 species of *Xenodon* from GenBank (Table 2) including *X. rabdocephalus*, which is absent in Zaher *et al*. (2019), and used *Erythrolamprus miliaris* as an outgroup. We chose this species as the outgroup since *Erythrolamprus* is the sister genus of *Xenodon* and is widespread within the Neotropics. We concatenated and aligned the 12S and 16S sequences in Geneious v9.1.2 using the MUSCLE algorithm with the default parameters (EDGAR, 2004). The final aligned dataset used in all analyses comprised 852 base pairs (bp). We used PartitionFinder 2 to identify partitioning schemes and the most appropriate nucleotide replacement models (LANFEAR et al., 2017a). According to our concatenated alignment, we found one partition evaluated by BIC, with the best model being TrN+G. For phylogenetic analysis, we performed a Bayesian phylogenetic analysis using BEAST v.2.6.3 (BOUCKAERT et al., 2019) for 50 million generations, sampling every 2,000 steps using a Yule Process tree prior. We checked for stationarity by visually inspecting trace plots and ensuring that all values for effective sample size were above 200 in Tracer v1.7.1 (RAMBAUT et al., 2018). The first 10% of sampled genealogies were discarded as burn-in, and the maximum clade credibility tree with median node ages was calculated with TreeAnnotator v.2.6.3 (BOUCKAERT et al., 2019).

Table 2. Accession Number

Species	12S	16S	Reference
X. dorbignyi	GQ457812	GQ457752	ZAHER et al. (2009)
X. guentheri	JQ598849	JQ598909	GRAZZIOTIN et al. (2012)
X. histricus	GQ457813	GQ457753	ZAHER et al. (2009)
X. matogrossensis	JQ598850	JQ598910	GRAZZIOTIN et al. (2012)
X. merremii	GQ457840	JQ598911	ZAHER et al. (2009)
X. nattereri	JQ598851	JQ598912	GRAZZIOTIN et al. (2012)
X. neuwiedii	GQ457841	GQ457779	ZAHER et al. (2009)
X. pulcher	JQ598852	JQ598913	GRAZZIOTIN et al. (2012)
X. rabdocephalus	-	MH141006	MULCAHY (UNPUBLISHED)
X. semicinctus	GU018156	GU018173	VIDAL et al. (2010)
X. severus	JQ598853	JQ598914	GRAZZIOTIN et al. (2012)
X. werneri	AF158468	AF158538	VIDAL et al. (2000)
Erythrolamprus miliaris	AF158409	AF158480	(VIDAL et al., 2000)

6.2 Ancestral character reconstruction

To evaluate the pattern of evolution of both types of rostral scales, and mimicry in the genus, we tested the best models of evolution using the *fitDiscrete* function in the geiger package

(PENNELL et al., 2014) for the software R3.6.0 (R CORE TEAM, 2019). This function fits various likelihood models of continuous time Markov models of trait evolution for discrete character, returning an estimate parameter along with the likelihood for univariate data (YANG, 2006). Transitions from one state to another can occur in different rates and directions. Three models of transition rates were used during ancestral character reconstruction, equal rates (ER), symmetric model (SYM), and all rates different (ARD). These models allow a random process where the probability of change between character states depends only on the current state (PENNELL et al., 2014; YANG, 2006). In the ER, the rate of changes between characters are assumed to be equivalent, the SYM allows different rates of changes between pair of states, but changes between all states are theoretically possible (for binary data, SYM results are equivalent to ER), and the ARD when all possible types of transition can have different rates (Paradis, Claude, & Strimmer, 2004; Revell, 2014). The best models were selected based on the smallest AICc (BURNHAM; ANDERSON, 2007). Since classification of the rostral scale is in binary data, as stated above, we only used the ER and ARD model, for mimicry we used all three models, ER, SYM and ARD.

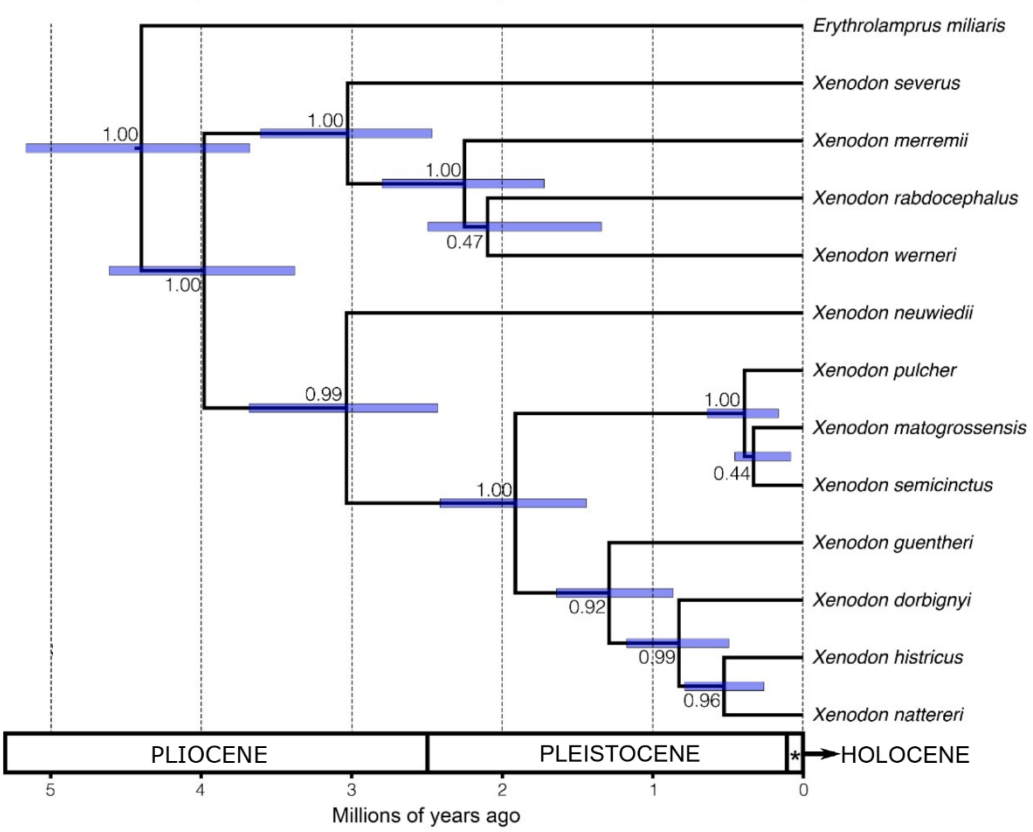
We used the method proposed by (BORGES et al., 2018) to test for phylogenetic signal in categorical traits. This method measures the degree of phylogenetic signals using the concept of Shannon's entropy, measuring the entropy contained in ancestral inferences using sigma (δ) as the value of phylogenetic signal. When δ increased the trait evolved according to the phylogeny and decreased when the trait evolved independently. Values of δ can be any positive real number, the higher the value of δ, higher the degree of phylogenetic signal between the trait and the phylogeny (BORGES et al., 2018). We performed this analysis in the software R3.6.0 (R CORE TEAM, 2019) following the methods described in Borges *et al*. (2018)

We reconstructed the ancestral state using the stochastic character mapping MCMC approach (HUELSENBECK, NIELSEN, & BOLLBACK, 2003) in the phytools package (REVELL, 2012), with the *make.simmap* function, a method for reconstruction that uses Bayesian inference. Both characters (rostral scale and mimicry) were mapped in the phylogeny, with the probability of the trait occurring among 100 stochastic trait histories (DUNOYER, SEIFERT, & VAN CLEVE, 2020). To analyze the correlation between the rostral scale and habitat we performed a threshold model of character evolution in phytools (FELSENSTEIN, ACKERLY, & MCPEEK, 2012; REVELL, 2014) with 1.000.000 generations, sampled every 100 generations, and rejected the first 200.000 generations as burn-in.

7 RESULTS

Our phylogenetic tree, containing all 12 species known for the genus (Fig. 2), presents two well-supported clades (pp=1.00) (Fig. 2). The first clade (pp=1.00) is composed by *Xenodon severus* as the sister taxon of *X. merremii*, which is the sister taxon of *X. werneri* and *X. rabdocephalu*s, all with a rounded rostral scale with wide distribution in South America (Fig. S1-3). The relationship between *X. rabdocephalus* and *X. werneri* showed low support value, and *X. merremii* could also be the sister species of one of both species (pp=1.00). The second clade is composed by two well-supported subclades (pp=0.99), with *X. neuwiedii* as the sister species of both subclades (Fig. 2), also well-supported (pp=0.99). One subclade is composed of *X. semicinctus* as a sister species of *X. matogrossensis*, with low support, and *X. pulcher* as the sister taxon of both. The remaining subclade is also well-supported (pp=0.99) and has *X. guentheri* as sister taxon of *X. dorbignyi, X. histricus* and *X. nattereri* (Fig. 2). In the second clade, all species have a keeled rostral scale, except for *X. neuwiedii* and *X. guentheri*.

Figure 2. Species tree of *Xenodon* inferred with BEAST, including *Erythrolamprus miliaris* as outgroup. Number at the nodes represent the posterior probability.



In addition, our calibrated time tree (Fig 2) indicates the first divergence between the two major clades around 3.98 Mya (95% HPD = 3.38–4.61) during the middle Pliocene. The beginning of the divergence within both subclades occurs in similar periods. The first clade, composed by *X. severus*, *X. merremii*, *X. rabdocephalus* and *X. werneri* started around 3.03 Mya (95% HPD = 2.47–3.61) at the end of the Pliocene and the other divergences occurred in the beginning of the Pleistocene. The second, and more diverse, subclade composed by the remaining species started its divergence around 3.04 Mya (95% HPD = 2.43–3.68), with other divergences from the beginning to the end of the Pleistocene.

Our stochastic character mapping suggests that the ancestor of *Xenodon* had a rounded rostral scale with *Bothrops* mimicry (Fig. 3A). The keeled rostral scale appears for the first time around 2 million years ago, during the Pleistocene in the subclade composed by

X. pulcher, *X. semicinctus* and *X. matogrossensis*, and them in the subclade composed by *X. dorbignyi*, *X. histricus* and *X. nattereri*, with one change around 1 million years ago in *X. guentheri* (Fig. 3B). The *Micrurus* mimicry pattern was constant around the evolution of the genus, with only two changes, when appear for the first time around 2 million years ago in the subclade composed by *X. pulcher*, *X. semicinctus* and *X. matogrossensis*, and then appear again in *X. dorbignyi* and *X. histricus* around 1 million years ago during the Pleistocene (Fig. 3B).

The best model for both rostral scale and mimicry pattern was the ER model (lowest AICc, Table 3). We found a strong phylogenetic signal for the rostral scale (δ=5.04, p=0.02), when $p<0.05$ there is evidence of phylogenetic signal between the trait and the phylogeny. Meaning that species with a keeled rostral scale are closely related species, which tend to resemble each other for a specific trait, evolving in close association within that phylogeny. In the case of mimicry, (δ=1.8, p=0.48), $p>0.05$, we found a weak phylogenetic signal or no evidence of phylogenetic signal, indicating that this trait evolved independently from the phylogeny. We found a positive correlation between the rostral scale and habitat where species inhabit with a correlation coefficient of r=0.5.

Figure 3. Stochastic Character Mapping reconstruction. A) Reconstruction rostral scale, black branches = keeled rostral scale, and red branches = normal rostral scale. B) Reconstruction of mimicry, green branches = *Bothrops* mimicry, orange branches = Micrurus and blue branch= both. The pie charts at the nodes represent the probability of ancestral state. This figure is illustrated with four *Xenodon* species: A) *Xenodon nattereri* at the top and *X. guentheri* at bottom, B) *X. pulcher* at the top and *X. merremii* at bottom.

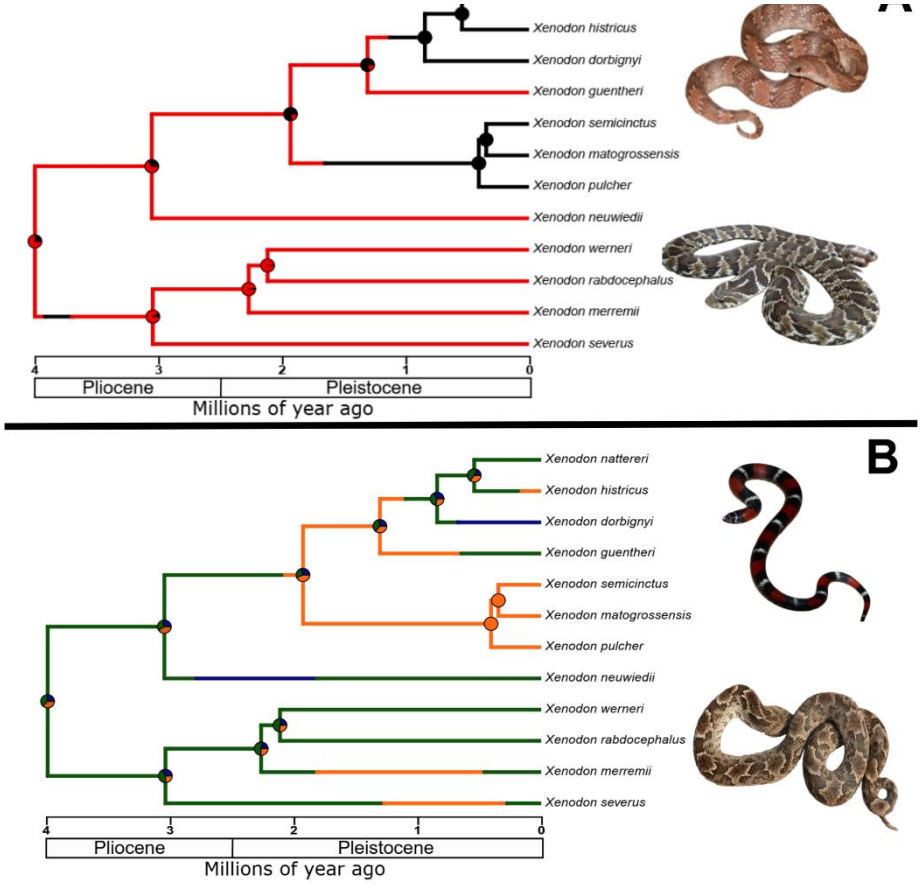


Table 3. Akaike information criterion of the three models of transition rates tested for rostral scale and mimicry. Bold values represent the best models for each trait.

				Rostral scale	
Model	AICc	ΔAICc	wAICc	Log Likelihood (-lnL)	Parameters
ER	**14.18**	0	0.38	-5.89	1
SYM	-	-	-	-	-
ARD	15.31	1.31	0.22	-4.99	2
				Mimicry	
ER	**24.70**	0	0.95	-11.15	1
SYM	30.68	5.98	0.04	-10.84	3
ARD	46.89	22.19	0	-9.04	6

8 DISCUSSION

Similarly to previous works (GRAZZIOTIN et al., 2012; ZAHER et al., 2009) we found two well-supported clades, along with the remaining two subclades (Fig. 2). Some differences can be found in the position of *X. pulcher* as the sister species of *X. semicinctus* and *X. matogrossensis*. Additionally, differences can be observed in the position of *X. guentheri*, *X. werneri*, and *X. rabdocephalus* (Fig. 2).

We found that rostral scale evolved in closely relation within the phylogeny of the genus (strong phylogenetic signal), contrary the weak or lack of phylogenetic signal shows that mimicry have evolved independently from the phylogeny. The reconstruction and selection of the ER model showed the same rate of transitions between both traits, rostral scale, and mimicry. The evolution of rostral scale and mimicry is unlikely to have been gradual, probably the rapid transition between the clades might explain these transitions, also those transitions have been occurring too fast. The differences between ER and ARD models (AICc) for the rostral scale are small, either of the models could be, however ΔAICc and

wAICc (Table 3) support ER model for rostral scale evolution. In ARD models every type of transition can have different rates.

Mimics is widely present in almost all genera of Colubridae and Dipsadidae, especially *Micrurus* mimics (RABOSKY et al., 2016), however only a few genera have the entire species of their genus with mimics. For example, the Elapomorphini tribe (*Apostolepis*, *Phalotris*, *Coronelaps*, *Elapomorphus*) have species that mimic species of *Micrurus* (CEI, 1993; DA SILVA, 2016). Nonetheless, all members of *Xenodon* have mimics with *Bothrops* or *Micrurus*, which made them an interesting subject of study, that's why we only analyzed the evolution of mimics between the genera, and not included other genera of snakes.

Our results suggest that species in the genus *Xenodon* evolved from an ancestor with a rounded rostral scale with a *Bothrops* color pattern. The evolution of the rostral scale and mimicry in the genus began around four million years ago, in the Plio-Pleistocene, a period with transitions from humid and warmer forest-like habitats to cooler and drier savannah-like habitats (HOOGHIEMSTRA; CLEEF, 1995). This period was characterized by a marked and pronounced dry season, associated with drastic lowering of global temperatures, and increasing aridity, resulting in the replacement of lowland rainforests by savannah woodlands (JACOBS, 2004; PLANA, 2004).

Those events related to extreme environmental heterogeneity have been reported in a range of Neotropical fauna, hypothesized to have driven the differentiation of the open biome communities from adjacent rainforests and from each other and consequently the biota of South America (GRAU et al., 2005; BRYSON, GARCÍA-VÁZQUEZ, & RIDDLE, 2011; WERNECK, 2011; DAZA et al., 2012; SOBRAL-SOUZA & LIMA-RIBEIRO, 2017). Therefore, the habitats where the species of *Xenodon* occur were directly impacted by these events. These changes in climate and habitats probably have shaped the diversification of the species, and the evolution of the keeled rostral scale of the genus, probably as an adaptation

to dry and open environments. The maintain of the rounded rostral scale in *X. guentheri* is probably due to evolutionary convergence, there was no need to change to a keeled rostral scale, due to its habits, the species has more terrestrial habits than semi-fossorial ones.

Overall, species with a keeled rostral scale exhibit a distribution associated to open areas, like Cerrado, Chaco, Pantanal, and Pampas (Fig. S4). On the other hand, species without keeled rostral scales, in general are associated to forested areas, such as Amazon Forest and the Atlantic Forest, except for *X. merremii* with a wide distribution associated with open and forested habitats (Fig. S1-3). The distribution of semi-fossorial species (those *Xenodon* species with a keeled rostral scale) in open areas is often related to habitat characteristics, such as temperature and precipitation (KINLAW, 1999; OLIVEIRA; SCHEFFERS, 2019; WU et al., 2015), and those species have adaptations to live underground, making them habitat specialist (GREENVILLE; DICKMAN, 2009; KINLAW, 1999). These adaptations, however, constrain many aspects of their ecology, bringing along challenges for moving underground over long distances (MARTÍN et al., 2021; PAPENFUSS, 1982; WEBB et al., 2000), something to be expected due to the energetic costs of burrowing (Dial, Gatten, & Kamel, 1987). In the case of *Micrurus*, there is a strong relation with the co-occurrence of coral snakes and their mimics (FRANÇA; BRAZ; ARAÚJO, 2017; RABOSKY et al., 2016; SAVAGE; SLOWINSKI, 1992), especially with triadal coral snake species, restricted to South America (DA SILVA, 2016). The presence of a keeled rostral scale in the genus *Xenodon* is related to semi-fossorial habits and has evolved as a strategy for adaptations to the new environment, with a positive correlation between diversification and colonization of new habitats.

Mimicry (coloration) has evolved independently in colubrid (RABOSKY et al., 2016), as an important defense system to avoid predation (BRODIE; BRODIE JR., 2004; SAVAGE; SLOWINSKI, 1992). This represents an important driver in the evolution of coral

snakes' mimicry for *Xenodon* species, especially with those of the *Micrurus frontalis* group, which are widely distributed in the center and southern South America (DA SILVA & SITES, 1999; DI-BERNARDO, BORGES-MARTINS, & DA SILVA, 2007). Species of the *Micrurus frontalis* group occur in sympatry with *Xenodon* species that mimic coral snakes. In the case of *X. pulcher*, *X. semicinctus* and *X. matogrossensis*, they inhabit in sympatry with *M. pyrrhocryptus* and in some regions with *M. frontalis* and *M. baliocoryphus* (Nogueira *et al*., 2019), while *X. dorbignyi* and *X. histricus* occur in sympatry with *M. altirostris*, *M. baliocoryphus* and *M. frontalis* (NOGUEIRA et al., 2019).

Regarding *Bothrops* mimicry, the same concepts apply, once there is a relationship between the presence of *Bothrops* with species that mimic them (BRODIE; BRODIE JR., 2004). Additionally, this mimicry is accompanied not only by coloration, but also by similar behaviors (BRODIE; BRODIE JR., 2004). The *Xenodon* species with *Bothrops* mimicry are more widespread, and the distribution of these species could be related to the potential model they imitate. *Xenodon rabdocephalus*, the only species of the genus with a distribution reaching Central America, apparently imitates *B. asper*, the only species of *Bothrops* in Central America (HAMDAN et al., 2020). *Bothrops asper* belongs to the *B. atrox* clade that began its diversification around 3.02–3.32 Mya (HAMDAN et al., 2020). Recent studies suggested that the first lineage within the *B. atrox* group to diversify was *B. asper* within the formation of the Panamanian bridge (HAMDAN et al., 2020). This information supports our results that the ancestor of *Xenodon* was a species with *Bothrops* mimicry, following the distribution of the *Bothrops* and *Xenodon* in northern South America. Another interesting example of mimicry that corroborates our findings is the case of *X. werneri*. This species is restricted to northern Amazonia (Nogueira *et al*. 2019), which perfectly imitates *B. bilineatus* (Fig. 1G), a *Bothrops* species with a disjointed distribution in Amazonian and the Atlantic Forest (Nogueira *et al*., 2019). The clade which *B. bilineatus* belongs to (*B. taeniatus* clade)

diverged during the Pliocene around 2–5 Mya in the Amazonian forest (HAMDAN et al., 2020), which could be one of the reasons for the evolution of mimicry in *X. werneri*, since mimicry coloration could evolved as a defense system to avoid predation, and is often associated with the presence of the model they are imitating, in this case species of *Bothrops,* both are one's of the driver in the evolution of *Bothrops* (BRODIE; BRODIE JR., 2004; SAVAGE; SLOWINSKI, 1992).

This mimicry of *Bothrops* and *Micrurus* is accompanied by behavioral postures, such as the triangulation of the head, tail rattling, hide the head, tail display, dorsoventral body compression, coil and s-coil body (BRODIE; BRODIE JR., 2004; CACCIALI, 2010; CEI, 1993; SAZIMA; ABE, 1991), evolving independently as a defense system to avoid predation (BRODIE; BRODIE JR., 2004). All these components together are important strategies for survival, because predators react to any signals associated with venomous snakes, whether these are coloration patterns or behavioral actions, relating to congenial responses (BRODIE; BRODIE JR., 2004; FRANÇA; BRAZ; ARAÚJO, 2017). Finally, evolution of venomous snakes can contribute to diversity within groups of snakes (e.g. families, genera) (FRANÇA; BRAZ; ARAÚJO, 2017; GREENE; MCDIARMID, 2005; RABOSKY et al., 2016), and mimicry as other strong ecological selections contribute to the speciation and radiation of the diversity of snakes (BRODIE; BRODIE JR., 2004).

With Batesian mimicry, and semi-fossorial habits with a preference for open areas, the rostral scale was modified as a shovel for burrowing. On the other hand, in species with terrestrial habits, their rostral scale remained rounded, probably due to the association for forested habitats (CABRAL et al., 2020; CEI, 1993; MARTINS; OLIVEIRA, 1998). In conclusion, the evolution of the rostral scale in *Xenodon* may be related to abiotic factors, as an adaptation for open and forested habitats, and mimicry are related to the presence of

venomous species like *Bothrops* or *Micrurus*, which through imitating them serve as a defensive strategy.

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APPENDIX A

Supporting information

Figure S1. Distribution of *Xenodon* with a rounded rostral scale in South America and their relations with the Ecoregions, adapted from (DINERSTEIN et al., 2017). White cross *X. severus*, black cross *X. werneri* and black diamond *X. rabdocephalus*.

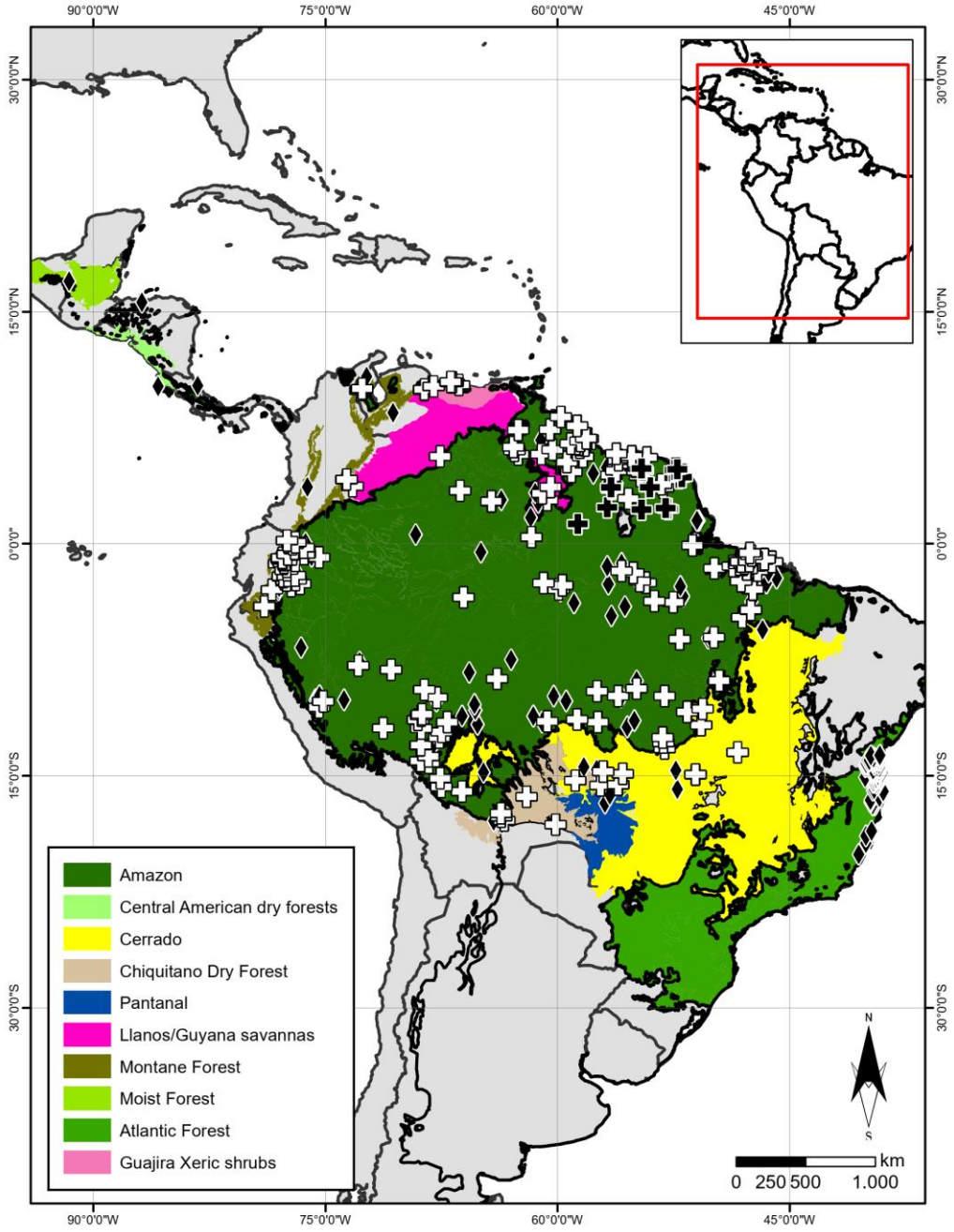


Figure S2. Distribution of *Xenodon* with a rounded rostral scale in South America and their relations with the Ecoregions, adapted from (DINERSTEIN et al., 2017). Black star *X. merremii*.

