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Climate change in open environments: Revisiting the current distribution to understand and safeguard the future of psammophilous squamates of the Diagonal of Open Formations of South America

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ABSTRACT

To identify regions that contribute to the persistence of biodiversity, we (1) predict the potential distribution of the psammophilous squamate species endemic of the Diagonal of Open Formations (DOF) in the current climate, (2) identify survey priority areas, (3) estimate the impacts of climate change in two future CO_2 emission scenarios, and (4) discuss strategies to safeguard these target species. We created an occurrence database and used environmental variables for the current and future periods to run the potential distribution models. We obtained models with high performance for all species and scenarios. Our study indicates potential occurrence areas for the psammophilous squamates of the DOF that still need to be sampled and are a survey priority for future inventories. In all future projections, climate change is predicted to shift the suitability and promote species range change, modifying the richness patterns for the psammophilous squamate reptiles of DOF. Finally, we demonstrate that future climatic conditions may decrease the effectiveness of current areas in protecting the diversity of these reptiles. Our results highlight the vulnerability of psammophilous squamates from South American Dry Diagonal to climate change and provide crucial information of the need of dynamic public policies for conservation of these species.

1. Introduction

The challenge of promoting the maintenance and conservation of biodiversity involves answering spatial questions: where are species distributed, what are the main predictors of their distribution, and how are they impacted by climate change (Ceron et al., 2021; Lara-Reséndiz et al., 2021). However, accessing well curated databases of current distribution and information on changes in geographic ranges of the species over time require time and resources (Meyer, 2016). In this sense, species distribution models (SDM) have been used to identify regions with high species richness (considering past, present, and future scenarios), of biogeographical relevance, and biodiversity hotspots (Raxworthy et al., 2003; Andrade-Díaz et al., 2019). Furthermore, SDM has been widely used to predict the impacts of anthropogenic global climate change on biodiversity (Lara-Reséndiz et al., 2021).

Climate change is known to modify the spatial axis of species, with populations being prone to colonize new habitats; cause changes in the abundance and distribution patterns at various spatial scales, and consequently also leading variation in species interaction networks (Ihlow et al., 2012; Sales et al., 2020). Unraveling the trajectory of the devastating impact that global change may have on biodiversity is complex because these consequences are unevenly distributed across taxa and probably vary geographically (Ihlow et al., 2012). In this context, identifying regions that contribute substantially to the persistence of biodiversity provides essential information for decision-making on conservation at a speed equivalent to that of the advance of destruction (Ihlow et al., 2012), such as the creation and maintenance of Protected Areas (PA) capable of safeguarding biodiversity and the functioning of current and future ecosystems (Prieto-Torres et al., 2021, 2022).

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South America is diagonally crossed by a southwest-northeast corridor of an open and dry vegetation called "the diagonal of open formations" (hereafter DOF; sensu Vanzolini, 1963) that comprises the domains of Caatinga in northeastern Brazil, Cerrado in central Brazil, and Chaco in southern South America (Werneck, 2011). These natural domains that form the DOF have historically been neglected in research on biodiversity and conservation priorities (Rodrigues, 2003; Guedes et al., 2014a). For example, knowledge about the reptile fauna, remains fragmented despite recent advances (e.g., Uchôa et al., 2022; Cabral et al., 2022a); and the rates of strictly PAs in the Caatinga (2%), Cerrado (10%), and Chaco (9%) are the lowest among many South America biomes (Nori et al., 2016a; Prieto-Torres et al., 2018).

The DOF has a high rate of squamate species ecologically and morphologically adapted for life in sandy soil environments — hereafter psammophilous squamates (Rodrigues, 2003; Recoder and Rodrigues, 2020). For instance, psammophilous lizards of the family Gymnophthalmidae are small-sized (<120 mm snout-vent length), lack eyelids, and show reduced or absent locomotor limbs (Recoder and Rodrigues, 2020); and psammophilous snakes of the family Dipsadidae usually have modified rostral scales (e.g., shovel-shaped rostral scale with a central keel; Cabral et al., 2022b). Among the DOF domains, the Caatinga harbors endemic genera and species of reptiles restrictedly distributed in sandy soil patches of the São Francisco River Dunes, thus demonstrating the unique biogeographic history of this region (Rodrigues, 2003; Recoder and Rodrigues, 2020). The DOF's psammophilous reptiles are, in general, poorly studied. For many species, distribution data are scarce, making it difficult to know their current ranges as well as to evaluate their vulnerability to climate change (Meyer, 2016).

Additionally, studies on the impacts of climate change on organisms are often biased. For example, there is a preference for studying charismatic and rare taxa (Sales et al., 2020) and model organisms related to ecosystem services, human food (Nascimento et al., 2022), and forested environments (Lourenço-de-Moraes et al., 2019). Non-charismatic, small-sized, narrowly distributed, and rarely sighted species (e.g., psammophilous species) are usually described late and are neglected in conservation status assessments (