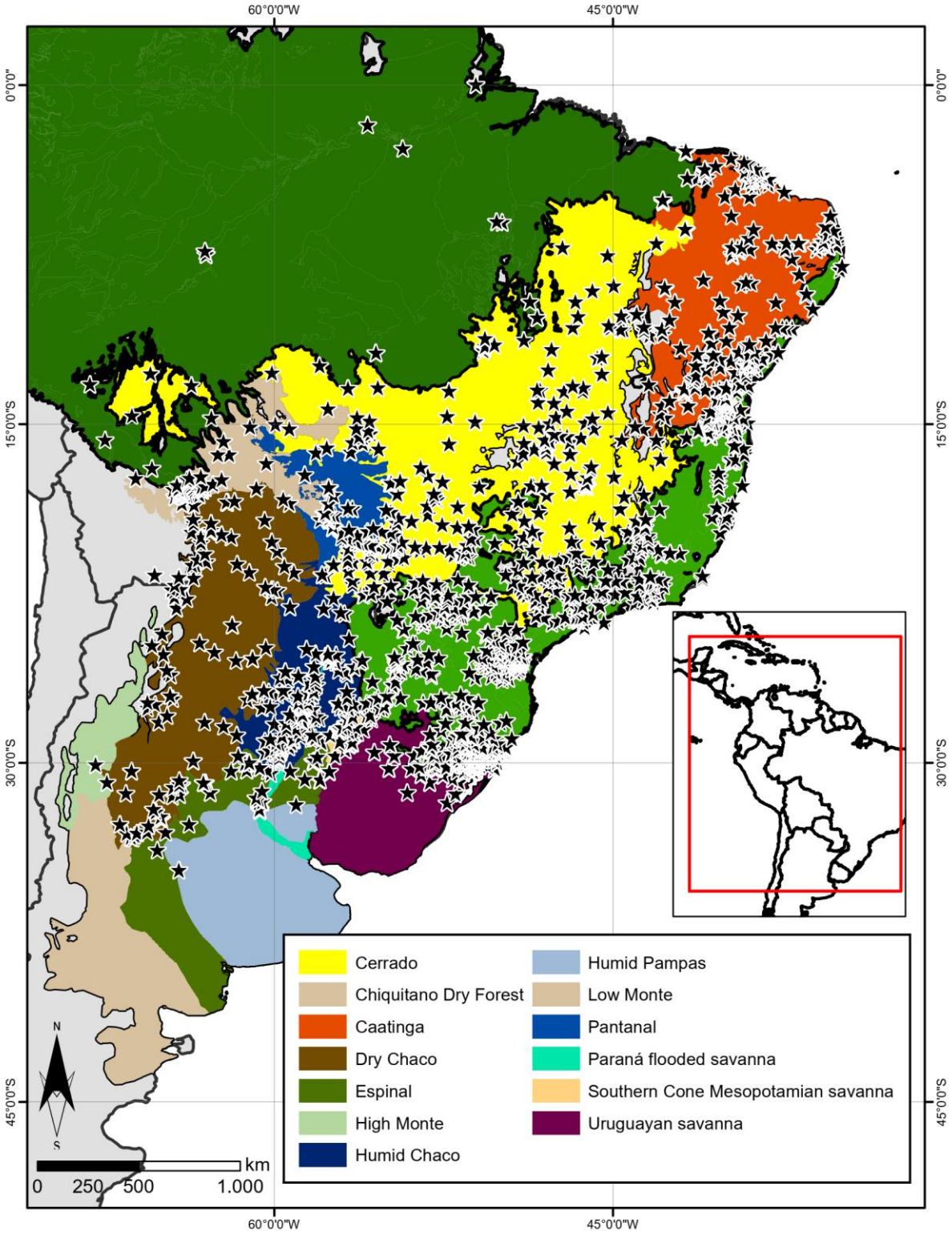


Figure S3. Distribution of *Xenodon* with a rounded rostral scale in South America and their relations with the Ecoregions, adapted from (DINERSTEIN et al., 2017). black triangle *X neuwiedii*, white circle *X. guentheri*.

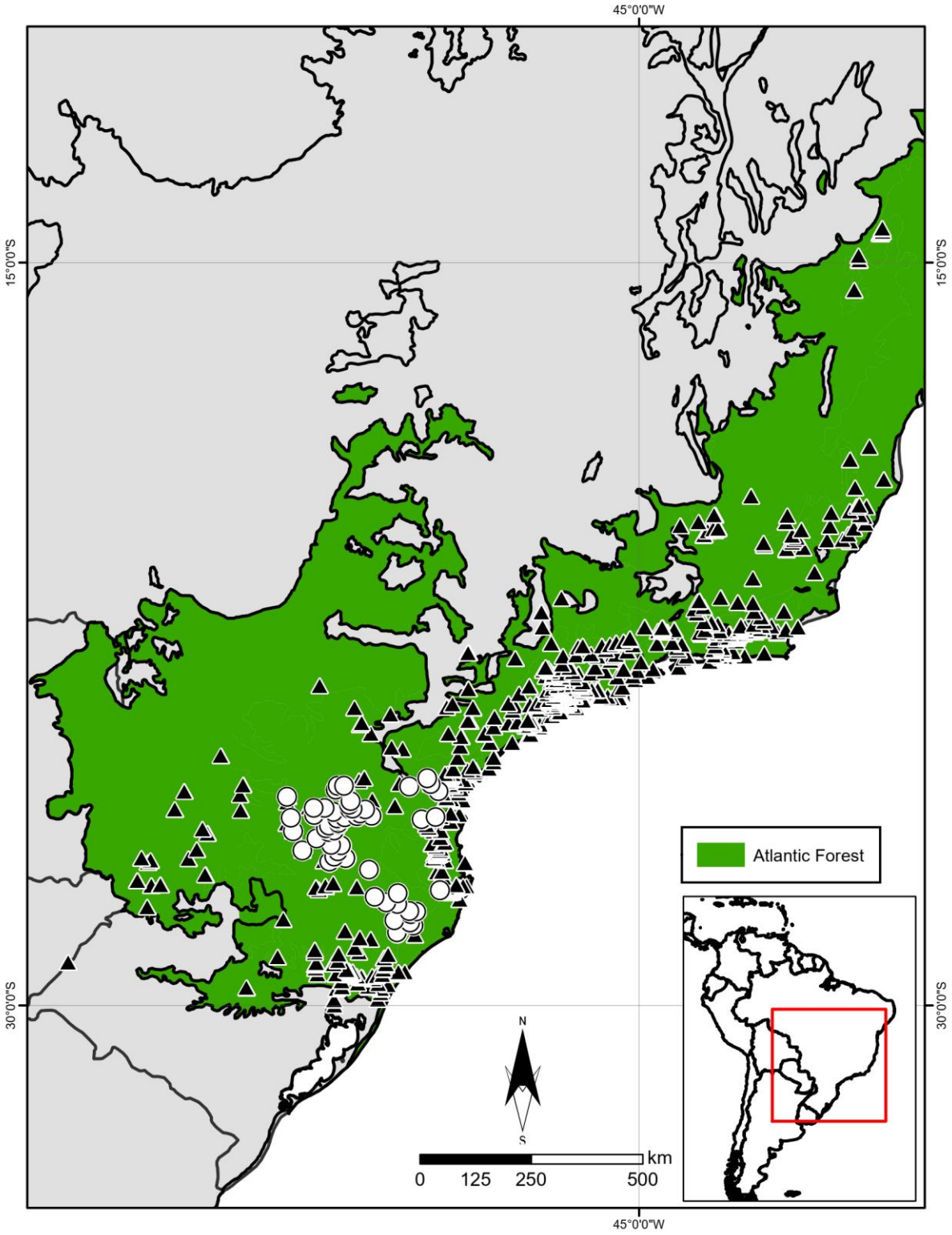
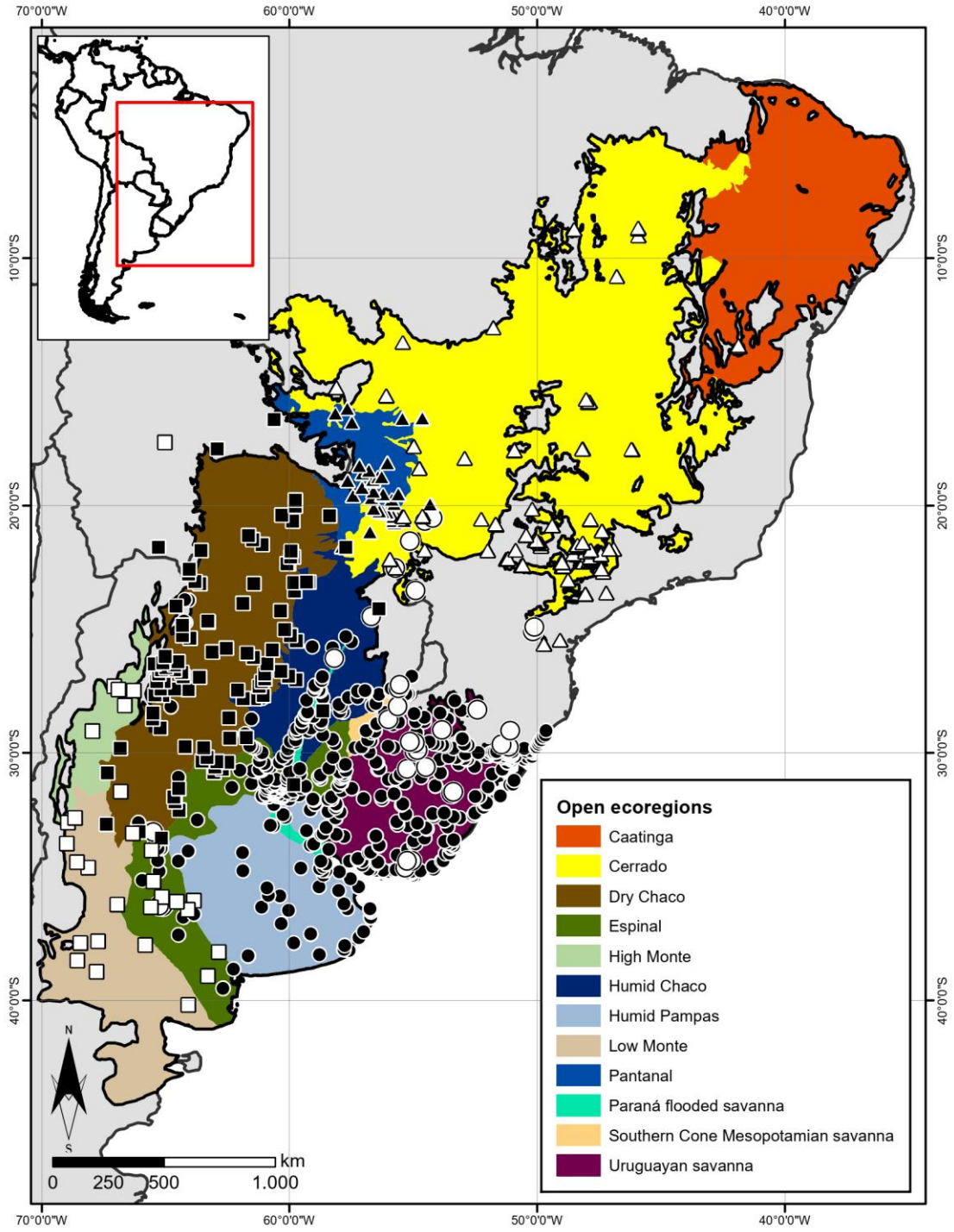


Figure S4. Distribution of *Xenodon* with keeled rostral scale in South America and his their relations with the Ecoregions, adapted from (DINERSTEIN et al., 2017). white triangle *X. nattereri*, white circle *X. histricus*, black triangle *X. matogrossensis*, black square *X. pulcher*, white square *X. semicinctus*, and black circle *X. dorbignyi*.



9 CHAPTER 2. FUNCTIONAL TRAITS AND PHYLOGENY EXPLAIN SNAKE DISTRIBUTION IN THE WORLD'S LARGEST DRY FOREST ECOREGION, THE GRAN CHACO

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10 ABSTRACT

Macroecological studies describe large-scale diversity patterns through analyses of species distribution patterns and allows us to elucidate how species differing in ecology, physical requirements, and life histories are distributed in a multidimensional space. Those patterns of distributions can be explained by vegetation, and climatic factors, and are determined by historical and current factors. The continuous accumulation of information on the distribution patterns of species is essential to understand the history and evolution of the biota. In this study, aimed to identify functional and evolutionary drivers that explain the geographic patterns of vertical stratification. We compiled morphological, ecological, and distribution data of 140 species of Chacoan snakes and constructed null models to map their geographic pattern. We used a range of environmental variables to assess which drivers are influencing these biogeographic patterns. Lastly, we used evolutionary data to build the first map of the phylogenetic regions of Chacoan snakes. We found a latitudinal pattern, with a marked verticality in the snake assemblies in the Chaco. Verticality and long-tailed species richness increased in areas with high stratify habitats and stable temperature. Fossoriality is driven mainly by soil conditions, especially soils with fewer sand particles and less stratify habitat. Phylogenetic regions in the Chaco showed a marked latitudinal pattern, like that observed in the geographic pattern of verticality. The distribution pattern of Chacoan snakes also reflects their evolutionary history, with a marked phylogenetic regionalization.

Keywords: Climate. Ecology. Habitat heterogeneity. Macroecology. Morphology. Phylogenetic region. Soil conditions. Species traits.

11 INTRODUCTION

Macroecological studies allow us to elucidate how species differing in ecology, physical requirements, and life histories are distributed in a multidimensional space (GOUVEIA et al., 2014a; MCGILL et al., 2006). To access the interaction between species assemblages and better describe the structure of species geographic ranges, macroecological studies usually consider landscapes features (e.g., environmental and climate variables), intra- and interspecific variation in functional traits (e.g., morphological measurements and ecological habits), and the interaction between species assemblages to describe the structure of species geographic ranges (GASTON; CHOWN; EVANS, 2008). These geographic ranges of species distribution are determined by historical and current factors, and changes in these patterns over time might result from environmental filtering, geographic distance, or natural barriers, and is reflected in the phylogenetic affinities of species (DARU et al., 2017; HORTAL; LOBO; JIMÉNEZ-VALVERDE, 2012).

Historical and current factors like forest structure variables along with climatic factors can help us to understand the differences in species richness and diversity spatial patterns in several groups of organisms (GATTI et al., 2017; ROLL; GEFFEN; YOM-TOV, 2015). For example, vertical stratification (i.e., the gradient formed by the vertical structuring of the habitat) can be used in different ways by different groups of species (Walther, 2002; Pereira et al., 2010). It provides opportunities for individuals of arboreal species to exploit a greater number of niches (i.e., verticality) compared to any strictly ground-dwelling species; these opportunities may result in morphological adaptations (GASTON; CHOWN; EVANS, 2008; HARRINGTON et al., 2018; SCHEFFERS et al., 2014). Additionally, soil conditions associated with changes in climatic factors also explain species richness and it is another important factor that helps predict

the diversity patterns in specific areas, as they are directly linked to microhabitat (FELDMAN; MEIRI, 2014; JACKSON et al., 2008; MOURA et al., 2016; SCHEFFERS et al., 2013, 2017). For instance, the body size of fossorial species decreases in areas with hottest temperature and low rainfall, making burrowing a critical ecological adaptation for survival in hot/dry areas (BURBRINK; MYERS, 2015; FELDMAN; MEIRI, 2014).

Thus, functional traits along with environmental variables could also explain the variation in species within communities across space, species adaptation to different environments and the trait-environment relationships to understand the processes that shape ecological communities (MCGILL et al., 2006; VIOLLE et al., 2014; WEIHER et al., 2011). For example, in tropical forested areas with medium temperature the diversity and richness arboreal species is higher when comparing with hottest areas (OLIVEIRA; SCHEFFERS, 2019; SCHEFFERS et al., 2013). This variation is followed by morphological adaptations, in which arboreal snakes show laterally compressed and slender bodies, long tails, and evident eyes (GUYER; DONNELLY, 1990; PIZZATTO; ALMEIDA-SANTOS; SHINE, 2007); in contrast, fossorial snakes, are known by having smaller bodies, a relatively small tail, eyes not evident, and modification in body scales for burrowing (CYRIAC; KODANDARAMAIAH, 2018; KINLAW, 1999; NAVAS et al., 2004).

The knowledge of diversity patterns and its relationship with evolutionary processes in large South American open areas are scarce, which is until now mainly focused on tropical forests (BRUSQUETTI et al., 2018a; WERNECK, 2011). This is the case of the Gran Chaco (hereafter Chaco), that is neglected in biodiversity research and harbors only few studies focusing mainly on conservation (NORI et al., 2016; SEMPER-PASCUAL et al., 2018). It is worth mentioning that in recent decades, the Chaco has been suffering high deforestation rates

(HANSEN et al., 2013) and landscape degradation, making it a priority area for conservation (DE LA SANCHA et al., 2021; FRATE et al., 2015; KUEMMERLE et al., 2017b). Therefore, understanding the ecological and evolutionary processes that have shaped the diversity pattern of species distribution in this region becomes increasingly relevant.

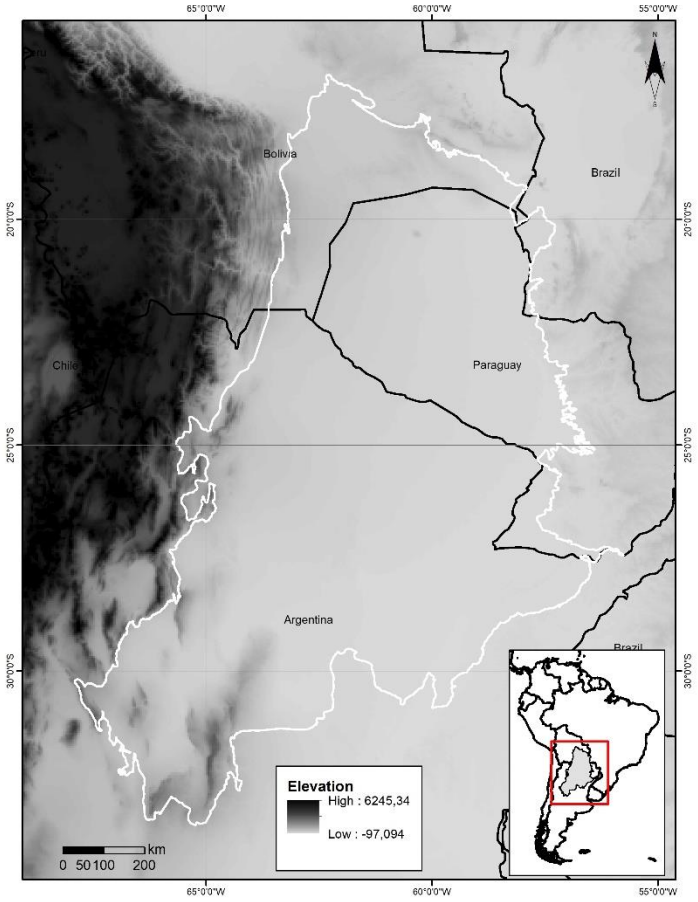
In this paper, we assess what drives geographic patterns of vertical stratification of snakes in the Chaco. To address this, we (i) describe the geographic patterns of vertical stratification of snake species; (ii) determine what and how environmental drivers explain these patterns; and (iii) assess whether these patterns can also be recovered by the phylogenetic relationships of snake species distributed in the Chaco. We tested the three following predictions: (1) As environments become more vertically stratified, arboreality becomes a beneficial attribute allowed by morphological specializations for perching, nesting, and foraging on branches of trees (HILDEBRAND; GOSLOW, 2001; GOMES et al., 2009); we expected more arboreality and species richness in areas were habitats become more vertical stratify. (2) Temperature act as a selective force on the body size of ecologically different snake species, resulting in miniaturization and morphological adaptations for burrowing in warmer areas (OLORI; BELL, 2012), we expected that richness of fossorial species would be higher in warmer and drier areas with lower proportion of sand particles. (3) We also expect the geographic distribution pattern to be reflected in the phylogenetic relations of Chacoan snake species. This geographic pattern might be favored by the climatic and environmental characteristics of the Chaco, which would act historically as a filter for species dispersion (DARU et al., 2017).

12 MATERIAL AND METHODS

12.1 Study Area

The Chaco is the largest continuous tropical dry forest in the world (Fig. 4) (GRAU; GASPARRI; AIDE, 2008), formed from the Andean uplift, marine introgressions, and several alluvial systems (GREGORY-WODZICKI, 2000; HERNÁNDEZ et al., 2005). The most important characteristics of the Chaco are its climatic seasonality and geomorphology; the latter consists of an extensive sedimentary alluvial plain with soils derived from the accumulation of Quaternary sediments (PENNINGTON; PRADO; PENDRY, 2000; PRADO, 1993). The Chaco is composed of xerophytic vegetation formed by a mosaic of grasslands, savannas, open woodlands, and thorn forests (PRADO, 1993; WILLIG et al., 2000). In general, the Chaco shows little variation in elevation; the only topographic relief (1000–1200 m a.s.l.) occurs at the western border, between Argentina and Bolivia (PRADO, 1993) (Fig. 1). Consequently, there appear to be no geographic barriers (e.g., large rivers or mountain ranges) that hinder the dispersal of organisms across the Chaco (BUCHER, 1982).

Figure 1 Geographical location of the Gran Chaco in South America (white polygon), with the elevation range (in meters) within the area. Notice the flatness topographic with the scarcity of elevation areas.



12.2 Data source and preparation

We first downloaded distribution data of snakes with confirmed occurrence in the Chaco from the Global Assessment of Reptile Distributions (GARD; http://www.gardinitiative.org/data.html). We then reviewed the literature and assembled a database containing ecological and morphological data for all species. Ecological data included information on habit (i.e., aquatic, arboreal, semiarboreal, fossorial, semifossorial, and terrestrial). Morphological data included information on total length (TT), tail length (TL),

snout-vent length (SVL), TL to TT ratio, body mass, and eye diameter (Table S1). Arboreal snake species tend to have longer tails, with slender bodies, and bigger eyes associated with verticality specialization (ALENCAR et al., 2017; HARRINGTON et al., 2018; VITT; CALDWELL, 2009); on the other hand, fossorial snake species tend to have smaller bodies, relatively small tail and reduction of eyes, modification of body scale structures (e.g., modified rostral scale in *Xenodon, Phimophis, Rena*) (CYRIAC; KODANDARAMAIAH, 2018; KINLAW, 1999; NAVAS et al., 2004; VITT; CALDWELL, 2009).

We recorded 140 snake species from eight families (Boidae, Colubridae, Elapidae, Anomalepididae, Typhlopidae, Leptotyphlopidae, Aniliidae, and Viperidae) in the Chaco region. These species were distributed along 458 grid cells covering the entire Chaco. We provide the first and most extensive open dataset on ecological and morphological traits of all snake species recorded in the Chaco (Table S1). Of the 140 snake species from the Chaco, 70 are terrestrial, 22 fossorial, 21 semifossorial, 17 arboreal, and 10 semiarboreal. The total length of the Chacoan snakes ranged from 103 to 4,000 mm, and the tail length ranged from two to 900 mm. In some cases, the tail represented almost 50% of the snakes' total length.

We used a range of environmental variables that potentially could reflect mechanisms that selects for species vertical niche: 19 climatic variables from WorldClim (at 2.5 min spatial resolution; (FICK; HIJMANS, 2017), three habitat productivity variables (ABATZOGLOU et al., 2018; TUCKER et al., 2005), three habitat heterogeneity variables (HANSEN et al., 2013; TUANMU; JETZ, 2015), two soil variables (HENGL et al., 2017), and one topographic variable (GRAHAM et al., 2014) (for details see Table S2). All environmental variables were tested for multicollinearity using the variance inflation factor (VIF) (Table S3), we also perform a Pearson correlation test, and no correlation was found between the variables cor >0.8 (Table S4). We

excluded all variables with VIF values >10 (which indicate strong multicollinearity) keeping only those with VIFs were < 10 (Zuur, Ieno, & Elphick, 2010). After multicollinearity tested, the final set of variables included annual mean temperature, precipitation seasonality, annual actual evapotranspiration (AET), net primary productivity (NPP), normalized difference vegetation index (NDVI), evenness and homogeneity of the Enhaced Vegetation Index (EVI), tree cover (TC), volumetric percentage of coarse fragments (FRAG), and proportion of sand particles in the soil (SAND).

We created a presence-absence matrix using the snake distribution data and a 55 × 55 km grid cell superimposed on the Chaco region. As we were interested in the Chaco region, we chose a grid size that reflected macroecological patterns (HURLBERT; JETZ, 2007). We discarded species-poor grid cells (those with less than five species), as they could affect the performance of the analyses (MOURA et al., 2018; OLIVEIRA; SCHEFFERS, 2019).

12.3 Analyses

12.3.1 Analyses of vertical stratification in snakes

To generate metrics of vertical stratification for each snake species, we performed a principal component analysis (PCA) using species-specific body mass, eye diameter, verticality, and tail proportion (TL/TT) (Fig. S1). We then extracted the score that each species received on the first PCA axis (species-specific mass, eye diameter, verticality, and tail proportion), which best explained our data. We used these scores as a metric; positive values indicated greater arboreality, and negative values indicated greater fossoriality. We used three verticality metrics as response variables: vertical niche or habitat (hereafter verticality), tail proportion, and PCA scores (fossoriality metrics) since it reflects the level of specialization of species, and therefore to their functional traits (ALENCAR et al., 2017; HARRINGTON et al., 2018; KINLAW, 1999;

OLIVEIRA; SCHEFFERS, 2019; WEBB et al., 2000), also the pattern of fossoriality is reflected in the first axis of the PCA, without overlapping and gradually.

To assess the geographical richness pattern of verticality, tail proportion and fossoriality we first constructed null models to control the effect of species richness on verticality metrics and maintain internal structure of species richness while randomizing the metrics (SWENSON, 2014). We adopted a weighted sampling scheme to control the influence widespread species, as they can overestimate the results compared to species with restricted distributions (OLIVEIRA; SCHEFFERS, 2019; SAFI et al., 2013). We repeated this procedure 1,000 times to generate a null distribution of verticality, tail proportion, and fossoriality and calculated the standardized effect size (SES) between the observed values and null values using the formula: SES = observed values - mean(null)/Standard Deviation(null). Hereafter, we refer to the SES values as verticality, tail proportion, or fossoriality. For verticality, positive values indicate assemblies containing more arboreal species, whereas negative values indicate assemblies containing more fossorial species. For tail proportion positive values indicate higher richness of snakes with longer tails and for the fossoriality metrics, positive values indicate higher richness of arboreality and negative values higher richness of fossoriality.

12.3.2 Environmental drivers of vertical stratification

To assess the environmental drivers that explain the geographical richness pattern of verticality, tail proportion and fossoriality we fitted spatial autoregressive (SAR) models using all possible combinations of predictor variables and applied a model averaging approach (BURNHAM; ANDERSON, 2007; MOURA et al., 2018). Spatial autoregressive models incorporate spatial autocorrelation with weighted matrices that specify the interaction strength between neighboring sites (DORMANN et al., 2007). We tested our three metrics in a multimodel inference

framework to investigate the contribution of our predictor variables. We constructed connectivity matrices for each metric (verticality, tail proportion, and fossoriality), defined by the distance at which Moran's I was strongest. Moran's I analyzes the spatial autocorrelation variations between neighboring sites, measuring whether there is a spatial autocorrelation between variables (MORAN, 1950).

We assessed the effects of multiple weighting functions when defining spatial weight matrices and selected the one that best accommodated the spatial structure present in the variables (OLIVEIRA; SCHEFFERS, 2019). Residuals from the models were tested for significant autocorrelation using Moran's I (Fig. S2), but no spatial autocorrelation was found in the spatial structures and metrics. We ranked the support of each model using Akaike's information criterion corrected (AICc) the weighted average model (wAICc) and used the standardized coefficient across all SAR models to compare with our explanatory variables (BURNHAM; ANDERSON, 2007)To estimate the variance explained by the averaged models, we calculated the pseudo-R^2 as the squared Pearson correlation coefficient between the weighted fitted values and the observed values (KISSLING; CARL, 2008). Higher values of pseudo-R^2 indicate better model fit. Statistical analysis was performed in R environment version 4.0.4 (R CORE TEAM, 2019) using *spdep* (BIVAND, 2020), *adespatial* (DRAY et al., 2020), and *MuMIn* (BARTÓN, 2020) packages.

Arboreal snakes are generally larger than non-arboreal snakes, and there is evidence that the body size of arboreal snakes is more constrained than in non-arboreal ones (HARRINGTON et al., 2018). Thus, to test the robustness of our results, we repeated the analysis of environmental drivers after removing genera containing mainly arboreal species (*Chironius*, *Corallus*, *Dipsas*, *Imantodes*, *Leptodeira*, *Leptophis*, *Siphlophis*, and *Spillotes*). We adopted this

approach because including these mainly arboreal genera could inflate the results in sites with higher arboreal diversity.

12.3.3 Phylogenetic regionalization

To explore whether the patterns of vertical stratification of snakes (verticality and fossoriality) have an evolutionary component, we performed a phylogenetic regionalization analysis using phylogenetic relationships and distribution data of Chacoan snake species. We used the most comprehensive phylogeny of squamates to date (TONINI et al., 2016), which includes all snake species recorded in the Chaco. We pruned the phylogeny to precisely match all snake species recorded in the Chaco (Fig. S8) using the package *picante* (KEMBEL et al., 2010a) in the R software version 4.0.4 (R CORE TEAM, 2019). Phylogenetic regionalization (phyloregion) procedures were performed using *phyloregion* package (DARU; KARUNARATHNE; SCHLIEP, 2020) in R environment version 4.0.4 (R CORE TEAM, 2019). This package uses a community matrix in a sparse format with phylogenetic information. The 'optimal phyloregion' function allows the user to find the optimal number of phylogenetic regions, cluster, and plot the results. To perform the phyloregion analysis, we used the presence-absence matrix and the snake phylogeny (see Data source and Preparation in Material and Methods).

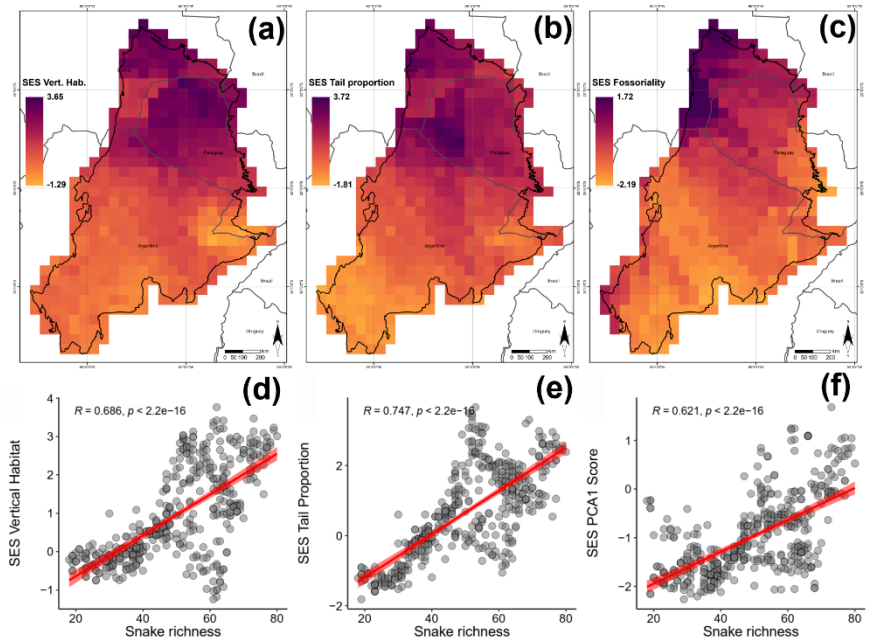
13 RESULTS

13.1 Patterns of vertical stratification of snakes

We found a latitudinal pattern of vertical stratification of snakes, with arboreality increasing towards the north and fossoriality becoming more restricted in the southern Chaco (Fig. 2a-c). Additionally, a small patch in the south-west of the Chaco can be noticed with presence of terrestrial, and arboreal species (Fig. 2c). We also found a marked pattern of verticality in the snake distribution of assemblages in the Chaco, increasing at north and decreasing southern.

Moreover, we found a positive correlation between species richness and verticality, tail proportion, and fossoriality (Fig. 2d-f).

Figure 2. Geographical pattern and correlation of species richness with metrics used in the analysis: (a) geographical pattern of verticality; (b) geographical pattern of tail proportion; (c) geographical pattern of fossoriality; (d) correlation between species richness and verticality; (e) correlation with tail proportion; and (f) correlation with fossoriality.

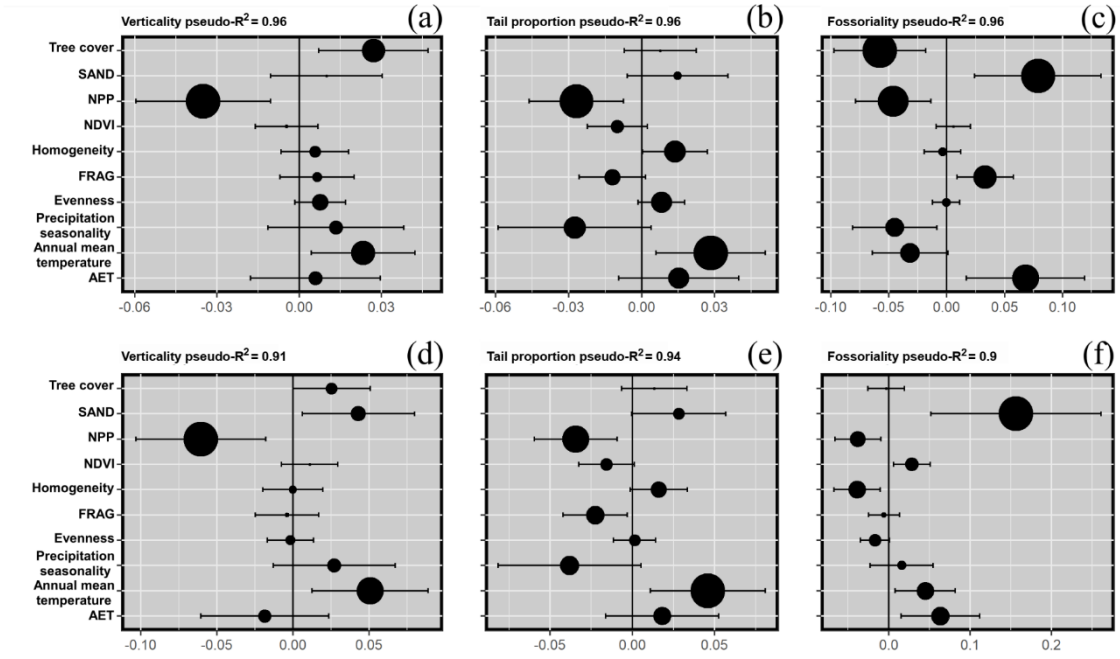


13.2 Environmental drivers of vertical stratification

The averaged models explained more than 90% of the variation in verticality, tail proportion, and fossoriality, as indicated by the pseudo-R^2 (Fig. 3a-c). Verticality was negatively correlated with NPP (r=-0.453, p<2.2e-16), but positively correlated with TC (r=0.619, p<2.2e-16) and annual mean temperature (r=0.794, p<2.2e-16) (Fig. S3). The NPP, TC, and annual mean temperature showed the strongest effect on the model (Fig. 3a), it was followed by homogeneity, evenness, and AET. Verticality and species richness increase in areas in the northern of the Chaco, and decrease gradually to the south, indicating that areas with greater vegetation structure have more

species that are more vertically stratified, when the habitat become less heterogeneous richness of arboreal species and richness decrease (Fig. 2a-c). For tail proportion, the variables with the strongest effect on the model were NPP, annual mean temperature, and precipitation seasonality (Fig. 3b). Tail proportion was positively correlated with annual mean temperature ($r=0.816$, $p<2.2e-16$) and homogeneity ($r=0.287$, $p<5.02e-10$), but negatively correlated with NPP ($r=-0.24$, $p<2.42e-07$), actual evapotranspiration ($r=-0.136$, $p<0.00384$), precipitation seasonality ($r=-0.0611$, $p<0.194$), evenness of vegetation ($p=-0.151$, $p<0.00127$), and FRAG ($r=-0.501$, $p<2.2e-16$) (Fig. S3). Long-tailed species are associated to habitats with high vertical stratification and stable climates, this is in somehow related to arboreality since arboreal species tend to have longer tails (Fig. 2b and Fig. S3). The most important variables affecting fossoriality were SAND, TC, and NPP (Fig. 3c). Fossoriality was positively correlated with SAND ($r=0.315$, $p<5.03e-12$), TC ($r=0.487$, $p<2.2e-16$), annual mean temperature ($p=0.658$, $p<2.2e-16$), and precipitation seasonality ($r=0.107$, $p<0.0229$) but negatively correlated with NPP ($r=-0.264$, $p<1.24e-08$), FRAG ($r=-0.267$, $p<6.85e-09$), and actual evapotranspiration ($r=-0.297$, $r<1.16e-10$) (Fig. S3). Fossoriality was frequent in the southern part of the Chaco where the habitats is characterized by soils with proportionally fewer sand particles, with less stratify habitats (Fig. 2c).

Figure 3. Model averaging showing the influence of each predictor variables explaining verticality habitat, tail proportion and fossoriality. Results derived from the SAR models, presenting all possible combinations of variables: (a-c) the entire dataset results are presented; (e-f) results from the sensitivity analysis. The size of circles represents the relative importance of each variable, plotted against the average standardized coefficients, and pseudo-R^2.



The analysis excluding the mostly arboreal genera (*Chironius*, *Corallus*, *Dipsas*, *Imantodes*, *Leptodeira*, *Leptophis*, *Siphlophis*, and *Spillotes*) showed the same general pattern, with slight differences (Fig. 3d-f and Fig. S4-S5). For verticality, the variables with the strongest effect on the model were NPP and annual mean temperature (Fig. 3d). For tail proportion, the variables with the strongest effect were NPP, annual mean temperature, and precipitation seasonality (Fig. 3e). However, for fossoriality, the SAND was the most important explanatory variable (Fig. 3f). This result was expected due to the biology of fossorial species, which are adapted to underground life. We also observed that tree cover had almost no effect on fossoriality, which complements the previous result (Fig. 3f). Fossorial species spend most of the

time buried and exhibit morphological adaptations for living underground, such as relatively small bodies and short tails (Fig. 2e, Table S1).

13.3 Phylogenetic regionalization

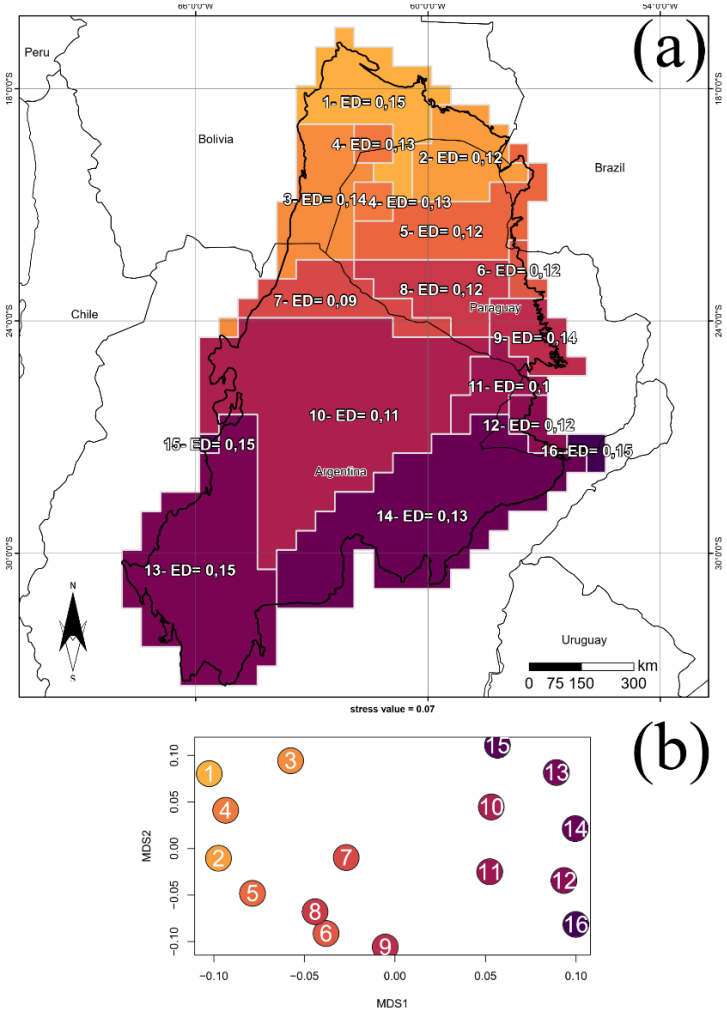
We recovered 16 phylogenetic regions in the Chaco, with a marked north-south pattern (Fig. 4a), similar to that observed for the geographic pattern of verticality (Fig. 2). Lineages of arboreal species is higher in northern part of the Chaco where habitat heterogeneity is higher and stratify. These arboreal lineages of species decrease as we move toward south, were lineage of fossoriality become more common, and the habitat heterogeneity decrease becoming less stratify. The north of the Chaco there are more clades associated to Colubrinae than in the south, especially the arboreal genus *Chironius*. On the other hand, in the south, lineages/clades of fossorial species (e.g., Scolecophidea, Elapomophini) become more common. Phylogenetic regions to the north are evolutionarily distinct from those to the south Fig 4a. Clades of mostly terrestrial species remain similar across phylogenetic regions.

Phylogenetic region 1, 13, 15, 16 have the highest evolutionary distinctness ED=0.15, follow by phylogenetic region 3 and 9 with ED=0.14 (Fig. 4a). These phylogenetic regions are in the north and south part of the Chaco, phylogenetic region with lowest ED is located mostly at the center of our study area (Fig. 4a). From these 16 regions, three main groups were identified, showing that different regions differ strongly in evolutionary distinctiveness (Fig. 4b and Fig. S6-7). These regions also showed a similar relationship between the evolution and environmental influence on the Chacoan snakes, shaping their actual distribution pattern. The NMDS ordination show this same patter, suggesting important division within the snake-fauna along the north–south axis of southern.

14 DISCUSSION

Our results recovered an evident geographic pattern of snake distribution related to verticality and fossoriality, in which the species richness of arboreal snakes is restricted to the northern Chaco where vertical stratify habitat and heterogeneity increases; while, in the opposite way, species richness of fossorial snakes is more common in the southern Chaco where habitat become less stratify and more heterogeneous (see Fig. 2a-c, f). The northern Chaco is strongly influenced by forested areas with more vertically stratify habitats, such as the Amazon, Chiquitania Dry Forest, and Andean Forest (SPICHIGER et al., 1995). In contrast, the southern Chaco is more influenced by open areas, such as the Pampas and Patagonia (NORI; GÓMEZ; LEYNAUD, 2011). This pattern corroborates that previously recorded for amphibians, in which fossorial species are more frequent in deserts and xeric environments characterized by dry climate, with high temperatures and low precipitation (BOLOCHIO et al., 2020; OLIVEIRA; SCHEFFERS, 2019).

Figure 4. Phylogenetic regionalization of snakes of the Gran Chaco: (a) all 16 phylogenetic regions showing the evolutionary affinities with evolutionary distinctness (ED) values of snake's assemblages; and (b) ordination of phylogenetic region in non-me tric multidimensional scaling (NMDS) space shows that different phylogenetic region differs in the evolutionary uniqueness, three groups can be noticed, following the ordination: phylogenetic region 1 to 5, 6 to 9 and 10 to 16.



As we predicted, verticality increases where areas are more vertically stratify with more habitat heterogeneity, and is driven by climatic factors and habitat conditions, especially tree cover and annual mean temperature (Fig. 3a). Vegetation structure and forest stratifications allow the arrangement of more niches and resources, enabling the co-occurrence of several arboreal species and increasing canopy richness (GOUVEIA et al., 2014b; SCHEFFERS et al., 2013). Arboreal species tend to have longer tails, a morphological adaptation to arboreality (HARRINGTON et al., 2018). Long tails are positively correlated with arboreality but negatively correlated with fossoriality, i.e., fossorial species tend to have smaller bodies and shorter tails (CYRIAC; KODANDARAMAIAH, 2018; KINLAW, 1999; NAVAS et al., 2004; WU et al., 2015). Like our results for snakes, vertically stratified habitats are known to play an important role in determining patterns of species richness and abundance in many other organisms worldwide (GOUVEIA et al., 2014a; STEIN; GERSTNER; KREFT, 2014). Climbing trees allows access to different microhabitats and resources, and this habit use is facilitated by morphological (functional) adaptations for survival and locomotion in snakes (HARRINGTON et al., 2018; SCHEFFERS et al., 2013, 2017).

In detail, our results also suggest that fossoriality in Chacoan snakes is mainly driven by soil conditions (Fig. 3d-f), corroborating our second prediction. The number of fossorial snake species tends to increase in areas with lower proportions of sand particles and warmer areas (Fig. 3f). In the Chaco, fossorial species tend to be smaller and have shorter tails than surface dwellers, possibly for burrowing and living underground, sheltering from extreme conditions, protecting, and feeding. This region, also known as the South American Pole Heat, has the highest absolute temperature in South America (maximum of 48.9 °C) and scarce precipitation (PRADO, 1993; PROHASKA, 1959). These characteristics result in a marked dry and rainy

season, a soil composed of fine sediments, and a rarity of rocky outcrops, which collectively drive and enable the species' ability to burrow (KINLAW, 1999). Consequently, these habitat characteristics may select for fossoriality acting as a barrier to the dispersion of arboreal snakes. These observations in the Chaco are likely due to environmental filtering, affecting the distribution of species (SCHEFFERS et al., 2017). Fossoriality has evolved multiple times in snakes (CYRIAC; KODANDARAMAIAH, 2018), apparently associated with diversification related to habitat adaptation (MOEN; MORLON; WIENS, 2016; WIENS; LAPOINT; WHITEMAN, 2015). In the Chaco, fossoriality occurs in Colubridae (Colubrinae and Dipsadinae), Elapidae (Elapinae), Scolecophidia (Anomalepididae, Leptotyphlopidae, and Typhlopiddae) (Fig. S8); the latter is the only snake group containing only fossorial species. However, the distribution of this specialized fossorial group is still poorly known. Thus, certain habitat conditions may favor the aggregation of fossorial taxa (CLINCHY; HAYDON; SMITH, 2002; O'BRIEN et al., 2008).

Finally, as predicted, we found that the spatial pattern reflects the phylogenetic affinities of the species in the Chaco, the geographic pattern of verticality and fossoriality is also reflected in the phylogenetic regions we found (Fig. 4). This result, is due to specialization in a single habitat component, allowing fossorial species to efficiently exploit underused parts of the available resource base (GREENVILLE; DICKMAN, 2009). Another explanation could be that the limited dispersal capacity of fossorial species makes them geographically restricted, resulting in evolutionary and geographically distant phyloregions (DARU et al., 2017). Furthermore, species distribution and range limits are determined by biotic and abiotic factors, movement, population dynamics, and intraspecific variability, which are related to the physiological tolerances of species (Gouveia et al., 2014a). This should facilitate an increase in species

richness of local communities, allowing specialist taxa to achieve high density in their selected habitats (PIANKA, 1994). Moreover, environmental filtering may be influencing the actual species distribution, showing a heterogeneous phyloregion with marked regionalization (DARU et al., 2017).

Our study fills an important gap in the knowledge of the distribution of snake species in the Chaco and the macroecology of South American open areas. We identified phyloregions, which are important for a better understanding of what shapes the distribution of biodiversity, and we provide information on the ecological properties of the species that comprise them (DARU et al., 2017). Therefore, phyloregions may function as an important unit for the conservation of evolutionary history in overlooked areas such as the Chaco (DARU et al., 2017; NORI et al., 2016). This suggestion is especially relevant as Chacoan vertebrates are facing conservation issues, with a poor representation in protected areas (ANDRADE-DÍAZ et al., 2019; NORI et al., 2016).

In conclusion, this is the first integrative approach study investigating macroecological and biogeographic patterns and the phylogenetic relationships of the Chacoan snakes, an unique area (SZUMIK et al., 2012). We found that as arboreality increases towards the north, fossoriality increases towards the south. The environmental pattern represents a marked vertical stratification in the Chaco, increasing as habitat heterogeneity increases. Fossoriality is strongly correlated with and thus driven by soil conditions. The distribution pattern in the Chaco is also explained by the evolutionary history of snakes in this region, with a marked phylogenetic regionalization.

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APPENDIX A

Supporting Information

Table S1. Dataset of species and traits used in the analysis. In the case of snout-vent length (SVL), tail length (TL) and body length we used the maximum measure, prioritizing measures of one individual, when possible. For the size of the eyes, we compared the size of the supralabial just below the eye and his relations with the head, the eye size/diameter was classified in small = 1, medium = 2 and large = 3, body mass was log10 transform. Mass values were taken from (Feldman *et al.*, 2016). For habitat use, we reclassify the categories into a range of 1 to 3: fossorial = 1, semifossorial = 1.5, aquatic and terrestrial = 2, semiarboreal = 2.5, arboreal = 3 (see OLIVEIRA & SCHEFFERS, 2019). Tail proportion was calculated in relation to total length. Measures are in millimeters and mass in grams. A total of 184 studies were compiled, including papers, book chapters, books, thesis, and unpublish data. Unpublish data of species measurements were taken from the first author's personal database and are marked with an asterisk (*).

Binomial	Habitat	BodyLength	SVL	TL	BodyMass	EyeSize	References
Amerotyphlops brongersmianus	Fossorial	325	207	7	18.4	Small	(ADALSTEINSSON et al., 2009; AVILA; FERREIRA; SOUZA, 2006; DIXON; HENDRICKS, 1979; DIXON; KOFRON, 2009; GRABOSKI et al., 2019; HEDGES et al., 2014; REIS MARTINS; LIMA SILVEIRA; FREIRE BRUNO, 2010; VANZOLINI, 1968)
Amerotyphlops reticulatus	Fossorial	522	496	22	105.8	Small	(DIXON; HENDRICKS, 1979; DIXON; KOFRON, 2009; GRABOSKI et al., 2019; HEDGES et al., 2014; VANZOLINI, 1968)
Anilius scytale	Fossorial	904	869	35	340.1	Small	(MARTINS; MARQUES; SAZIMA, 2008; MARTINS;

							OLIVEIRA, 1998; MASCHIO et al., 2007)
Apostolepis ambiniger	Fossorial	500	460	40	50.2	Small	(DE LEMA, 2001; FRANÇA et al., 2018; NOGUEIRA; BARBO; FERRAREZZI, 2012)
Apostolepis assimilis	Fossorial	200	186	14	29.1	Small	(CABRAL; PEREZ, 2015; CEI, 1993; GIRAUDO; SCROCCHI, 1998; HARVEY, 1999)
Apostolepis breviceps	Fossorial	419	387	32	9.3	Small	(HARVEY, 2008)
*Apostolepis dimidiata**	Fossorial	571	518	53	90.6	Small	(CABRAL; DE LEMA; RENNER, 2017; CEI, 1993; GIRAUDO; SCROCCHI, 1998; HARVEY, 1999; HARVEY et al., 2008)
Apostolepis dorbignyi	Fossorial	411	362	49	37.4	Small	(HARVEY, 1999; LOEBMANN; DE LEMA, 2012)
Apostolepis intermedia	Fossorial	351	319	32	6.6	Small	(DE ALBUQUERQUE; DE LEMA, 2012; ENTIAUSPE-NETO; DE LEMA; CABRAL, 2014)
Apostolepis multicincta	Fossorial	384	333	51	40.7	Small	(EMBERT; REICHLE, 2003; FRANÇA et al., 2018; HARVEY, 1999)
Apostolepis nigroterminata	Fossorial	387	370	17	22.8	Small	(DOS SANTOS et al., 2018; HARVEY, 1999)
Apostolepis vittata	Fossorial	493	460	33	39.8	Small	(FRANÇA et al., 2018; HARVEY, 1999; PETERS; OREJAS-MIRANDA, 1972)
Atractus bocki	Fossorial	447	370	77	18.4	Small	(CEI, 1993; PASSOS; AGUAYO; SCROCCHI, 2009)

Atractus latifrons	Fossorial	613	521	92	52.5	Small	(ALMEIDA et al., 2014; HOOGMOED, 1980; MARTINS; OLIVEIRA, 1993)
*Atractus paraguayensis**	Fossorial	502	490	12.7	37.9	Small	(CABRAL, 2014; GIRAUDO; SCROCCHI, 2000; PASSOS et al., 2010)
Atractus reticulatus	Fossorial	346	295	51	20.7	Small	(BALESTRIN; DI-BERNARDO, 2005; GIRAUDO; SCROCCHI, 2000; PASSOS et al., 2010; PIZZATTO; JORDÃO; MARQUES, 2008)
Boa constrictor	Semiarboreal	4000	3777	223	35283.8	Large	(BERTONA; CHIARAVIGLIO, 2003; BOBACK, 2005, 2006)
Boiruna maculata	Terrestrial	1640	1340	300	748.8	Medium	(CEI, 1993; PIZZATTO, 2005; SCOTT et al., 2006; ZAHER, 1996)
Bothrops alternatus	Terrestrial	1216	1114	102	2399.7	Medium	(CABRAL et al., 2017; CEI, 1993)
Bothrops ammodytoides	Terrestrial	712	570	80	521.2	Medium	(CARRASCO; LEYNAUD; SCROCCHI, 2010; CEI, 1993)
Bothrops diporus	Terrestrial	1000	860	140	687.8	Medium	(DA SILVA; RODRIGUES, 2008; HARVEY; APARICIO; GONZALES, 2005)
Bothrops itapetiningae	Terrestrial	576	510	66	141.9	Medium	(LEÃO et al., 2014)
Bothrops jararacussu	Terrestrial	2000	1800	200	5169.5	Medium	(CEI, 1993; GIRAUDO, 2002; HARVEY; APARICIO; GONZALES, 2005)
Bothrops matogrossensis	Semiarboreal	1001	878	123	1118.3	Medium	(DA SILVA; RODRIGUES, 2008; HARVEY; APARICIO; GONZALES, 2005; MONTEIRO et al., 2006)

Bothrops moojeni	Terrestrial	1060	954	106	5883.4	Médium	(CEI, 1993; HARVEY; APARICIO; GONZALES, 2005; NOGUEIRA; SAWAYA; MARTINS, 2003)
Bothrops pauloensis	Terrestrial	1001	878	123	470	Médium	(DA SILVA; RODRIGUES, 2008; VALDUJO; NOGUEIRA; MARTINS, 2002)
Chironius bicarinatus	Arboreal	1390	890	500	521.4	Large	(ALMEIDA-SANTOS; MARQUES, 2002; BAILEY, 1955; CACCIALI; CABRAL, 2015; DIXON; WIEST; CEI, 1993; MARQUES et al., 2009)
Chironius exoletus	Arboreal	1531	973	558	353.7	Large	(BAILEY, 1955; CACCIALI; CABRAL, 2015; DIXON; WIEST; CEI, 1993; HAMDAN; FERNANDES, 2015; TORRES-CARVAJAL et al., 2019)
Chironius flavolineatus	Arboreal	1404	880	524	186.2	Large	(CACCIALI; CABRAL, 2015; DIXON; WIEST; CEI, 1993; HAMDAN; FERNANDES, 2015; HAMDAN; SCALI; FERNANDES, 2014)
Chironius fuscus	Arboreal	1597	1095	502	384.8	Large	(DE SOUZA FILHO et al., 2012; DIXON; WIEST; CEI, 1993; HOLLIS, 2006; TORRES-CARVAJAL et al., 2019)
Chironius laurenti	Arboreal	2152	1445	707	820.5	Large	(DIXON; WIEST; CEI, 1993; TORRES-CARVAJAL et al., 2019)
Chironius maculoventris	Semiarboreal	1155	785	370	183.5	Large	(CACCIALI; CABRAL, 2015; DIXON; WIEST; CEI, 1993; HOLLIS, 2006)

Chironius quadricarinatus	Semiarboreal	1067	1444	377	186.2	Large	(CACCIALI; CABRAL, 2015; DIXON; WIEST; CEI, 1993; HOLLIS, 2006)
Chironius scurrulus	Arboreal	2243	1515	728	1117	Large	(DIXON; WIEST; CEI, 1993)
Clelia clelia	Terrestrial	2240	1840	400	1722.6	Medium	(GAIARSA; DE ALENCAR; MARTINS, 2013; SCOTT et al., 2006; SCROCCHI; VIÑAS, 1990)
Corallus hortulanus	Arboreal	1700	1241	459	3922.3	Large	(HENDERSON; PAUERS, 2012; HENDERSON; PAUERS; COLSTON, 2013; PIZZATTO; ALMEIDA-SANTOS; SHINE, 2007)
Crotalus durissus	Terrestrial	1800	1674	126	2883	Medium	(CEI, 1993; HARVEY; APARICIO; GONZALES, 2005)
Dipsas bucephala	Arboreal	571	426	145	49.6	Large	(HARVEY; EMBERT, 2008; HOGE; ROMANO, 1975; LIONS; ALVAREZ; CÉSPEDEZ, 2000; TORELLO-VIERA; ARAÚJO; BRAZ, 2012)
Dipsas catesbyi	Arboreal	777	542	235	69.5	Large	(HARVEY; EMBERT, 2008)
Dipsas lavillai	Terrestrial	534	405	129	36.7	Large	(FERREIRA; ÁVILA, 2009; SCROCCHI; PORTO; REY, 1993)
Dipsas mikanii	Terrestrial	400	322	78	72.1	Large	(BRAZ; FRANCO; ALMEIDA-SANTOS, 2008; PIZZATTO et al., 2008; TORELLO-VIERA; MARQUES, 2017)
Dipsas turgida	Terrestrial	515	415	100	48.2	Large	(CEI, 1993; SCROCCHI; PORTO; REY, 1993)

Dipsas ventrimaculata	Terrestrial	509	393	116	71.2	Large	(CEI, 1993; SCROCCHI; PORTO; REY, 1993)
Drymarchon corais	Semiarboreal	2406	2005	401	1365.4	Medium	(BERNARDE; ABE, 2006; CEI, 1993; MARTINS; OLIVEIRA, 1998)
Epicrates alvarezi	Semiarboreal	1613	1443	170	1883.7	Large	(CEI, 1993; PASSOS; FERNANDES, 2008; PIZZATTO; MARQUES, 2007)
Epictia albipuncta	Fossorial	340	316	24	8	Small	(FRANCISCO; PINTO; FERNANDES, 2012; KRETZSCHMAR, 2006; LAURENT, 1984; PINTO et al., 2010)
Epictia australis	Fossorial	160	153	7	1.4	Small	(CEI, 1993; LAURENT, 1984; SCROCCHI, 1990a)
Epictia vellardi	Fossorial	155	149	6	2.3	Small	(CABRAL; NETTO, 2016; CEI, 1993; LAURENT, 1984)
Erythrolamprus aesculapii	Terrestrial	1130	1005	125	139.2	Large	(CURCIO; SCALI; RODRIGUES, 2015; MARQUES; PUORTO, 1994; TORELLO-VIERA; MARQUES, 2017)
Erythrolamprus albertguentheri	Terrestrial	655	545	110	74.1	Medium	(CEI, 1993; DIXON, 1987)
Erythrolamprus almadensis	Terrestrial	524	392	132	58.8	Large	(CEI, 1993; DIXON, 1987; GIRAUDO, 2002)
Erythrolamprus ceii	Terrestrial	524	430	94	32.8	Medium	(CEI, 1993; DIXON, 1987)
Erythrolamprus jaegeri	Aquatic	539	395	144	62.5	Large	(CARREIRA; MENEGHEL; ACHAVAL, 2005; DIXON, 1987; GIRAUDO, 2002)
Erythrolamprus miliaris	Terrestrial	798	644	154	110	Medium	(CEI, 1993; DIXON; TIPTON, 2003; GIRAUDO;

							ARZAMENDIA; CACCIALI, 2006; PIZZATTO; MARQUES, 2006)
Erythrolamprus poecilogyrus	Terrestrial	793	616	177	68.3	Medium	(ANDRADE et al., 2020; CABRAL; BUENO-VILLAFAÑE; ROMERO-NARDELLI, 2017; DIXON; MARKEZICH, 1992; PRIETO; GIRAUDO; LPEZ, 2012)
Erythrolamprus reginae	Terrestrial	960	698	262	98.8	Large	(ASCENSO; COSTA; PRUDENTE, 2019; CEI, 1993; GIRAUDO, 2002)
Erythrolamprus sagittifer	Terrestrial	925	648	277	177.3	Large	(CEI, 1993; DIXON; THOMAS, 1982)
Erythrolamprus semiaureus	Aquatic	1457	1259	220	168.7	Medium	(DIXON, 1983; GIRAUDO; ARZAMENDIA; CACCIALI, 2006; PIZZATTO; JORDÃO; MARQUES, 2008; TORELLO-VIERA; MARQUES, 2017)
Erythrolamprus typhlus	Terrestrial	740	590	150	112.7	Large	(CEI, 1993; DIXON, 1987)
Eunectes notaeus	Aquatic	2550	2,180	370	25204.8	Medium	(CACCIALI, 2009; CEI, 1993; PIZZATTO; MARQUES, 2007; STRUSSMANN; SAZIMA, 1993)
Helicops angulatus	Aquatic	795	560	235	179.6	Medium	(COSTA et al., 2016; KAWASHITA-RIBEIRO; ÁVILA; MORAIS, 2013; ROSSMAN, 1973)
Helicops infrataeniatus	Aquatic	693	500	193	168.7	Medium	(CEI, 1993; COSTA et al., 2016; KAWASHITA-RIBEIRO; ÁVILA; MORAIS, 2013; ROSSMAN, 1973)

Helicops leopardinus	Aquatic	731	530	201	98.8	Medium	(CEI, 1993; COSTA et al., 2016; GIRAUDO, 2002; KAWASHITA-RIBEIRO; ÁVILA; MORAIS, 2013; ROSSMAN, 1973)
Helicops polylepis	Aquatic	1052	767	285	191.8	Medium	(COSTA et al., 2016; KAWASHITA-RIBEIRO; ÁVILA; MORAIS, 2013; ROSSMAN, 1973)
Hydrodynastes gigas	Aquatic	2009	1439	530	2193.6	Medium	(CEI, 1993; FRANCO; FERNANDES; BENTIM, 2007; GIRAUDO, 2002)
Hydrops caesurus	Aquatic	663	570	93	80	Small	(CEI, 1993; GIRAUDO, 2002; SCROCCHI et al., 2005)
Imantodes cenchoa	Arboreal	1170	825	345	515.8	Large	(CEI, 1993; DE SOUSA; PRUDENTE; MASCHIO, 2014; DONNELLY; MYERS, 1991; PIZZATTO et al., 2008)
Leptodeira annulata	Semiarboreal	655	485	170	185.4	Large	(ÁVILA; MORAIS, 2007; CEI, 1993; PIZZATTO et al., 2008)
Leptophis ahaetulla	Arboreal	1440	956	484	918.7	Large	(CACCIALI, 2009; CEI, 1993; DE ALBUQUERQUE; GALATTI; DI-BERNARDO, 2007; DE ALBUQUERQUE; PASSOS; GOTTE, 2012; DE ALBUQUERQUE, 2009; GIRAUDO, 2002)
Liotyphlops beui	Fossorial	326	321	5	21	Small	(CEI, 1993; CENTENO; SAWAYA; GERMANO, 2010; DIXON; KOFRON, 2009; FREIRE; CARAMASHI; ARGOLO, 2007; PARPINELLI;

							MARQUES, 2008; SANTOS; REIS, 2018)
Liotyphlops ternetzii	Fossorial	413	400	13	18.4	Small	(CEI, 1993; CENTENO; SAWAYA; GERMANO, 2010; DIXON; KOFRON, 2009; FREIRE; CARAMASHI; ARGOLO, 2007; GIRAUDO, 2002; SANTOS; REIS, 2018)
Lygophis anomalus	Terrestrial	713	529	184	84.1	Medium	(CARREIRA; MENEGHEL; ACHAVAL, 2005; CEI, 1993; DIXON, 1985)
Lygophis dilepis	Terrestrial	690	531	159	44.9	Medium	(CACCIALI, 2009; CEI, 1993)
Lygophis flavifrenatus	Terrestrial	746	627	206	82.7	Medium	(CACCIALI, 2009; CARREIRA, 2002; CARREIRA; MENEGHEL; ACHAVAL, 2005; CEI, 1993)
Lygophis meridionalis	Terrestrial	598	606	221	96.2	Medium	(CACCIALI, 2009; CEI, 1993)
Lygophis vanzolinii	Terrestrial	748	545	203	81.3	Medium	(CEI, 1993; DIXON, 1985)
Mastigodryas boddaerti	Terrestrial	1800	895	305	331	Large	(MONTINGELLI et al., 2019; SIQUEIRA; NASCIMENTO; SANTOS-COSTA, 2012)
Micrurus altirostris	Semifossorial	783	732	51	483.4	Small	(DA SILVA, 2016; DA SILVA; SITES, 1999; HARVEY; APARICIO E.; GONZALEZ A., 2003; SCROCCHI, 1990b)
Micrurus baliocoryphus	Semifossorial	1449	1374	75	616.2	Small	(DA SILVA, 2016; DA SILVA; SITES, 1999; HARVEY; APARICIO E.; GONZALEZ A., 2003; SCROCCHI, 1990b)
Micrurus diana	Semifossorial	1052	954	54	257.2	Small	(DA SILVA, 2016; DA SILVA; SITES, 1999)

Micrurus frontalis	Semifossorial	1794	1728	66	584.9	Small	(DA SILVA, 2016; DA SILVA; SITES, 1999; SCROCCHI, 1990b)
Micrurus lemniscatus	Semifossorial	1650	1550	100	557.5	Small	(HARVEY; APARICIO E.; GONZALEZ A., 2003; MARQUES; ALMEIDA-SANTOS; RODRIGUES, 2006; PIRES et al., 2014)
*Micrurus pyrrhocryptus**	Semifossorial	1747	1666	81	966.5	Small	(CEI, 1993; DA SILVA, 2016; DA SILVA; SITES, 1999; SCROCCHI, 1990b)
*Micrurus silviae**	Semifossorial	1113	1050	63	676.1	Small	(DA SILVA, 2016; DI-BERNARDO; BORGES-MARTINS; DA SILVA, 2007)
Micrurus surinamensis	Semifossorial	1378	1198	180	496.8	Small	(DA SILVA, 2016; ROZE, 1996)
Mussurana bicolor	Semifossorial	870	710	160	177.8	Medium	(GAIARSA; DE ALENCAR; MARTINS, 2013; GOUTURIER; FAIVOVICH, 1996; PIZZATTO, 2005; SCOTT et al., 2006; SCROCCHI; VIÑAS, 1990; ZAHER, 1996)
Mussurana quimi	Terrestrial	1090	860	230	352.8	Medium	(FRANCO; MARQUES; PUORTO, 1997; SCOTT et al., 2006; SILVEIRA; COTTA, 2006)
Oxybelis aeneus	Arboreal	1138	838	300	341.7	Large	(JADIN et al., 2019, 2020, 2021)
Oxyrhopus guibei	Terrestrial	955	745	210	354.5	Large	(PIZZATTO, 2005; TORELLO-VIERA; MARQUES, 2017; ZAHER; CARAMASCHI, 1992)
Oxyrhopus petolarius	Terrestrial	910	690	220	1245.6	Large	(CABRAL; SCOTT, 2014; CEI, 1993; GIRAUDO, 2002; MACCULLOCH et al., 2009)

*Oxyrhopus rhombifer**	Terrestrial	712	596	116	129.1	Large	(CEI, 1993; GIRAUDO, 2002; TORELLO-VIERA; MARQUES, 2017)
Palusophis_bifossatus	Terrestrial	2007	1520	487	450.9	Large	(CEI, 1993; GIRAUDO, 2002; LEITE, 2006; MARQUES; MURIEL, 2007; MONTINGELLI et al., 2019)
Paraphimophis rusticus	Terrestrial	890	800	190	1406.8	Medium	(CEI, 1993; SCOTT et al., 2006; SCROCCHI; VIÑAS, 1990; ZAHER, 1996)
Phalotris bilineatus	Semifossorial	320	290	30	13.6	Small	(CABRAL; CACCIALI, 2015; CARREIRA; MENEGHEL; ACHAVAL, 2005; CEI, 1993; GIRAUDO, 2002; PUORTO; FERRAREZZI, 1993)
Phalotris lemniscatus	Semifossorial	368	338	30	40.5	Small	(CABRAL; CACCIALI, 2015; CARREIRA; MENEGHEL; ACHAVAL, 2005; CEI, 1993; GIRAUDO, 2002; PUORTO; FERRAREZZI, 1993)
Phalotris matogrossensis	Semifossorial	495	463	32	30.1	Small	(CACCIALI; MOTTE, 2007; LEMA; D'AGOSTINI; CAPPELLARI, 2005; LEYNAUD; CABRERA; CARRASCO, 2005)
Phalotris sansebastiani	Semifossorial	524	475	49	49.4	Small	(JANSEN; KÖHLER, 2008; SCROCCHI; GIRAUDO, 2012)
Phalotris tricolor	Semifossorial	770	725	45	121.1	Small	(CACCIALI; MOTTE, 2007; CEI, 1993; JANSEN; KÖHLER, 2008; LEMA; D'AGOSTINI; CAPPELLARI, 2005;

							LEYNAUD; CABRERA; CARRASCO, 2005)
*Philodryas aestiva**	Terrestrial	929	628	301	168.7	Large	(CARREIRA; MENEGHEL; ACHAVAL, 2005; CEI, 1993; CELSI; MONSERRAT; KACOLIRIS, 2008; GIRAUDO, 2002; THOMAS, 1976)
Philodryas agassizii	Terrestrial	307	297	10	29.1	Medium	(CEI, 1993; DI PIETRO; CHRISTIE; WILLIAMS, 2012; MARQUES et al., 2006)
*Philodryas baroni**	Semiarboreal	1500	1211	499	471.6	Large	(BRIGUERA et al., 2006; CACCIALI, 2009; CEI, 1993)
*Philodryas livida**	Terrestrial	693	530	163	113.8	Medium	(SMITH et al., 2014; THOMAS; FERNANDES, 1996)
*Philodryas mattogrossensis**	Terrestrial	1522	1039	483	471.6	Large	(CACCIALI et al., 2016a; THOMAS, 1976)
*Philodryas olfersii**	Semiarboreal	1400	718	354	452.7	Large	(CARREIRA; MENEGHEL; ACHAVAL, 2005; CEI, 1993; GIRAUDO, 2002; HARTMANN; MARQUES, 2005; THOMAS, 1976)
*Philodryas patagoniensis**	Terrestrial	1500	860	311	512.5	Large	(CEI, 1993; HARTMANN; MARQUES, 2005; LÓPEZ; GIRAUDO, 2008)
*Philodryas psammophidea**	Terrestrial	1285	1015	270	168.7	Large	(CEI, 1993; QUINTEROS-MUÑOZ; PEÑARANDA; NAVARRO, 2010; THOMAS, 1976)
Philodryas trilineata	Arboreal	1304	908	396	647.8	Large	(CEI, 1993; THOMAS, 1976)
Philodryas varia	Arboreal	1151	861	290	361	Large	(CEI, 1993; THOMAS, 1976)

Phimophis guerini	Terrestrial	1161	965	196	320.2	Medium	(CEI, 1993; FILHO et al., 2012; GIRAUDO, 2002; MARQUES; ETEROVIC; SAZIMA, 2001)
Phimophis vittatus	Semifossorial	700	600	100	68.3	Medium	(ALENCAR; GAIARSA; MARTINS, 2013; CEI, 1993)
Pseudoboa coronata	Terrestrial	723	644	179	203.1	Medium	(ALENCAR; GAIARSA; MARTINS, 2013; MARTINS; OLIVEIRA, 1998)
Pseudoboa nigra	Terrestrial	1215	930	285	527.1	Medium	(CACCIALI, 2009; CEI, 1993; DE PAULA OROFNO; PIZZATTO; MARQUES, 2010; GIRAUDO, 2002)
Pseudoeryx plicatilis	Aquatic	826	655	171	200.2	Small	(CABRAL; CABALLERO, 2012; CEI, 1993; SCARTOZZONI; TREVINE; GERMANO, 2010)
Pseudotomodon trigonatus	Terrestrial	400	355	45	22.3	Medium	(CEI, 1993; HARVEY; MUÑOZ, 2004)
Psomophis genimaculatus	Terrestrial	387	302	85	22.3	Large	(MARQUES et al., 2005, 2015; NENDA, 2007)
Psomophis obtusus	Terrestrial	359	300	95	22.9	Large	(CEI, 1993; MARQUES et al., 2015)
Rena unguirostris	Fossorial	103	101	2	2	Small	(CEI, 1993; LAURENT, 1984; PINTO et al., 2010)
Simophis rhinostoma	Terrestrial	887	691	196	112.3	Medium	(CACCIALI et al., 2009; MARQUES et al., 2005)
Siphlophis compressus	Arboreal	1420	1136	284	418.5	Large	(GUEDES et al., 2011; SHEEHY et al., 2014)
Siphlophis worontzowi	Arboreal	1107	885	222	137.4	Large	(COSTA; SÃO-PEDRO; FEIO, 2010; DAL VECHIO et al., 2015; PRUDENTE et al., 2017)

Spilotes pullatus	Arboreal	2100	1200	900	3030.1	Medium	(CEI, 1993; GIRAUDO, 2002; HAUZMAN; COSTA; SCARTOZZONI, 2005)
Taeniophallus occipitalis	Terrestrial	504	379	125	40.5	Large	(MYERS; CADLE, 1994; MYERS, 1974)
Taeniophallus poecilopogon	Terrestrial	390	278	112	21.4	Large	(CARREIRA; MENEGHEL; ACHAVAL, 2005; CEI, 1993; MYERS; CADLE, 1994; MYERS, 1974)
Tantilla melanocephala	Semifossorial	370	290	80	15.4	Medium	(BURGOS GALLARDO; RAMOS; BALDO, 2012; CEI, 1993; SAWAYA; SAZIMA, 2003; WILSON, 1999)
Thamnodynastes chaquensis	Terrestrial	793	619	174	95.8	Large	(BAILEY; THOMAS; DA SILVA, 2005; BELLINI; GIRAUDO; ARZAMENDIA, 2014; BERGNA; ALVAREZ, 1993)
Thamnodynastes hypoconia	Aquatic	730	537	193	56.6	Large	(BAILEY; THOMAS; DA SILVA, 2005; BELLINI; GIRAUDO; ARZAMENDIA, 2014; FRANCO et al., 2003)
Thamnodynastes lanei	Terrestrial	648	479	169	56.1	Large	(BAILEY; THOMAS; DA SILVA, 2005)
Thamnodynastes pallidus	Terrestrial	764	600	164	22.3	Large	(BAILEY; THOMAS; DA SILVA, 2005; BELLINI; GIRAUDO; ARZAMENDIA, 2014)
Thamnodynastes strigatus	Semiarboreal	860	640	220	95.8	Large	(BAILEY; THOMAS; DA SILVA, 2005; BELLINI; GIRAUDO; ARZAMENDIA, 2014; CEI, 1993)

Tomodon dorsatum	Terrestrial	707	532	175	94.7	Medium	(BIZERRA; MARQUES; SAZIMA, 2005; CEI, 1993; HARVEY; MUÑOZ, 2004)
Tomodon ocellatus	Terrestrial	377	334	43	35.3	Medium	(CEI, 1993; HARVEY; MUÑOZ, 2004)
Tomodon orestes	Terrestrial	515	448	67	31.3	Medium	(HARVEY; MUÑOZ, 2004)
Xenodon dorbignyi	Semifossorial	443	372	71	95.8	Medium	(CARREIRA; MENEGHEL; ACHAVAL, 2005; CEI, 1993; NENDA; CACIVIO, 2007; TOZETTI; OLIVEIRA; PONTES, 2009; YANOSKY; CHANI, 1988)
Xenodon histricus	Semifossorial	333	282	51	11.3	Medium	(ALVES et al., 2013; CARREIRA; MENEGHEL; ACHAVAL, 2005; CEI, 1993)
*Xenodon matogrossensis**	Semifossorial	462	395	67	21.1	Medium	(CABRAL et al., 2020)
Xenodon merremi	Terrestrial	783	656	127	168.7	Medium	(CACCIALI, 2010; PIZZATTO; JORDÃO; MARQUES, 2008)
*Xenodon pulcher**	Semifossorial	510	440	70	68.3	Medium	(CEI, 1993; NENDA; CACIVIO, 2007; SCROCCHI; CRUZ, 1993)
Xenodon semicinctus	Semifossorial	412	366	46	46.2	Medium	(CEI, 1993; NENDA; CACIVIO, 2007; SCROCCHI; CRUZ, 1993)
Xenodon severus	Terrestrial	1000	840	160	978.2	Medium	(CHIPPAUX, 1986; KAHN, 2010; SILVA; SOUZA; BERNARDE, 2010)
Xenopholis undulatus	Terrestrial	465	395	70	24.2	Medium	(COSTA; CLARA; GURGEL, 2013; GOMES et al., 2020; JANSEN; ÁLVAREZ; KÖHLER, 2009)

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Table S2. Predictor variables used in the study. Climatic variables were download from the WorldClim (FICK; HIJMANS, 2017); http:// www.worldclim.org). The annual actual evapotranspiration (AET) was used from (ABATZOGLOU et al., 2018) and net primary productivity (NPP from https://lpdaac.usgs.gov/, and the Normalized difference vegetation index (NDVI) from (TUCKER et al., 2005). Habitat heterogeneity variables were download from http://www.earthenv.org// (TUANMU & JETZ, 2015), tree cover from the http://earthenginepartners.appspot.com/science-2013-global-forest (HANSEN et al., 2013), mean elevation download from https://asterweb.jpl.nasa.gov/gdem.asp (GRAHAM et al., 2014), and soil variables from https://soilgrids.org/ (HENGL et al., 2017).

Climatic variables	
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range
BIO3	Isothermality (BIO2/BIO7) (* 100)
BIO4	temperature seasonality
BIO5	Max Temperature of Warmest Month
BIO6	Min temperature of coldest month
BIO7	Temperature Annual Range (BIO5-BIO6)
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter

BIO19	Precipitation of Coldest Quarter
	Productivity
AET	Actual evapotranspiration
NPP	Net primary productivity
NDVI	Normalized difference Vegetation index
	Habitat Heterogeneity
EVENNESS	Evenness of Enhanced Vegetation Index (EVI)
HOMOGENEITY	Similarity of Enhanced Vegetation Index (EVI)
TC	Tree cover in the year 2000, canopy closure
	Soil
FRAG	Volumetric fraction of coarse fragments (> 2 mm)
SAND	Proportion of sand particles (> 0.05 mm) in the fine earth fraction
	Topographic
ELEV	Mean elevation

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Table S3. variance inflation factor (VIF) and Pearson correlation test of the variables using in the analysis.

Environmental variables		VIF
Climatic	Annual mean temperature	5
	Precipitation seasonality	2
Habitat Heterogeneity	Evenness of the Enhaced Vegetation Index (EVI)	2
	Homogeneity of the Enhaced Vegetation Index (EVI)	3
	Tree cover	2
Productivity	Actual evapotranspiration	2
	Net primary productivity	2
	Normalized difference vegetation index	2
Soil	Volumetric percentage of coarse fragments	3
	Proportion of sand particles in the soil	1

Table S4. Pearson correlation test for all the 10 environmental variables. No correlation between variables cor >0.8.

	Annual mean temperature	Precipitation seasonality	Evenness of the Enhaced Vegetation Index (EVI)	Actual evapotranspiration	Volumetric percentage of coarse fragments	Homogeneity of the Enhaced Vegetation Index (EVI)	Net primary productivity	Proportion of sand particles in the soil	Tree cover	Normalized difference vegetation index
Annual mean temperature	1.0	0.0	0.5	0.1	-0.5	0.5	-0.1	0.0	0.6	0.5
Precipitation seasonality	0.0	1.0	0.2	-0.3	0.5	0.5	-0.2	0.2	0.1	-0.3
Evenness of the Enhaced Vegetation Index (EVI)	0.5	0.2	1.0	0.5	-0.2	0.1	0.2	-0.2	0.1	0.2
Actual evapotranspiration	0.1	-0.3	0.5	1.0	-0.3	-0.4	0.4	-0.4	0.0	0.3
Volumetric percentage of coarse fragments	-0.5	0.5	-0.2	-0.3	1.0	0.1	0.2	0.2	-0.4	-0.4
Homogeneity of the Enhaced Vegetation Index (EVI)	0.5	0.5	0.1	-0.4	0.1	1.0	-0.4	0.3	0.3	0.0
Net primary productivity	-0.1	-0.2	0.2	0.4	0.2	-0.4	1.0	-0.3	-0.2	0.0
Proportion of sand particles in the soil	0.0	0.2	-0.2	-0.4	0.2	0.3	-0.3	1.0	0.2	0.1
Tree cover	0.6	0.1	0.1	0.0	-0.4	0.3	-0.2	0.2	1.0	0.5
Normalized difference vegetation index	0.5	-0.3	0.2	0.3	-0.4	0.0	0.0	0.1	0.5	1.0

Figure S1. Principal components of our trait data. Fossorial species are located at the left and arboreal species at right.

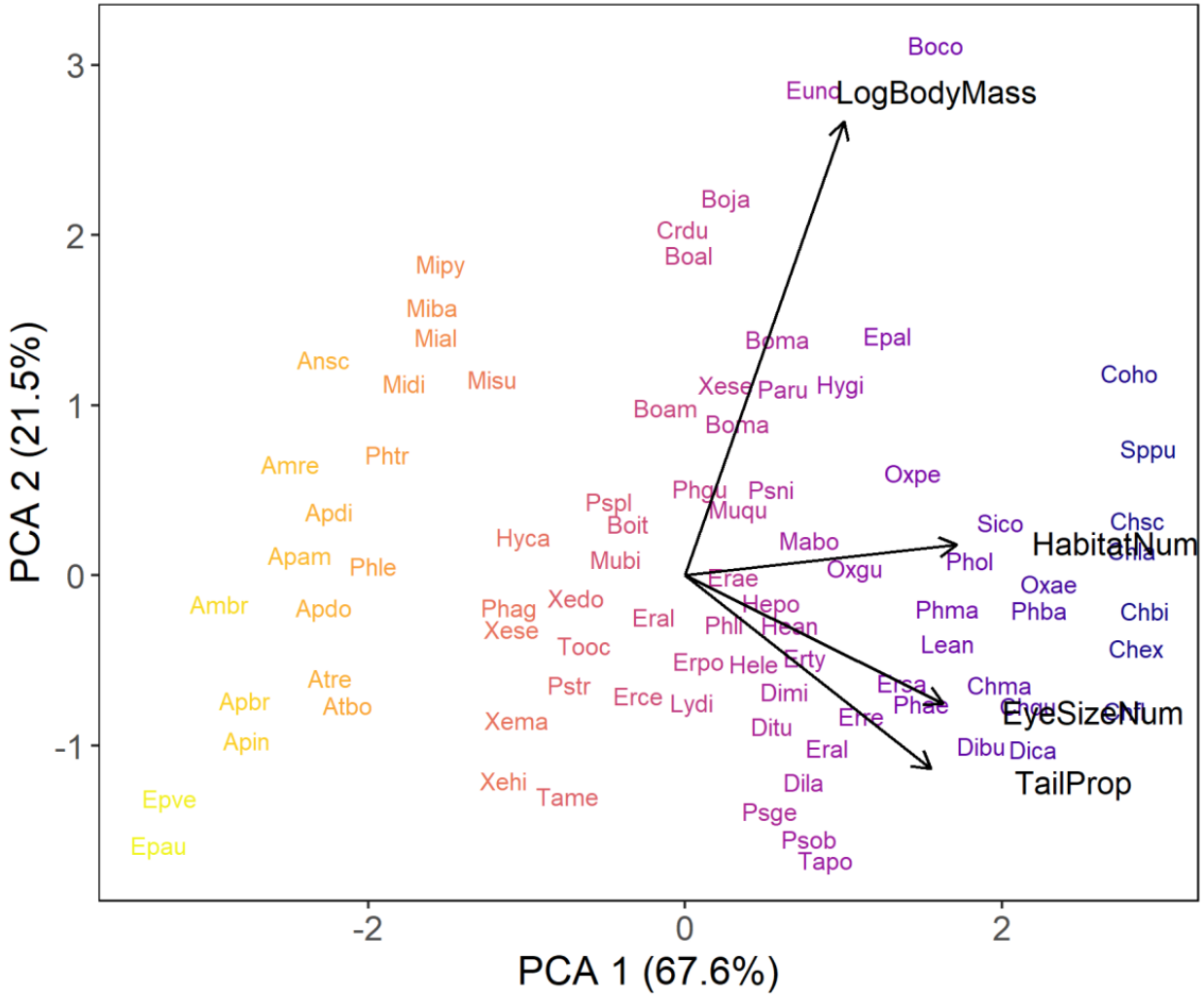

Figure S2. Regional autocorrelograms. Red line represents spatial autocorrelation in vertical habitat, tail proportion and fossoriality. of our response and predictors variables. Blue lines are the spatial autocorrelation in our spatial autoregressive (SAR) models. Averaged residuals represent the difference between raw values from an explanatory variable and the averaged fitted values (weighted AICc x fitted values) from SAR models.

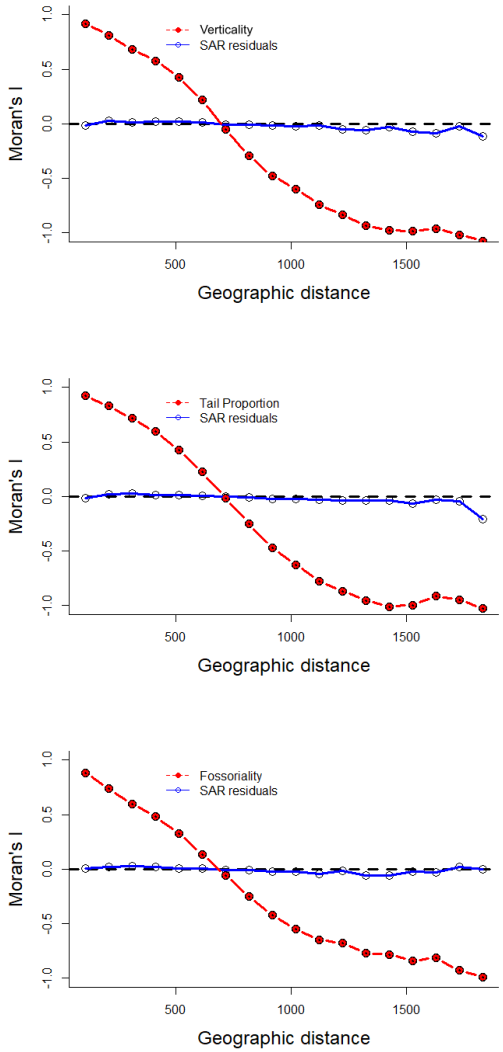

Figure S3. Correlation between our response and predictors variables. Numbers on top represent Pearson correlation with significance probability.

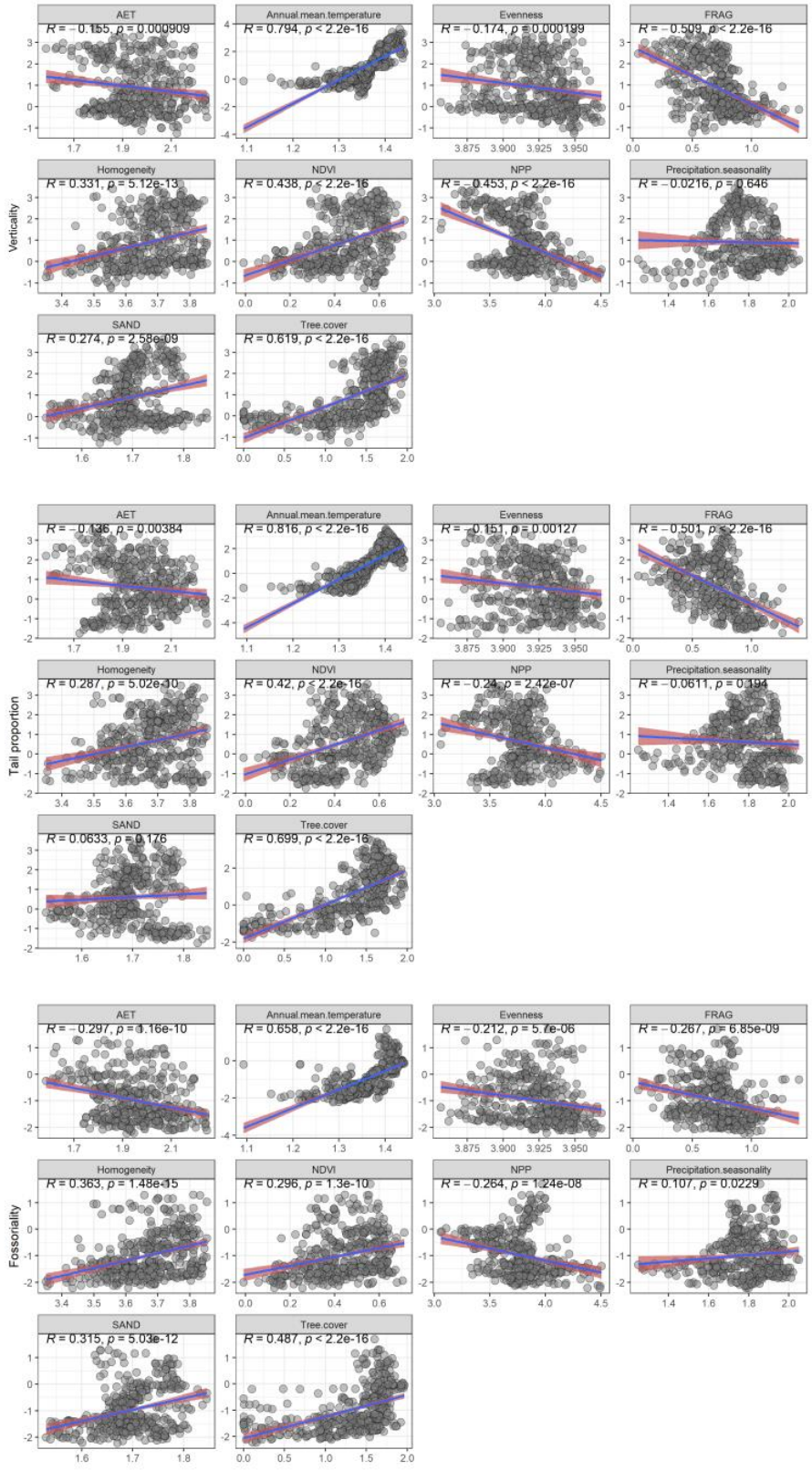

Figure S4. Regional autocorrelograms from our sensitivity analysis. Red line represents spatial autocorrelation in vertical habitat, tail proportion and fossoriality. of our response and predictors variables. Blue lines are the spatial autocorrelation in our spatial autoregressive (SAR) models. Averaged residuals represent the difference between raw values from an explanatory variable and the averaged fitted values (weighted AICc x fitted values) from SAR models.

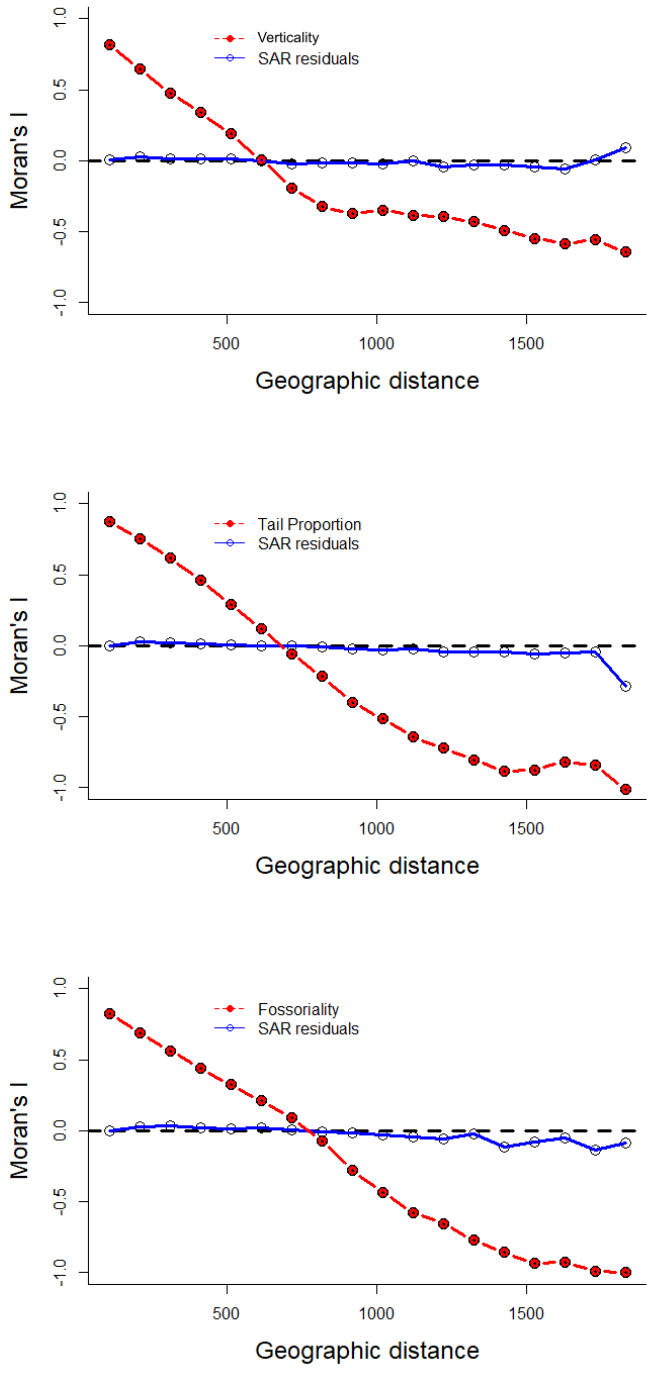

Figure S5. Correlation between our response and predictors variables from our sensitivity analysis. Numbers on top represent Pearson correlation with significance probability.

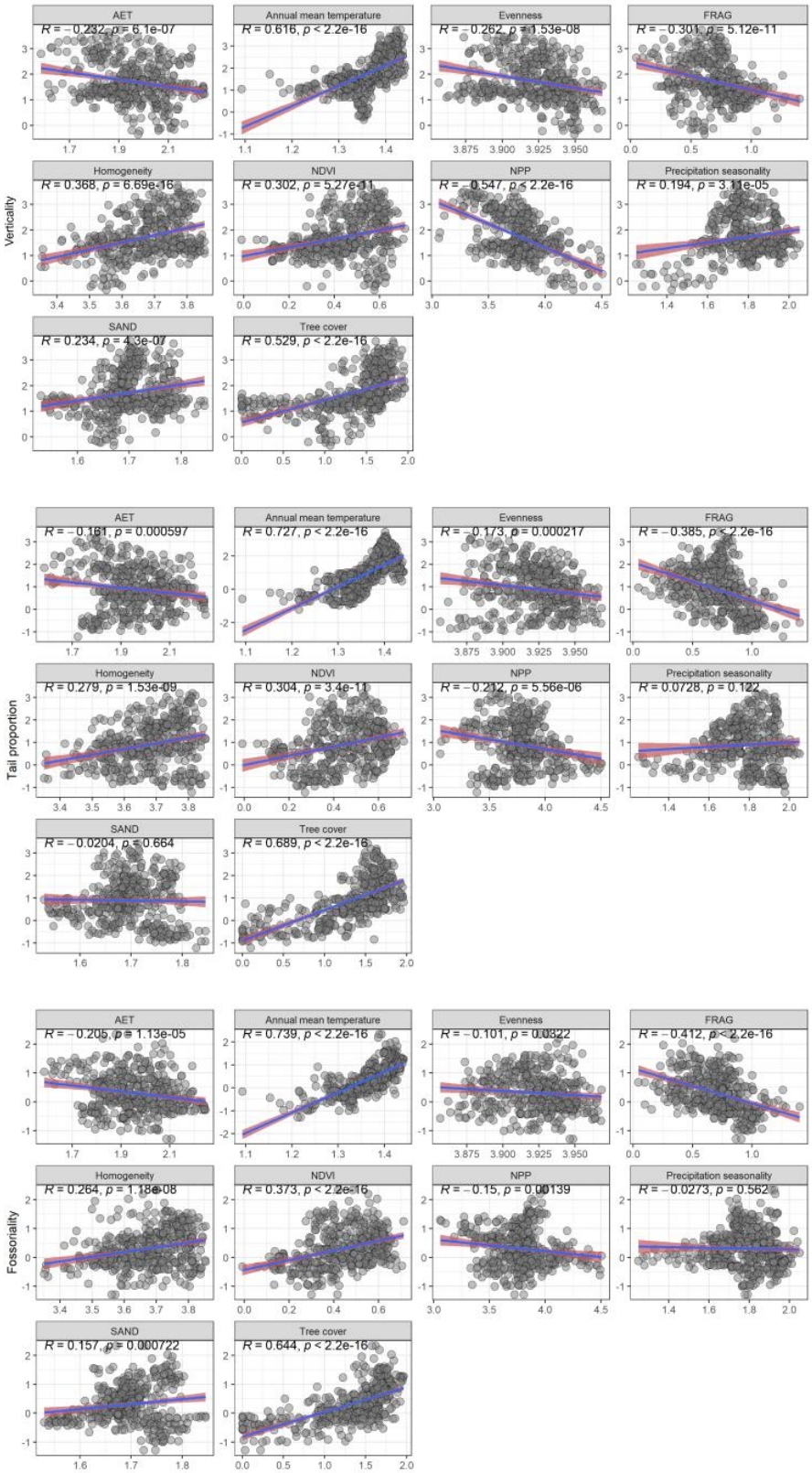

Figure S6. The threshold of explained variances to identify the optimal number of phylogenetic regions. Red line and circle in the graph represent the optimal numbers of phylogenetic region.

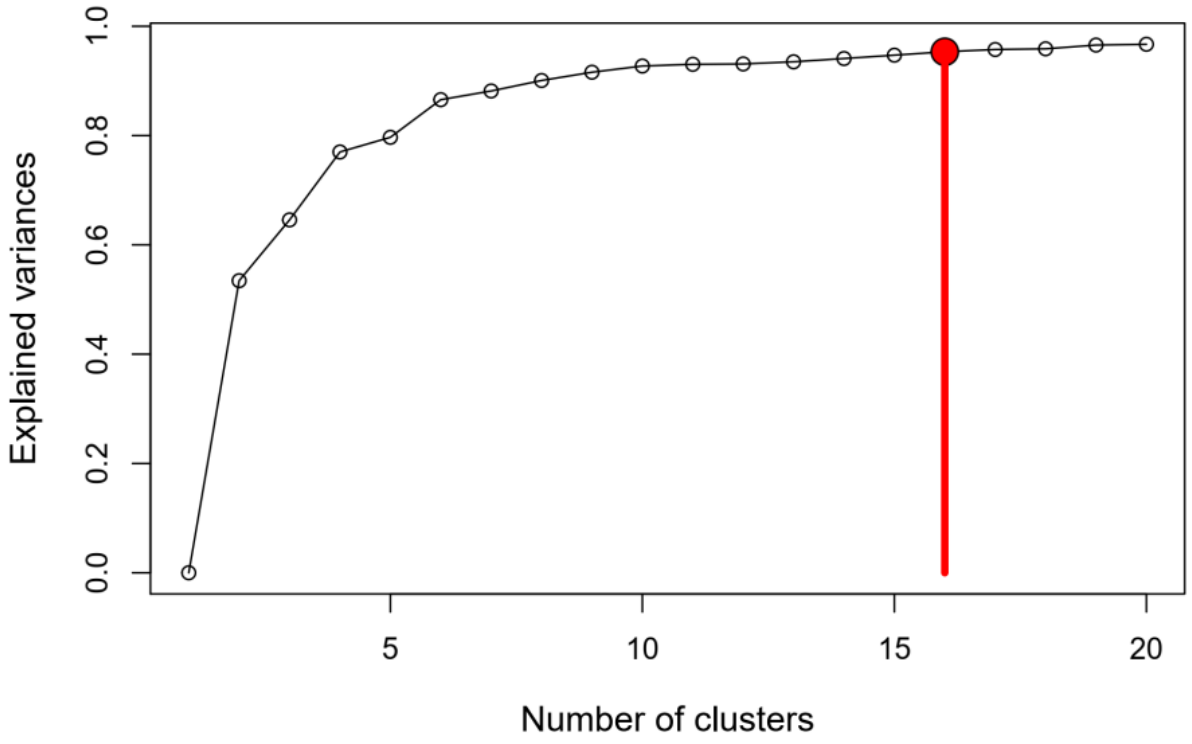

Figure S7. Geographical pattern of phylogenetic endemism PE, phylogenetic diversity PD, phylogenetic species variability (PSV). Phylogenetic endemism measures endemism based on the relatedness of species (DARU; KARUNARATHNE; SCHLIEP, 2020; ROSAUER et al., 2009), calculate the spatial uniqueness of each branch in the tree taking the reciprocal of its range, multiplying by branch length, and summing for all branch lengths present at a sample/site (ROSAUER et al., 2009). Phylogenetic diversity is a measure to compared diversity in geographic areas, evolutionary history shared between areas (GRAHAM; FINE, 2008; LAFFAN et al., 2016), and describe the evolutionary distinctiveness of component taxa (FAITH, 1992; HELMUS et al., 2007). How phylogenetically related are species in a community was measure through phylogenetic species variability (HELMUS et al., 2007). PSV is standardized to vary between zero when species are closely related and one when species are distantly related, indicating maximum variability. As relatedness increases, the index approaches 0, indicating reduced variability (BURBRINK; MYERS, 2015; HELMUS et al., 2007; PYRON; BURBRINK, 2014b).

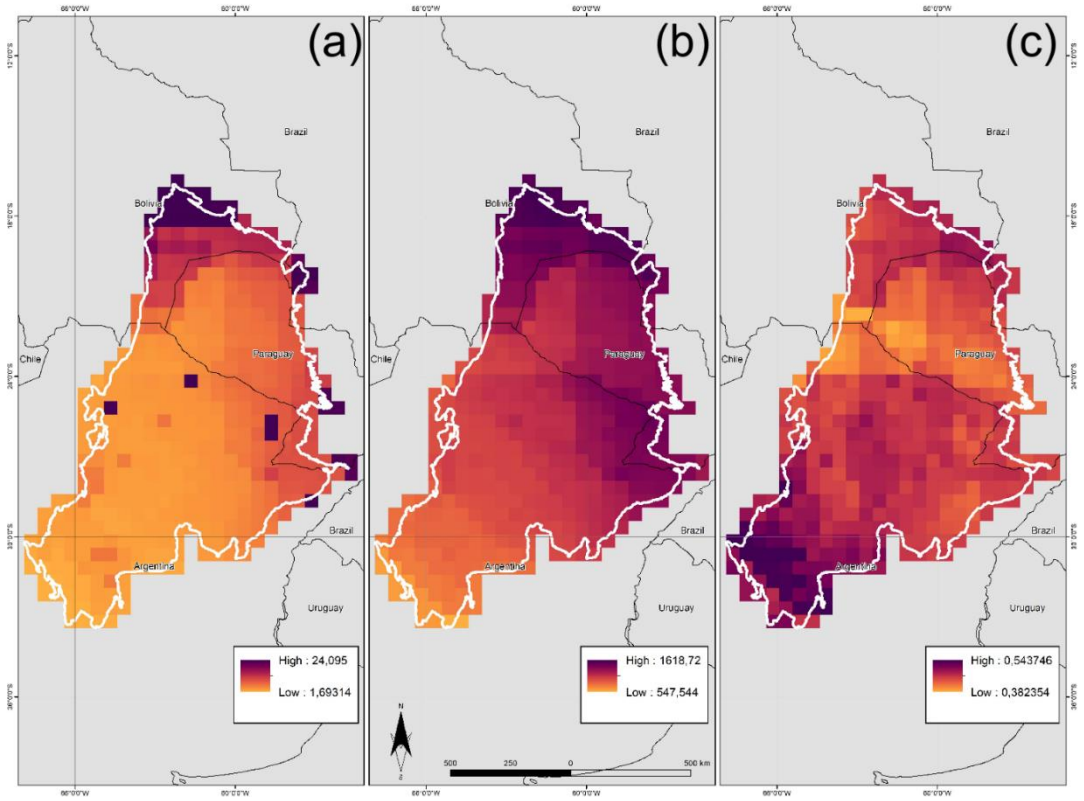

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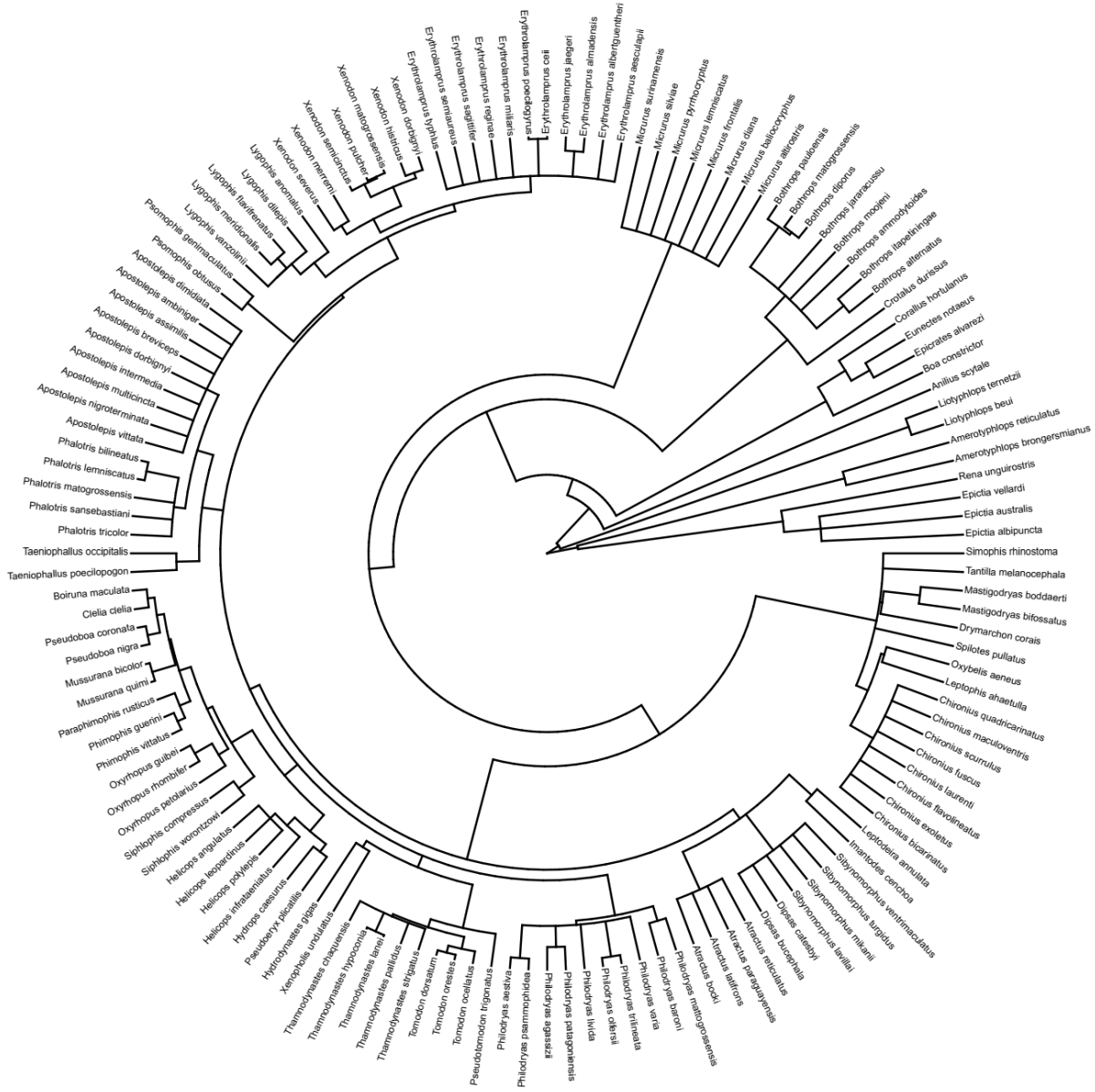
Figure S8. Phylogeny of snakes from the Gran Chaco, representing the 140 species used in this study. Phylogeny data was extracted and pruned from TONINI et al. (2016).



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15 CHAPTER 3. PHYLOGEOGRAPHY AND DIVERSIFICATION OF TWO CHACOAN SNAKES

16 ABSTRACT

The Gran Chaco, hereafter the Chaco, is one of the biggest and continuous dry forest ecoregions, is in the center of South America, covering the northwest of Argentina, southeast of Bolivia, west of Paraguay, and a small area in the center-west of Brazil. The Chaco is the result of Andean uplift, marine introgressions, and several alluvial systems. The Pleistocene glaciations and Miocene marine introgressions could have played an important role in the evolutionary processes of the Chaco biota such as plants, amphibians, birds, and mammals. In this research we used mitochondrial genes to assess what historical events may have acted as drivers of the diversification of; *Erythrolamprus poecilogyrus caesius*, *Xenodon pulcher* and *X. matogrossensis*. Our ASAP and GYMC analysis show three lineages of *E. poecilogyrus caesius* in the Chaco, with species not isolated by distance but with a high level of haplotypic and nucleotic diversity. Marine introgressions, climatic oscillations, and landscape heterogeneity in southern South America during this period are important drivers of the genetic structure and demographic history of *Erythrolamprus poecilogyrus caesius*. *Xenodon pulcher* and *X. matogrossensis* split at the end of the Miocene. The split of *X. pulcher* and *X. matogrossensis* could be the result of marine introgressions, and the formation of the Pantanal Basin.

Keywords: Dipsadidae. Xenodontinae. South America. DNA. Evolution.

17 INTRODUCTION

The Gran Chaco (hereafter the Chaco), is one of the biggest and continuous dry forest ecoregions, is in the center of South America, and covering the northwest of Argentina, southeast of Bolivia, west of Paraguay and a small area in the center-west of Brazil (BUCHER, 1982; PRADO, 1993). The Chaco, along with the Caatinga and Cerrado form the Dry Diagonal (VANZOLINI, 1970; WERNECK, 2011) and are important biodiversity hotspots with medium to high levels of species richness and endemism (OLSON et al., 2006; WERNECK, 2011). Currently, the Chaco is considered one of the most threatened ecoregions of the world, with the higher rates of deforestation (GRAU; GASPARRI; AIDE, 2008; HANSEN et al., 2013).

The most important characteristic of the Chaco is its geomorphology, which consists of an extensive sedimentary alluvial plain with soils derived from the massive accumulation of Quaternary sediments (PENNINGTON; PRADO; PENDRY, 2000; PRADO, 1993). This vegetation of the Chaco is composed by xerophytic vegetation formed by a mosaic of grasslands, savannas, open woodlands, and thorn forests (PRADO, 1993; WILLIG et al., 2000). This area shows an impressive monotony along its distributions (PRADO, 1993), resulting in a horizontal terrain, with four main allochthonous rivers crossing the Chaco, from west to east (PRADO, 1993).

Pleistocene glaciations and Miocene marine introgressions have played an important role in the evolutionary processes of the biota of South America (MORANDO et al., 2004; WERNECK, 2011; ROCHA et al., 2020). This period was also characterized by the second flooding pulse of the Paranense Sea, which isolated large and depressed areas in the Chaco, especially in the areas covering by the Michicola and Asunción Arch (BRUSQUETTI et al., 2018; HERNÁNDEZ et al., 2005; RUSKIN et al., 2011). Recent studies suggests that

Pleistocene glaciations and Miocene marine introgressions may been influenced the evolutionary history of plants, amphibians, birds, and mammals of the Chaco (BRUSQUETTI et al., 2018, 2019; CAMPS et al., 2018; DELSUC et al., 2012; ROCHA et al., 2020). Those events could have different influence on the Chaco biota, for example, for frogs of the genus *Lepidobatrachus*, marine introgressions during the late Miocene may act as a driver of diversification and affect the historic demography (BRUSQUETTI et al., 2018) and Pleistocene glaciations may influence the demographic history of *Leptodactylus bufonius* (BRUSQUETTI et al., 2019). For plants, climate refugia during the Pliocene may have acted as drivers of diversification (CAMPS et al., 2018). Finally, marine incursions during Middle Miocene may have acted as drivers of diversification for mammals (DELSUC et al., 2012). Nevertheless, studies regarding the events that shaped the vertebrate community are still scarce in the Chaco, especially for reptiles.

In this research we evaluate the genetic structure and demographic history of *Erythrolamprus poecilogyrus caesius* in the Chaco (CEI, 1993; NOGUEIRA et al., 2019). *Erythrolamprus poecilogyrus caesius* can be easily recognized by its coloration and geographic distribution (ENTIAUSPE-NETO et al., 2021; GIRAUDO, 2002). *Erythrolamprus poecilogyrus caesius* is endemic and widely distributed in the Chaco in Argentina, Bolivia, Brazil, and Paraguay (CABRAL; BUENO-VILLAFAÑE; ROMERO-NARDELLI, 2017; NOGUEIRA et al., 2019). This subspecies has a preference for habitats with temporary ponds, and feeds mainly on anurans, and can be found foraging mainly during the night (CABRAL; BUENO-VILLAFAÑE; ROMERO-NARDELLI, 2017; CEI, 1993).

Furthermore, in this work, we would like to assess what drives the diversification of the *Xenodon pulcher* and *X. matogrossensis*, a closely related species distributed in the Chaco and

Pantanal, with sympatric distribution. *Xenodon pulcher* is distributed in the Chaco (CABRAL et al., 2015; SCROCCHI; CRUZ, 1993) and *Xenodon matogrossensis* (Scrocchi and Cruz, 1993) (Fig. 1) in the Pantanal wetlands (CABRAL et al., 2020; SCROCCHI; CRUZ, 1993). Both species have semifossorial habits and are characterized by a keeled rostral scale modified as a shovel, and color pattern consisting in white, red, and black rings around the body, with one white between two black rings (CABRAL; CACCIALI; SANTANA, 2022; CEI, 1993).

In this research we used mitochondrial genes for assessing the genetic structure and demographic history of *Erythrolamprus poecilogyrus caesius* and what drives the diversification of *Xenodon pulcher* and *X. matogrossensis*, to answer the following questions: 1) Is there a differentiation between the populations of *E. poecilogyrus caesius* in the Chaco? 2) Have the Pleistocene glaciations or marine introgressions influenced the genetic structure of *E. poecilogyrus caesius*? 3) and at what time and during what event mentioned above occur the split between *X. pulcher* and *X. matogrossensis*?

18 MATERIALS AND METHODS

18.1 Data sampling and laboratory methods

We obtained 21 tissues from 15 localities of *Erythrolamprus poecilogyrus caesius* in the Chaco, and 10 tissues (five each each) of *X. pulcher* (5 localities) and *X. matogrossensis* (3 localities) from areas between transition of the Chaco and Pantanal, and inside Chaco and Pantanal. Tissues samples were kindly provided by the following institutions: Instituto de Investigación Biológica del Paraguay (IIBP), Asunción, Paraguay; Colección del Laboratorio de Genética Evolutiva, Posadas, Argentina (LGE); Coleção Zoológica Universidade Federal Mato Grosso do Sul, Campo Grande, Brazil; and the personal collection of Vanda L. Ferreira, from the UFMS. We used the phenol-chloroform extraction protocol (SAMBROOK; FRITSCHE; MANIATISR,

1989), and the DNeasy Blood and Tissue kit, Qiagen, Valencia, CA, USA extraction protocol following the manufacturer's protocol. For the three species, we amplified the partial sequences of the mitochondrial Cytochrome b (CytB), this gene is helpful in determine phylogenetic relationships due to its variability (SEDDIGH; DARABI, 2018), using the standard Polymerase Chain Reaction (PCR) technique as described by (CARVALHO et al., 2020; MORAES-DA-SILVA et al., 2019; POOK; WÜSTER; THORPE, 2000).

18.2 Molecular methods

We aligned the sequences with the ClustalW algorithm (SIEVERS et al., 2011) and checked by eye in Geneious 9.1.2. The final alignment consists of 549 bp for *Erythrolamprus poecilogyrus caesius* and 908 bp for *Xenodon pulcher* and *X. matogrossensis*. We used PartitionFinder 2 to identify partitioning schemes and the most appropriate nucleotide replacement models (LANFEAR et al., 2017). Two partitions were identified for *E. poecilogyrus caesius* with the best nucleotide substitution models being HKY+I and TRN+I, also two partitions were identified for *X. pulcher* and *X. matogrossensis* alignment, with the best nucleotide substitution models being TRN and HKY+G.

We analyzed our sequence data using Bayesian inference (BI), conducted in BEAST and construct a calibrated phylogeny to delimitate our lineages. We ran two independent runs of four Markov chains for 10 million generations sampling every 1,000 generations and discarding 10% as burn-in. We evaluated the stability of the analysis in Tracer v1.6, ensuring that all ESS values were above 200 (RAMBAUT et al., 2014). We used a Yule Process as a more simplified speciation model, and a Strict clock using the mutation rate of CytB (1.34% per million of year, DAZA et al., 2009). This mutation rate was used because fossil record of Dipsadidaeis very limited, thus our calibration point would not be accurate, also this rate is often used in several

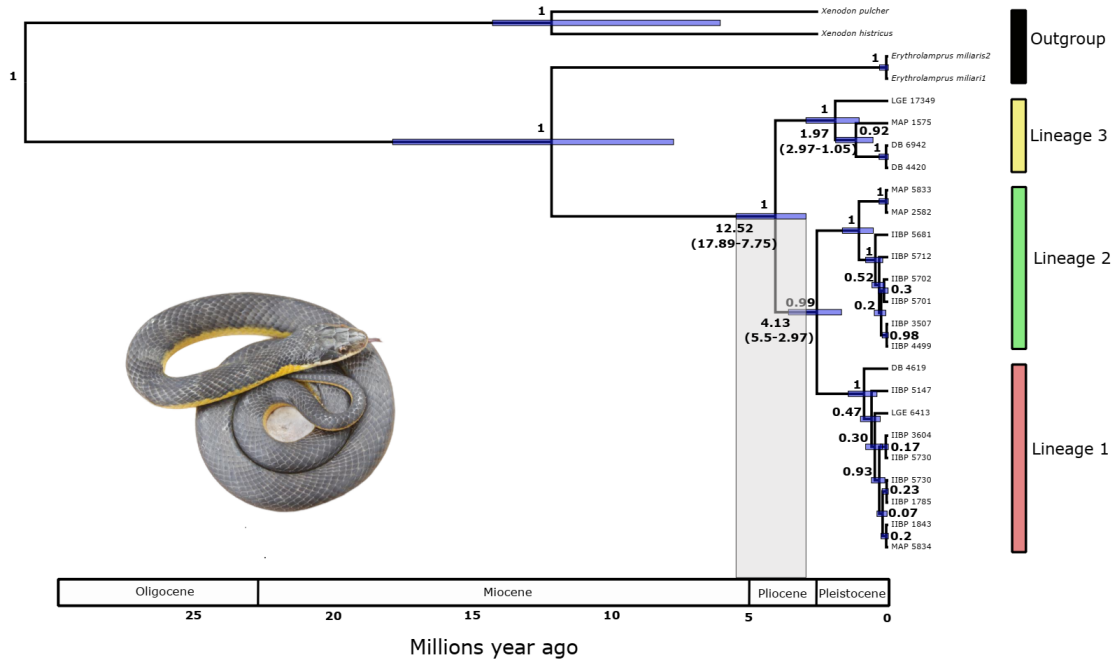
phylography studies of snakes (DAZA et al., 2009; CARVALHO et al., 2020). These parameters were conducted to estimate a species tree and diversification-time estimation for the phylogeographic analysis of *E. poecilogyrus caesius* and diversification between *X. pulcher* and *X. matogrossensis*. For the phylogeographic analysis of *Erythrolamprus poecilogyrus caesius* we used the following outgroups available on GenBank: *Xenodon pulcher* (accession number GQ895877.1), *X. histricus* (JQ598962.1), and *E. miliaris* (JQ598931.1 and KX694884.1), we choose those outgroups because *Xenodon* is the sister genus of *Erythrolamprus*, and *E. miliaris* is a sister species of *E. poecilogyrus caesius* (GRAZZIOTIN et al., 2012; ZAHER et al., 2009). For analyzing the diversification of *X. pulcher* and *X. matogrossensis* we used *Xenodon histricus* as an outgroup (JQ598962.1), we selected this species as outgroup because is the sister species of *X. pulcher* and *X. matogrossensis* (GRAZZIOTIN et al., 2012; ZAHER et al., 2009).

We used two approaches to identify the genetic structure in *Erythrolamprus poecilogyrus caesius*: we choose these methods because they are recommended for a single locus analysis; assemble species by automatic partitioning (ASAP) (PUILLANDRE; BROUILLET; ACHAZ, 2021) and Single threshold (GMYC) (FUJISAWA; BARRACLOUGH, 2013). The first method identifies barcode gaps which can be used to distinguish intraspecific differences caused by the divergence between species (PUILLANDRE et al., 2012). The second method uses an ultrametric tree to estimate the coalescence process of alleles and cladogenesis (FUJISAWA; BARRACLOUGH, 2013). We used this approach because single-locus methods are to be used as a first step of the species delimitation (PUILLANDRE; BROUILLET; ACHAZ, 2021).

We generated a haplotype network using the Median Joining Networks algorithm in PopART (BANDELT; FORSTER; RÖHL, 1999). Haplotype networks use any grouping to verify genealogical relationships and haplotype frequency (e.g., populations or localities)

(BANDELT; FORSTER; RÖHL, 1999). We used the lineages delimited with ASAP and GMYC to group the populations. For testing isolation by distance (IBD) we perform a Mantel test in Alleles in Space 1, genetic and geographic distance were calculated also in Alleles in Space 1 (MILLER, 2005). To assess genetic diversity, we estimate haplotype (Hd) and nucleotide diversity (π), number of polymorphic sites (S), and number of haplotypes (H). We also apply neutrally tests of Tajima's *D* (TAJIMA, 1989) and Fu's *Fs* (FU, 1997) to detect significance deviance from the null hypothesis of neutral evolution and constant population size. All statistics were performed in DnaSP software (ROZAS et al., 2017). We perform an analysis of molecular variance (AMOVA) to detect population differentiation, using the lineages/cluster define with ASAP and GMYC, performed in Arlequin software (EXCOFFIER; LISCHER, 2010), data were previously prepared in DnaSP.

Figure 1. Calibrated tree of *E. poecilogyrus caesius* samples in the Chaco. Number above the nodes represent the posterior probability. The light blue bar and numbers at the bottom of the nodes represents the 95% highest posterior density (HPD). Grey bar is showing the 95% highest posterior density (HPD). Grey bar is showing the 95% HPD split of the lineages of *E. p. caesius* in the Chaco. Colors at the right represent the lineages define by GYMC and ASAP. At the left an illustrative photograph of the typical coloration of *E. p. caesius* from the



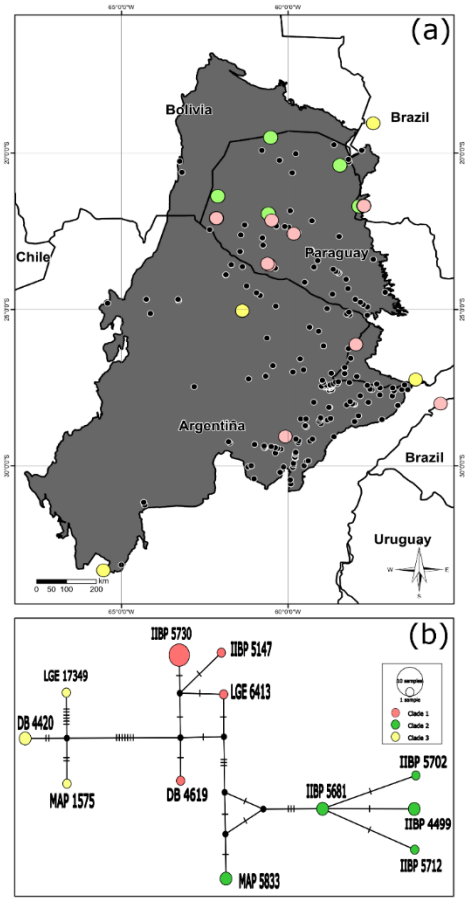
We perform a Bayesian Skyline analysis in Beast to analyze the historical demography of *Erythrolamprus poecilogyrus caesius.* This methodology allows us to estimate historical patterns of population size from a genealogy (DRUMMOND et al., 2005). We used the same mutation rate described above, and the same parameters, however in this case we ran two independent iterations of four Markov chains for 20 million generations sampling every 2,000 generations. We evaluated the stability of the analysis and performed a Bayesian Skyline Reconstruction in Tracer v1.6, ensuring that all ESS values were above 200 (RAMBAUT et al., 2014).

19 RESULTS

19.1 *Erythrolamprus poecilogyrus caesius*

We found three lineages of *Erythrolamprus poecilogyrus caesius* in the Chaco (Fig. 1) using two different methods (ASAP and GMYC). The southern lineage is composed of specimens from southeast of the Chaco in Argentina, the east of Chaco in Brazil, and center of the Chaco in Paraguay with high support (posterior probability (PP=1); the northern lineage occurs in northern part of the Chaco in Paraguay and east of the Chaco in Brazil (PP=1), and the third lineage is composed of one specimens from the southern part of the Chaco, one from the east part of the Chaco in Argentina and one in the northeast of the Chaco in Brazil (PP=1). The estimate time of split of lineages occur at 4.13 mya (5.5-2.97 mya of highest posterior density, HPD) (Fig. 1). Three haplogroups were define with our data (Fig. 2). The haplotype genealogies showed no shared haplotypes within *Erythrolamprus poecilogyrus caesius* samples. The northern lineage was grouped in one haplogroup with five haplotypes and his distributed at the north of the Chaco in Paraguay and Brazil; the southern lineage was grouped in another haplogroup with four haplotypes, distributed at the southeast of Argentina, east of the Chaco in Brazil and center of the Chaco in Paraguay and the third haplogroup with three haplotypes populations in the south and east of the Chaco in Argentina and northeast of the Chaco in Brazil (Fig. 2).

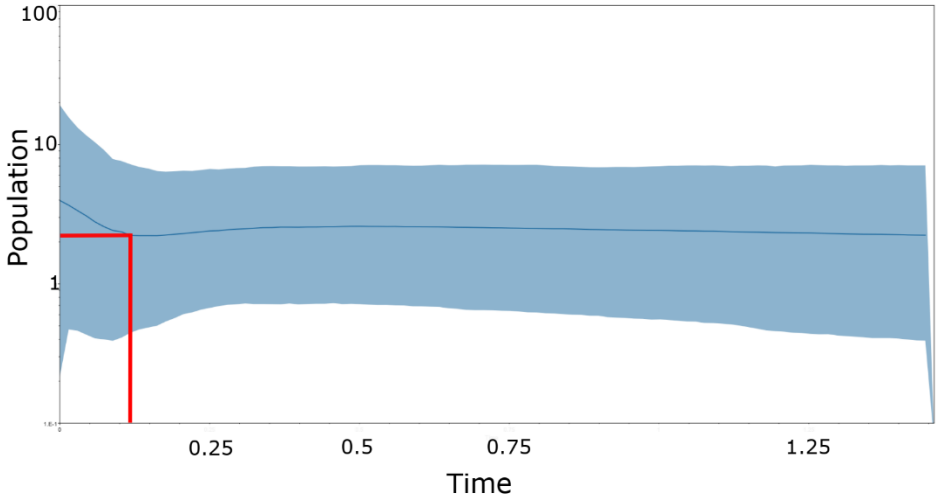
Figure 2. Distribution of analyzed samples of *Erythrolamprus poecilogyrus caesius* in the Chaco (grey area) (a) Distribution (black points) of *E. poecil*ogyrus and tissue samples analyzed (rose, green and yellow points) separated by the lineage identify. (b) Mitochondrial haplotype networks of *E. p. caesius* in the Chaco. Colors represent to each lineage found in the GYMC and ASAP analysis. Black dots indicate unsampled mutations, and circle size corresponded to haplotype frequencies.



Mantel test results showed no isolation by distance among populations of *Erythrolamprus poecilogyrus caesius* (r=0.7, p=0.7). We found high levels of haplotypic diversity (Hd=0.9) and nucleotide diversity (π=0.02). Recent population expansions were not supported by the neutrality test (D=-0.1, pp=0.5; Fs= -0.01, p=0.5). Genetic variation is higher inside Fst=0.52 than between

lineages (Fst=0.48), populations are in demographic stability. Bayesian skyline analysis showed that there is no evidence for recent expansion thought time in *E. poecilogyrus caesius*.

Figure 3. Bayesian skyline plots (BSP) of mitochondrial data of *E. poecilogyrus caesius*. Red line represents the mean and 95% highest posterior density limits for the effective population size per generation time (y-axis). The x-axis shows the time in millions of years.



19.2 *Xenodon pulcher* and *X. matogrossensis*

The analysis for *Xenodon pulcher* and *X. matogrossensis* show shows two well-differentiated lineages with high support (both with PP=1) for *Xenodon* species. *Xenodon pulcher* and *X. matogrossensis* split 5.75 mya (4.47-7.15 mya 95% HPD) (Fig. 4), at the end of the Miocene and beginning of Pliocene. Also, both species started their diversification recently at 2.22 mya (1.57-2.94 mya 95% HPD) and 2.22 (1.36-3.15 mya 95% HPD), during the Pleistocene (Fig. 4).

20 DISCUSSION

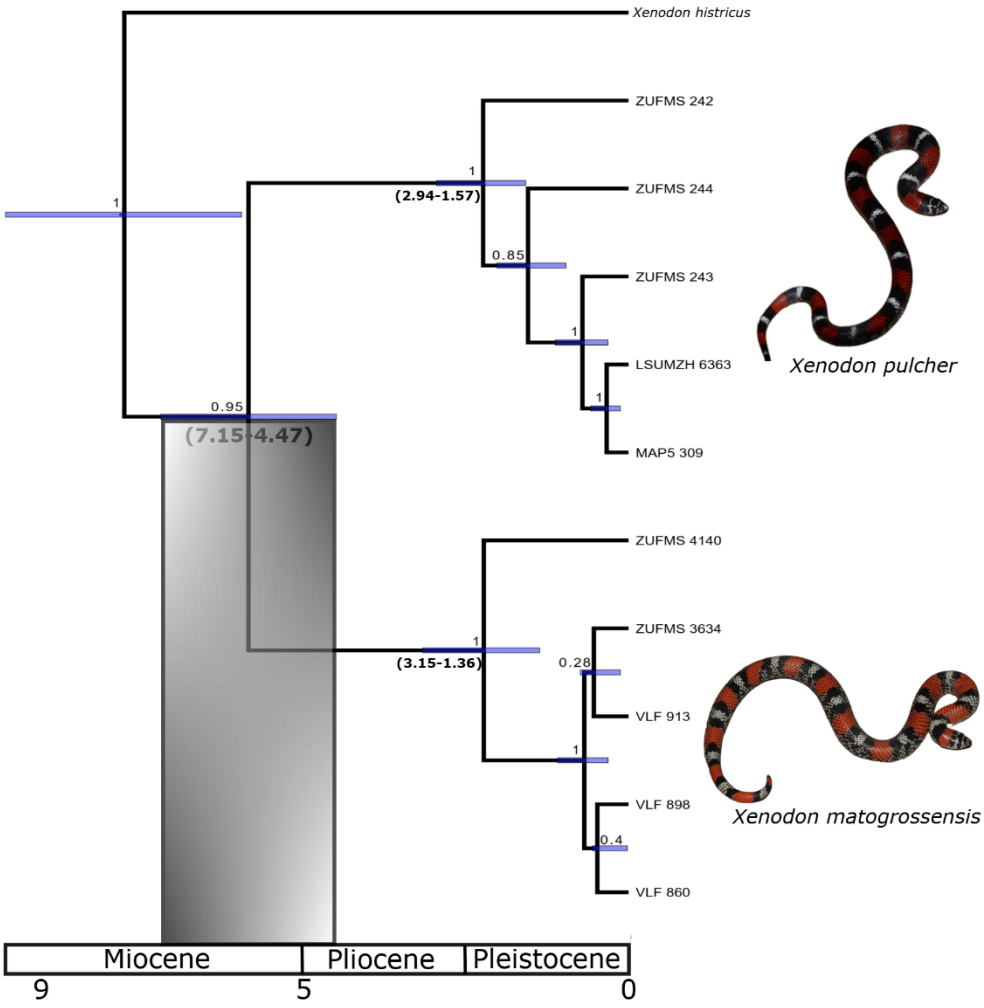
20.1 Phylogeography of *Erythrolamprus poeciogyrus caesius*

We found three lineages with structuration within the mitochondrial genealogy of *E. poecilogyrus caesius*, with no haplotype sharing, which is consistent with the geographic distribution of the specimens. We found high haplotypic and nucleotide diversity within each

lineages in *E. poecilogyrus caesius*, the neutrality test shows no recent expansion in *E. poecilogyrus caesius*, which is corroborated in the Bayesian Skyline plot, suggesting that a climatic refugia during marine introgressions and glaciations in the late Pleistocene have influence genetic structure of *E. poecilogyrus caesius* (Fig. 2-3), which agree for other populations of species in the Chaco (BRUSQUETTI et al., 2018, 2019; DELSUC et al., 2012).

Species with large geographical distributions in the dry diagonal may have limited gene flow across their range due to isolation by distance (VAN STRIEN; HOLDEREGGER; VAN HECK, 2015; WRIGHT, 1946). However, our results were not congruent with this since we found no isolation by distance in *E. poecilogyrus caesius*. The isolation by distance in populations with continuous distribution occur when dispersion capacities decrease with increasing geographical distance (HARDY; VEKEMANS, 1999), which is not the case of *E. poeciogyrus caesius* which probably have more dispersion capacities along their distribution in the Chaco (ROCHA et al., 2020).

Figure 4. Calibrated tree of *Xenodon pulcher* and *X. matogrossensis*. Number near at the nodes represent the posterior probability. The light blue bar at the nodes represents the 95% highest posterior density (HPD). Grey bar is showing the 95% HPD split of the of *X. pulcher* and *X. matogrossensis*. At the right can be notice an illustrative photograph of *Xenodon pulcher* and *X. matogrossensis* (Photographs of Marcio Martins).



We found that lineage 3 diverge from lineage 2 and 1 at 4.13 mya and lineage 2 diverge from lineage 1 at 2.62 mya, during events occurring during the Pliocene and beginning of Pleistocene (Fig. 1), probably related to the end of marine introgressions, climatic oscillations (ORTIZ-JAUREGUIZAR; CLADERA, 2006; WERNECK et al., 2012). Marine introgression and the Pliocene and Pleistocene fluctuations and glaciations probably have influenced the

genetic and demographic structure of *E. poecilogyrus caesius*. This habitat fragmentation because of changes during the marine introgressions and glaciations and oscillations associated with global climate cycles have impacted the evolution of the organisms (ROCHA et al., 2020). During this period the Paranense Sea experienced its second flooding pulse, isolating the low areas in the Chaco, which could explain the distribution of our third lineages (HERNÁNDEZ et al., 2005; RUSKIN et al., 2011).

20.2 Diversification of *Xenodon pulcher* and *X. matogrossensis*.

The split between *Xenodon pulcher* and *X. matogrossensis* diverge during the Mid-Late Miocene (Fig. 4). A possible explanation for the split of both species are the marine introgressions during the Mid-late Miocene, which are being reported for other organisms in the Chaco (BRUSQUETTI et al., 2018; DELSUC et al., 2012). *Xenodon pulcher* started its diversification during the Pleistocene (a period with heavy climatic oscillations), which is marked by an increase in temperature and drier conditions (ORTIZ-JAUREGUIZAR; CLADERA, 2006).

Considering *X. matogrossensis* we believe that the formation of the Pantanal Basin has directly influenced the diversification and differentiation of the species. Tectonic activity during late Miocene drastically modifies this region, with subsidence of depressions and intensification of their differences in relation to other South American regions (ASSINE et al., 2016). This changes in the habitat causing the depression of land in the Pantanal with flooded areas, which have probably act as drivers of diversification of the species. This probably influence the differentiation of *X. matogrossensis*, this species is highly related to sand areas in the Pantanal, which are not fully flooded in the Pantanal.

As was reported in other research, marine introgressions, and the events occurring during Pliocene/Pleistocene have shaped and were important drivers in the process of shaping the biota

of southern South America, in this case snakes in the Chaco (BRUSQUETTI et al., 2018, 2019; CAMPS et al., 2018). We think that the evolution of fossorial habits related to abiotic factors along with the events occurring during this period have influenced the diversification process of *X. pulcher* in the Chaco and *X. matogrossensis* in the Pantanal. Nevertheless, we believe that with more data and other analysis we can have a better understanding of the evolutionary process of the Chaco and Pantanal. In this sense, this represents the first integrative approach that evaluated the evolutionary processes that have shaped and influenced the distribution of snakes in the Chaco.

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21 CHAPTER 4. A NOT PROMISING FUTURE FOR THE SNAKES OF THE GRAN CHACO: IMPACT OF CLIMATE CHANGES IN SNAKES COMMUNITY

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22 ABSTRACT

The impacts of anthropogenic activities largely contributed to recent and future climate changes worldwide. The future impacts on biodiversity produced by climate change have been intensively investigated in the last two decades around the globe. Dry ecoregions are currently considered the most threatened ecosystems in the world. In South America, those dry ecoregions are the Cerrado, Caatinga and the Gran Chaco. Of those three, and the Chaco. Of those three, the Chaco has been suffering high deforestation rates and landscape degradation in the last 10 years, making it a priority area for conservation. In this work, we estimate by ecological niche modeling, the present and future distribution area of snakes, to assess how the future snake richness will changes with climate changes across the geographic space in the Chaco. We found that snakes' assemblages in the Chaco would change with future climatic conditions, with a clear trend to biotic homogenization of the ecoregion with a decrease of species richness. These negative changes would be reflected in the protected areas of the Chaco, with suffering biotic homogenization, and loss of species richness. Urgent changes are needed, if we want to prevent the impacts of climate changes and the loss of habitats in the Chaco and maximize the conservation of species.

Keywords: Biotic Homogenization. Conservation. Functional diversity. Phylogenetic diversity. South America.

23 INTRODUCTION

The impacts of anthropogenic activities largely contributed to recent and future climate changes worldwide, of those impacts the deforestation is one of the most important with negative effects on biodiversity (BELLARD et al., 2012; HIDASI-NETO et al., 2019; MOONEY et al., 2009; ZANK et al., 2014). These impacts and their consequences would disproportionately affect ecosystems with some regions being more affected than others (DRYFLOR et al., 2014; HIDASI-NETO et al., 2019; KUEMMERLE et al., 2017b; LOARIE et al., 2009). These regions would suffer drastic changes in climate conditions (e.g., intense drought, heat waves, storms), mainly due to by their lack of topographic complexity (HIDASI-NETO et al., 2019; LOARIE et al., 2009), with negative impacts on their biodiversity.

The future impacts on biodiversity produced by climate changes have been intensively investigated in the last two decades in different regions around the globe (e.g., HIDASI-NETO et al., 2019; LOURENÇO-DE-MORAES et al., 2019; MEDINA; PONSSA; ARÁOZ, 2020; NAVAS; OTANI, 2007; ZANK et al., 2014). Climate change produces species-specific responses and, the co-occurrence patterns are also likely to be modified, resulting in a reorganization of assemblages (PETERSON et al., 2002; WALTHER, 2010). This reorganization of assemblage can make those assemblages more homogeneous, with a decrease in the number of specialists, restricted and endemic species, with the replaced by widespread and niche generalist species (CLAVEL; JULLIARD; DEVICTOR, 2011; MCKINNEY; LOCKWOOD, 1999), phylogenetic and functional diversity often also decrease. This brings consequences to ecosystems services, by potentially decreasing the resilience, stability, and adaptability of natural environments (HIDASI-NETO et al., 2019; OLDEN et al., 2004).

Moreover, current agricultural-driven habitat loss and associated anthropogenic pressures negatively affect populations by reducing landscape connectivity and the movement of individuals and genes (FAHRIG, 2003, 2007). In this sense, if species show low levels of dispersal or adaptations to climate changes, the species persistence would be threatened, or go extinct, and opportunistic and exotic species may thrive, also species related to open areas would be favored by those changes taken advantage of the savannization of the habitat (BOULANGEAT; GRAVEL; THUILLER, 2012; KISSLING et al., 2012; MEDINA; PONSSA; ARÁOZ, 2020; NIELSEN et al., 2019; SALES; GALETTI; PIRES, 2020; THUILLER et al., 2013). Deforestation for agricultural expansion is the most significant impact that affect vertebrates' abundance, and richness, increasing the extinction risk, which would have negative impacts on communities leading to regional extinction and biotic homogenization (BELLARD et al., 2012; HIDASI-NETO et al., 2019; MENÉNDEZ-GUERRERO; GREEN; DAVIES, 2020; ROMERO-MUÑOZ et al., 2020; SEMPER-PASCUAL et al., 2018).

Arid ecoregions are currently considered the most threatened ecosystems of the world (BAUMANN et al., 2017; DRYFLOR et al., 2014; KUEMMERLE et al., 2017a; WERNECK, 2011), and is expected to be more affected in future scenarios of climate change (LOARIE et al., 2009). One of those ecoregions is the Gran Chaco (hereafter, Chaco) the Chaco is highly threatened and considered one of the most extensive continuous dry forest areas in South America (BUCHER, 1982; KUEMMERLE et al., 2017a). In recent decades, the Chaco has been suffering high deforestation rates (HANSEN et al., 2013) and landscape degradation, making it a priority area for conservation (DE LA SANCHA et al., 2021; FRATE et al., 2015; KUEMMERLE et al., 2017a).

Several studies have pointed out the importance of taking conservation actions in the Chaco (KUEMMERLE et al., 2017b; NORI et al., 2016; ROMERO-MUÑOZ et al., 2020; SEMPER-PASCUAL et al., 2018). However, most of those works focused on mammals, birds, and amphibians, and evaluated just the taxonomic or conservation facet of the biodiversity (CACCIALI et al., 2016; NORI et al., 2016; ROMERO-MUÑOZ et al., 2020; SEMPER-PASCUAL et al., 2018) neglecting the non-charismatic animals such as snakes and the other facets of biodiversity. On another way, ANDRADE-DIAZ et al. (2019) identified priority conservation areas of 12 endemic snakes of the Dry Chaco. Although this work is restricted to the Dry Chaco in Argentina, it shows that expansion of the agricultural frontier has potential negative effects on the distribution of snakes in this region. Not just for the Chaco, but in the Neotropics, there is a lack of studies associating climate change and spatiotemporal biodiversity patterns (BROOK; SODHI; BRADSHAW, 2008). In addition, research seeking understand how biotic homogenization of ecosystems caused by climate change are scarcer.

In this work, using ecological niche modeling, we estimate the present and future distribution of Chacoan snakes, seeking to assess how the future snake diversity will change with climate changes across the geographic space in the Gran Chaco. We aim to answer: (1) would be a decrease in the number of the species between assembles (regional extinction) caused by climate changes, leading to a biotic homogenization? (2) Are we going to lose snake species in the Gran Chaco, phylogenetic clades, and functional diversity due to the expected changes in climate? (3) Where those changes going to happen and how are the relations of future changes in species composition within the Protected Areas of the Chaco?

24 MATERIAL AND METHODS

24.1 Study Area

The Chaco is an ecoregion, with stressful environments and marked climatic seasonality (CABRERA, 1994; PRADO, 1993), which resulted of the Andean uplift, marine introgressions, and several past alluvial systems (GREGORY-WODZICKI, 2000; HERNÁNDEZ et al., 2005; IRIONDO, 1993). The most important characteristic of the Chaco is its geomorphology, which consist in an extensive sedimentary alluvial plain with soils derived from the massive accumulation of Quaternary sediments (PENNINGTON; PRADO; PENDRY, 2000; PRADO, 1993). This region is characterized by xerophytic vegetation formed by a mosaic of grasslands, savannas, open woodlands, and thorn forest (PRADO, 1993; WILLIG et al., 2000). This area shows an impressive flattened, with scarce high-elevation hills, with few elevations' hills located mostly in their western limit in Argentina and Bolivia (PRADO, 1993).

24.2 Occurrence data

We compiled occurrence data of snakes with confirmed records in the Chaco. Occurrence data were compiled by reviewing museums and literature. We review specimens from the following collections: Museo Nacional de Historia Natural del Paraguay (MNHNP), Instituto de Investigación Biológica del Paraguay (IIBP-H), Fundación Miguel Lillo (FML), Colección Herpetologica Universidad Nacional del Nordeste (UNNEC), Laboratorio de Genetica Evolutiva/Instituto de Biología Subtropical (LGE), Coleção Zoológica da Universidade Federal Mato Grosso do Sul (ZUFMS). Occurrence data of literature were gathered from recent works (CABRAL; WEILER, 2014; CACCIALI et al., 2016; NOGUEIRA et al., 2019). We only considered accurate localities, avoiding the use of records with only information on states, departments, etc. All records were verified to make sure that species records are accurate and within the species distribution (Neotropics). We also discarded duplicated records (same species,

different specimen, same locality), this procedure was made with CoordinateCleaner package in R The final occurrence data consist on 51081 records of 141 species (Table S1).

24.3 Climatic data

We download 19 climatic variables from WorldClim at 10arc-min (~20km) resolution (FICK; HIJMANS, 2017). Present variables cover aspects of precipitation and temperature of the world between 1950-2000, and future variables cover between (2081-2100) (IPCC, 2021). For future, we considered the non-mitigation scenario (SSP585) from Shared Socioeconomic Pathways (SSP). We choose only this scenario because in the Chaco actions to mitigate climate change are scarce, and the ecoregion are facing real challenges for mitigate future impacts of climate change in the biodiversity (BAUMANN et al., 2017; GRAU; GASPARRI; AIDE, 2005; KUEMMERLE et al., 2017b; MERELES; RODAS, 2014). We used three generalized circulation models (GCM) CNRM-CM6-1, MIROC6 and MRI-ESM2-0 for future climate projections, because the selection of different GCM is recognized as a source of uncertainty in projecting the future habitat suitability of species.

24.4 Ecological niche modeling

Ecological niche modeling (ENM) was performed with package ENMTML (ANDRADE; VELAZCO; DE MARCO JÚNIOR, 2020) in R (R CORE TEAM, 2019). This package provided a series of options for niche modelling. For the pseudoabsence allocation method we used the RND method, which is the random allocation of pseudo-absences throughout the area used for model fitting, and a presence-absence ratio of 0.5 (ANDRADE; VELAZCO; DE MARCO JÚNIOR, 2020). We performed ENM using three different algorithms, combining the prediction of them, since this is recommended to detect the best model of uncertainty (ALENCAR et al., 2022; ARAÚJO; NEW, 2007; NORBERG et al., 2019; THUILLER et al., 2019). Therefore, we

used the following algorithms: Bioclim BIO (presences) (HIJMANS; ELITH, 2017), Maximum Entropy default (all features) MXD (PHILLIPS, 2021), (presence and background points) and Generalized Linear Models GLM (presence and pseudoabsences). For the threshold of presence-absence predictions, we used Jaccard similarity index (LEROY et al., 2018). To reduce multicollinearity, we perform a Principal Component Analysis (PCA) to reduce the dimensionality of the bioclimatic data and retained the first six axes representing the principal components as climate predictors (Supplemental Material). When modeling future ENM we used the occurrence-based restriction (OBR), which uses the distance between points to exclude far suitable patches, to apply spatial restrictions to model projection (future) (ANDRADE; VELAZCO; DE MARCO JÚNIOR, 2020).

The best model was created based on the ensemble procedure, calculated by the arithmetic average of the suitability of the best algorithms, best algorithms was evaluated with the weighted average of models based on their performance, in this case using average Jaccard (ANDRADE; VELAZCO; DE MARCO JÚNIOR, 2020). Cross-validation of the models was performed by the method of random bootstrap partition, with two replicates with 70% of data used for model training, and 30% for model testing (ANDRADE; VELAZCO; DE MARCO JÚNIOR, 2020). We create ENM for species with minimum of 10 records. Our final database has 141 snake species with occurrence record in the Chaco, of those we generated ENM models for 125 species (Supplemental Material). We create ENM of species in the entire Neotropics (background area).

24.5 Presence-absence matrix

With the ENM data, we then create a presence-absence matrix of the present and future to perform subsequent analysis. The presence-absence matrix data were saved with grid of

10x10km of spatial resolution. We also calculated the species geographic range shifts between temporally different scenarios, in the entire distributions of species and within our study area. We estimated the area of polygons in km^2 of each species, for calculating the expected changes in species ranges and assemblages of widely and narrowly distributed species. Species with less than $50km^2$ where define as narrowly distributed and more than $50km^2$ as widely distributed.

24.6 Phylogenetic procedure

To compute the phylogenetic metrics, we pruned the phylogeny of TONINI et al. (2016), to include only the species in our study area. If species were absent in the phylogeny, or with other names, we replaced it by the correct names, or added the species based on the phylogenetic relationship artificially at the genus-level (or another desired clade). This procedures of manipulating the phylogeny were made with packages *phangorn* (SCHLIEP, 2011) and *ape* (PARADIS; CLAUDE; STRIMMER, 2004).

24.7 Functional data

To compute functional diversity, we created a matrix of attributes (Table S8) with the potential to link morphological, physiological, and phenological variations at individual level to ecosystem processes and patterns (BERRIOZABAL-ISLAS et al., 2017; FELDMAN et al., 2016; PETCHEY; GASTON, 2006; TODD et al., 2017). These attributes were related to body size, reproduction strategies, microhabitat use, and daily activity. Data were gathered from CABRAL et al. (2022) (see Supplemental Material). From this matrix, we generated a multidimensional space, in which functional diversity indices were computed by performing a PCoA using the trait-based distances (MOUILLOT et al., 2013). Then we evaluated the quality of PCoA-based multidimensional spaces according to the deviation between trait-based distances and distances in the functional space (MAIRE et al., 2015) and chose the dimensionality that

shows the best fit (4 axis in our case, Table S9). From the four first PCoA axis, we created a functional dendrogram using UPGMA agglomeration method. These analyses were performed using the mFD package (MAGNEVILLE et al., 2022) in R (R Core Team, 2008).

24.8 Biodiversity metrics

We estimated beta-diversity of the current and future scenario using the package *betapart* (BASELGA; ORME, 2012). We calculated spatial beta-diversity for each grid using Jaccard multiple site dissimilarity index on the focal cell and its surrounding neighbor cells. We make a subsampling procedure to randomly select four neighbor cells around each focal cell to compute the average value of Beta-Jaccard across interactions to diminish a possible effect of cell sizes on the index (BASELGA; GÓMEZ-RODRÍGUEZ; LOBO, 2012).

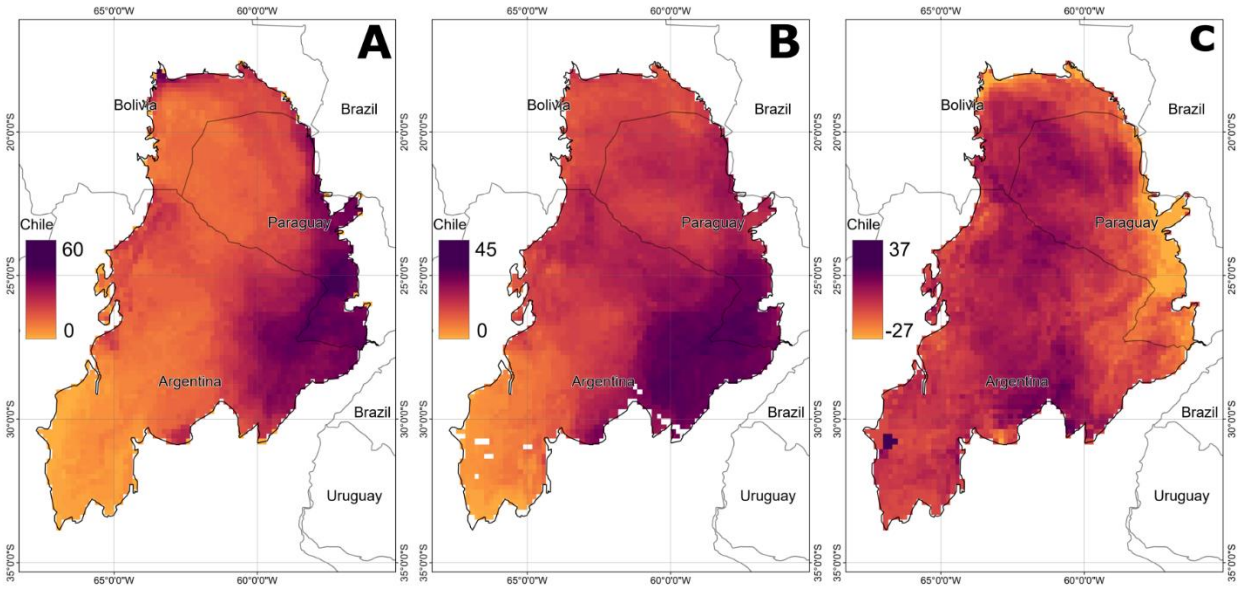
We calculated the phylogenetic-beta diversity across species assemblages for the current and future scenarios. After, we run a null model to calculate the Standardized Size Effect (SES) of the phylogenetic-beta diversity, to quantify phylogenetic diversity (PD) corrected for species richness under both current and future climate scenarios. SES was calculated by comparing observed PD values to null expectations through shuffling tip labels multiple times (1000 runs), tip shuffle model was performed in *phyloregion* package (DARU; KARUNARATHNE; SCHLIEP, 2020). Negative SES values indicate that species in the assemblages are more related than expected by chance (i.e., species are clustering in the phylogeny), and positive values indicate that species in the assemblages are less related than expected by chance (i.e., species are overdispersal in the phylogeny).

24.9 Temporal changes and Biotic Homogenization

We then calculated the temporal changes in the spatial gradients of taxonomic and phylogenetic diversity, for current and future scenarios, and the differences between current and

future scenarios, using the ratio of Beta Diversity between future and current scenarios. The differences between both, future, and present climate were used to identify assemblages subject to biotic homogenization (values < 0) or heterogenization (> 0). We also calculated the changes in species richness between current and future scenario, the proportion of widely and narrowly distributed species between species assemblages for current and future scenario, and the differences between both. Species with less than 50km^2 were define as less distributed and more than 50km^2 as widely distributed. We calculated the species distribution range considered the biology of species, since fossorial species tend to have restricted distribution, on the other hand some terrestrial and generalist species have wide range of species.

Figure 1. Current (A) and future (B) species richness from the Chaco, and the projected difference in species richness between current and future (C). For present the maximum number of species per assemblages is 60, for the future 45 and the differences between present and future show a maximum of 37 species per assemblages, with a maximum loss of 27 species.



We also calculated the temporal changes in assemblages' functional diversity to better explain the temporal changes in taxonomic and phylogenetic diversity. From the species functional dendrogram, for present and future scenarios, we calculated the standardized effect size of mean pairwise distance (SesFuncMPD) between all species in each community, using null models created with 1000 randomizations of tip labels. Significant positive values indicate greater functional diversity than null expectation and negative values indicate lower functional diversity than the null expectation. We also calculated three complementary indices for each community: Functional richness (FRic), which represents the amount of functional space filled by the community (VILLÉGER; MASON; MOUILLOT, 2008); Functional evenness (FEve), which describes the evenness of abundance distribution in a functional trait space (VILLÉGER; MASON; MOUILLOT, 2008); and Functional dispersion (FDis), which is the mean distance of individual species to the centroid of all species in the community (LALIBERTE; LEGENDRE, 2010). These analyses were performed using the mFD (MAGNEVILLE et al., 2022) and picante (KEMBEL et al., 2010) packages in R.

24.10 Biotic homogenization and Protected Areas

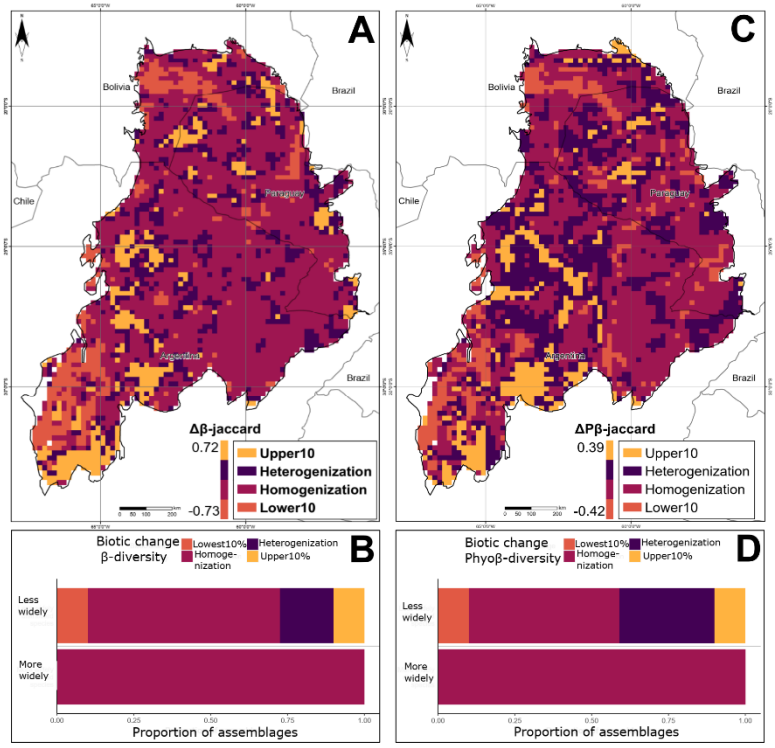
We combined the information about snakes' biodiversity in the future with the information on the terrestrial Protected Areas (PA) of the world and selected only the PA inside the Chaco with designated categories (I to IV). Information on shapefile was downloaded from WDPA; https://www.iucn.org/ theme/protected-areas/our-work/world-database-protected-areas, accessed on 16 January 2021. We combined our database of biodiversity metrics with PAs to see how biotic homogenization, would affect assembles inside PAs.

25 RESULTS

25.1 Species richness

Overall, in the future, snake richness will decrease in the Gran Chaco, with a loss of 28 species regionally. The highest species richness per regions would decrease in the future (Fig. 1A-C). The current species richness per area is more than 60 species, and future projection show that the highest species richness per area would be 40. A loss of species at local level and regional level is observed for the snakes in the Chaco, with areas that would loss 27 species (Fig. 1C). More than 20% of the species assemblages would have a decrease in richness (Fig. 1C). Changes in the composition of species is expected in the entire Chaco, and these changes are most noticeable at southern and northern parts of the Chaco (Fig. 2A-D). Furthermore, some species might likely be locally extinct, by losing their suitable habitat in the Chaco (e.g., several *Chironius* spp., *Erythrolamprus aesculapii, E. typhlus, Micrurus frontalis, Pseudoboa nigra*).

Figure 2. Spatial pattern of expected biotic homogenization of Chaco (A-D). Taxonomic biotic homogenization Δβ-jaccard) (A) and proportion of biotic changes at assemblages' levels in β-diversity in the Chaco (B); Phylogenetic biotic homogenization ΔPβ-jaccard) (C) and proportion of biotic changes at assemblages' levels in Pβ-diversity in the Chaco (D). Biotic homogenization (values < 0), heterogenization (value > 0). The 10% heterogenized assemblages (Upper 10) and the 10% more homogenized assemblages (lower 10).

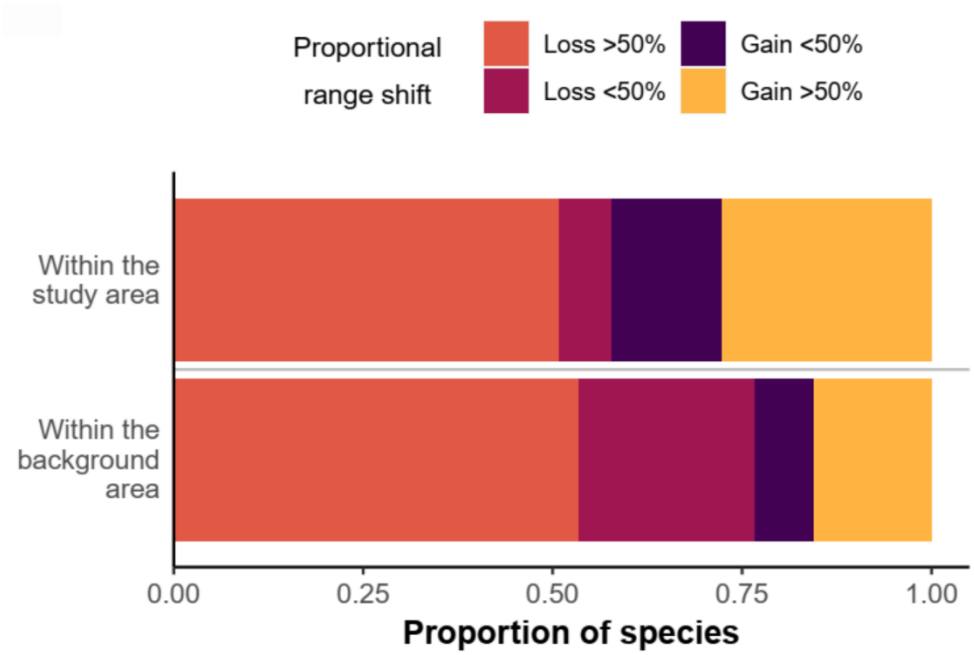


25.2 Biotic homogenization

Biotic taxonomic homogenization is expected to occur in the entire snake assemblages of the Chaco (Fig. 2A-B). Widely distributed species are present in all future assemblages, is expected the loss of less distributed species in most of the assemblages. Heterogenization with less distributed species is expected to occur in at least 30% of assembles. Also, is expected that widely distributed species will dominate the species assemblages of snakes in the Chaco (Fig. 2A-B). Biotic homogenization using phylogenetic diversity metrics shows that at least 60% of snake assemblages will suffer phylogenetic homogenization. This biotic homogenization will be frequent in the entire Chaco (Fig. 2C-D). More than 50% of the assemblage's current encompassing species with less distribution are going to suffer biotic homogenization and widely distributed species are expected to be present in 100% of the current assemblages.

Severely, more than 50% of snake species of the Chaco lose suitable areas in the future (year 2100), and more than 70% of species within their entire distribution (Fig. 3). In the Chaco and Neotropics, half of the species will loss more than 50% of their suitable areas, and only a small percentage of species will lose less than 50% in the Chaco (Figure 3). At least 20% of these species will lose less than 50% of suitable areas in their entire distribution (Fig. 2). On the other hand, almost half of the species will gain suitable areas in the Chaco, and at least 25% of the species would gain suitable areas within his distribution (Fig. 3).

Figure 3. Projected changes in species range shift between the Chaco (study area) and Neotropics.



25.3 Functional richness

The functional richness (FRic) is expected to increase by 74% in the future assemblages, but both, rises and decreases, will not modify the index value by more than 10% (Fig. 4). Changes in assemblages' functional evenness (FEve) and dispersion (FDis) were also small, around 2% and 3%, respectively. Despite these low values and the increase in FRic, almost all assemblages (93%) will probably loose species with functional attributes more distant from the centroid of the assemblage functional space (decrease their FDis) or will not show change in index with species replacement. The temporal change in FEve didn't point to any trend, with 53% of the assemblages decreasing the index value and 47% increasing it.

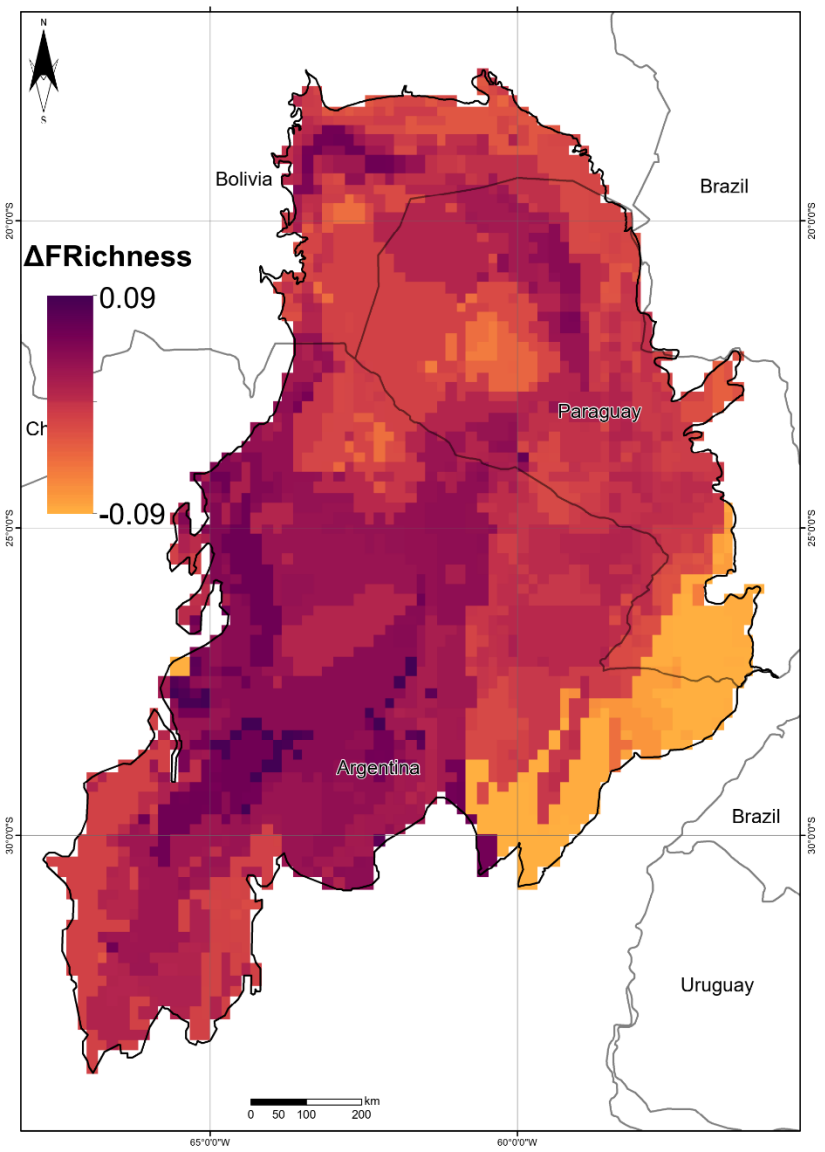
In the present and future, most Chaco snake communities showed functional diversity (SesFuncMPD, calculated from functional dendrogram) lower than the mean value of communities assembled by chance. In the future, this index will decrease even more in 74% of

the communities. However, the values are significantly different from null models in just 8.97% of the contemporary assemblages and change to 10.69% in the future snakes' communities. A summary of all functional diversity indexes is in Table S10.

25.4 Biotic homogenization and Protected Areas

In total, 56 protected areas were identified in the Chaco, with PAs concentrated in the northern, center, and south-east of the Chaco with a few PAs located in the south (Fig. 5A, Table S8). From the 56 PAs, we identify loss of species richness at assembles level in 23 PAs, in which some lose PAs lose at least 2 species, while others at least 15 species (Figure 4A). Widely distributed species are going to be present in all PAs (Fig. 5B), while some PAs would be entirely homogenized (Fig. 5C). Almost all PAs in the Chaco will also suffer from spatial-temporal changes between species composition (Fig. 5D).

Figure 4. Projected changes in Functional Richness between current and future scenarios for snakes' communities from the Chaco.



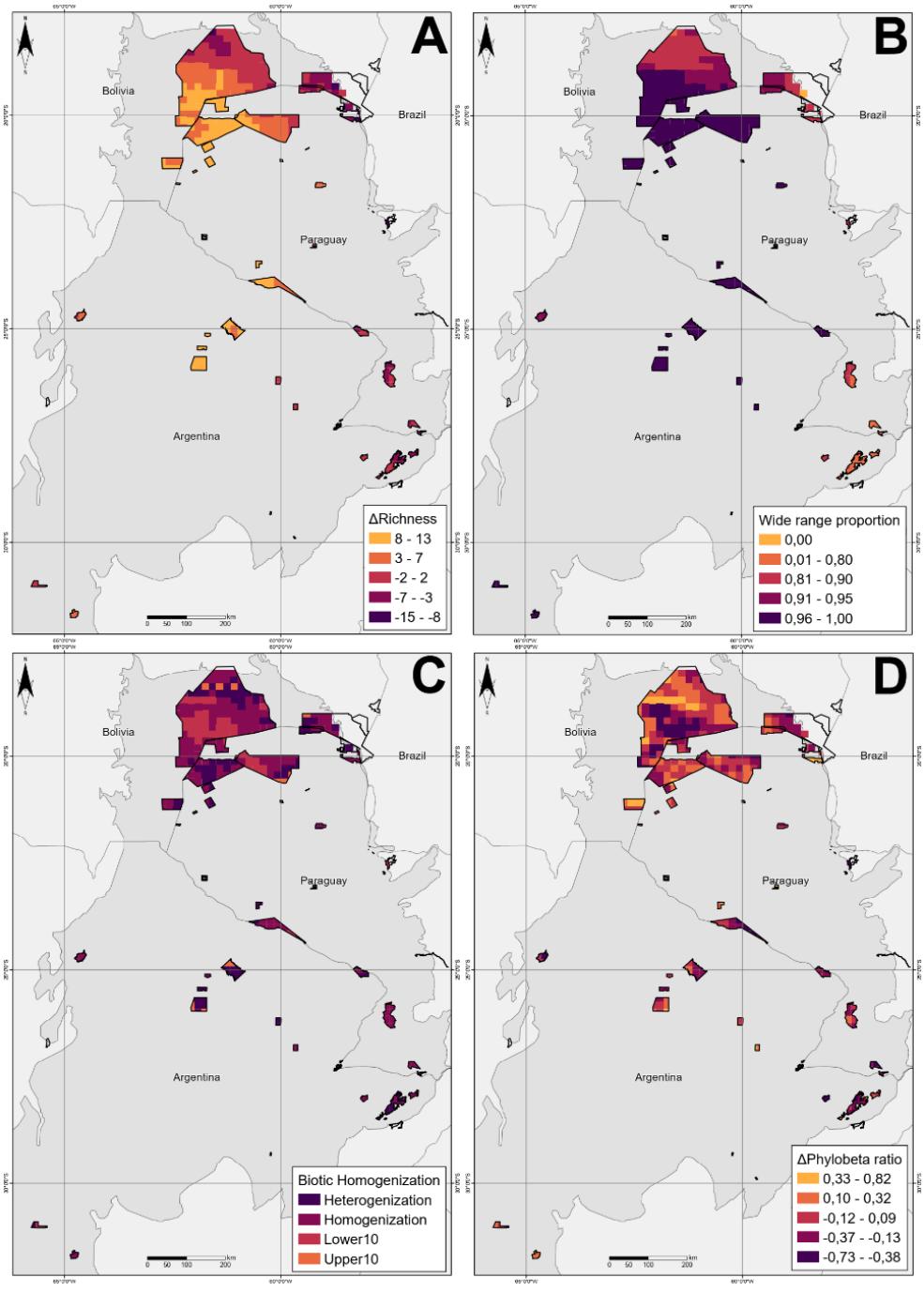
26 DISCUSSION

The ecological niche modelling estimates that snakes' assemblages in the Chaco will change with future climatic scenarios (in the year 2100), with a clear trend toward biotic homogenization throughout the ecoregion. This biotic homogenization will be characterized by the replacement of narrowly distributed species by widely distributed species, with consequent homogenization of phylogenetic and functional diversity of local assemblages. This pattern is expected in biotic

homogenization events, with a decrease in the number of specialists, restricted and endemic species, that tend to be replaced by widespread and niche generalist species (CLAVEL; JULLIARD; DEVICTOR, 2011; MCKINNEY; LOCKWOOD, 1999). Any changes in the forested environment, have negative consequences for species associated with forest habitats. In this sense, the replace of forest by open areas tend to produce a savannization effect, with increasing the number of species related in open areas in areas where landscape was replaced from forest to open areas (SALES; GALETTI; PIRES, 2020).

Our estimations about taxonomic, phylogenetic, and functional diversity in future scenarios agree with a species replacement driven by the restriction of species occurrence due to their habitat requirements and vegetation change (BASELGA; GÓMEZ, 2019; BASELGA; ORME, 2012; OLDEN et al., 2004). For example, the trend to the future assemblages had lower functional diversity than the expected by chance (decreasing of SESMPD values in the future, compared to present values). This indicates that the environmental restriction will play an important role in assembling future snake communities, preventing some species with specific ecomorphological traits to remain in modified areas (OLDEN et al., 2004). At the same time, the small increase in functional richness in almost all snakes' communities in the future (Fig. 4) probably is an outcome of the entry of widely distributed species (habitat and morphology generalists, or with typically fossorial morphologies). This also causes a decrease in the values of functional dispersion in these assemblages, because they probably will be dominated by snakes with morphology more like each other's (OLDEN et al., 2004; BERRIOZABAL-ISLAS et al., 2017).

Figure 5. Expected changes in Protected Areas in the Chaco, richness (A), proportion of widely distributed species (B), biotic homogenization (C), and spatial temporal changes in species composition (D).



Negative effects of biotic homogenization would be reflected in phylogenetic diversity, because a reduction in the number of species, or less diverse assembles would make the phylogenetic diversity in the entire area and between communities decrease. Phylogenetic diversity measures to what extent these assemblages differ in terms of the evolutionary relationships of their members (GRAHAM; FINE, 2008; LEPRIEUR et al., 2012). Biotic homogenization in Chaco, would lead to species assemblages becoming less diverse, with significant consequences in the ecosystems, probably leading to reductions in overall community ecosystem function, stability, and adaptability (OLDEN et al., 2004). The homogenization would also impact the resilience of communities to environmental disturbances by preventing the colonization of species regionally extirpated (OLDEN et al., 2004). Those changes are distributed among the entire Chaco.

Many studies show the effects of climate changes on South America biodiversity in long periods (future scenarios), with a decrease in species richness due the loss of suitable areas of species and homogenizing the environment (ANDRADE-DÍAZ et al., 2019; HIDASI-NETO et al., 2019; LOURENÇO-DE-MORAES et al., 2019; ROMERO-MUÑOZ et al., 2020). ANDRADE-DÍAZ et al. (2019) have demonstrated negative impacts of the agricultural frontier on endemic snakes of the Chaco, and here we reinforced that.

Deforestation in the Chaco is leading to the fragmentation of habitats, which provoke a reduction in the number and composition of species in the Chaco and represent an important driver in climate change (KUEMMERLE et al., 2017b; MERELES; RODAS, 2014; ROMERO-MUÑOZ et al., 2020; SEMPER-PASCUAL et al., 2018). Deforestation in the Chaco is related to cattle ranch and agricultural activities (BAUMANN et al., 2017; MERELES; RODAS, 2014; VALLEJOS et al., 2015; WWF, 2021) and has increased in the last 20 years (HANSEN et al.,

2013; MERELES; RODAS, 2014). This fragmentation not only affects biodiversity, but also have their effect on species of fauna and flora that will be affected by the climate changes and the landscape composition (MERELES; RODAS, 2014). These effects may result in population reductions, as some species are unable to adapt to these changes in such a short space of time (MERELES; RODAS, 2014).

The negative impact of climate change would be reflected in the PAs of the Chaco, with many PAs suffering biotic homogenization, and loss of species richness. This reinforces the idea that Chaco is a priority area for conservation, and conservation actions should seek to maximize the conservation of biodiversity in this threatened region (NORI et al., 2016; ROMERO-MUÑOZ et al., 2020; SEMPER-PASCUAL et al., 2018; WWF, 2021). Current PAs in the Chaco are isolated and may not be enough for the conservation of vertebrates (NORI et al., 2016). As stated by KUEMMERLE et al. (2017a), the Chaco is threatened and should not be neglected when raising awareness of the urgent conservation needs in the often-forgotten Neotropical dry forests. Urgent actions are needed, if we want to prevent the impacts of climate changes and the loss of habitats in the Chaco and maximize the conservation of species.

In conclusion, snakes' assemblages in the Chaco would change with climatic scenarios in a near future (in the year 2100), with a clear trend to the biotic homogenization of the ecoregion. This biotic homogenization would be characterized by the replacement of narrowly distributed species by widely distributed species, with consequent homogenization of phylogenetic and functional diversity of local assemblages. Moreover, some species might likely be locally extinct, by losing their suitable habitat in the Chaco. Negative effects of biotic homogenization would be reflected in the phylogenetic diversity, because a reduction in the number of species, or less diverse

assembles. These negative changes would be reflected in the PAs of the Chaco, with many PAs suffering biotic homogenization and loss of species richness.

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APPENDIX A

The code and supporting information that supports this work is freely available at https://github.com/hugodryas/ENM-of-Chacoan-snakes. This dataset contains more than 50.000 unique records of snakes from the Chaco (more than 1.000 pages).

27 FINAL CONCLUSIONS

1. In *Xenodon* species with Batesian mimicry, and semi-fossorial habits with a preference for open areas, the rostral scale was modified as a shovel for burrowing. On the other hand, in species with terrestrial habits, their rostral scale remained rounded, probably due to the association for forested habitats. In conclusion, the evolution of the rostral scale in *Xenodon* may be related to abiotic factors, as an adaptation for open and forested habitats, and mimicry are related to the presence of venomous species like *Bothrops* or *Micrurus*, which through imitating them serve as a defensive strategy.
2. We present the first integrative approach that investigated macroecological and biogeographic patterns and the phylogenetic relationships of the Chacoan snakes, which represent a unique area. We found that as arboreality increases towards the north, fossoriality increases towards the south. The environmental pattern represents a marked vertical stratification in the Chaco, increasing as habitat heterogeneity increases. Fossoriality is strongly correlated with and thus driven by soil conditions. The distribution pattern in the Chaco is also explained by the evolutionary history of snakes in this region, with a marked phylogenetic regionalization.
3. As was reported in other research, marine introgressions, and the events occurring during Late Miocene and Pliocene/Pleistocene have shaped and were important drivers in the process of shaping the biota of southern South America, in this case snakes in the Chaco. However, the formation of the Pantanal has never been proposed as a driver of diversification for reptiles. We think that the evolution of fossorial habits related to abiotic

factors along with the events occurring during this period have influence the diversification process of *X. pulcher* in the Chaco and *X. matogrossensis* in the Pantanal. Nevertheless, we believe that with more data and other analysis we can have a better understanding of the evolutionary process of the Chaco and Pantanal. This represents the first integrative approach that evaluated and try to understand the evolutionary process that have shape and influence the distribution of snakes in the Chaco.

4. We found that snakes' assemblages in the Chaco would change with climatic scenarios in a near future (in the year of 2100), with clear trend to the biotic homogenization of the ecoregion. This biotic homogenization would be characterized by the replacement of less distributed species by widely distributed species, with consequent homogenization of phylogenetic and functional diversity of local assemblages. Also, it is likely that some species might be locally extinct, by losing their suitable habitat in the Chaco. Negative effects of biotic homogenization would be reflected in the phylogenetic diversity, because a reduction in the number of species, or less diverse assembles would make that the phylogenetic diversity in the entire area and between communities decrease. These negative changes would be reflected in the PAs of the Chaco, many PAs would suffering biotic homogenization, and loss of species richness.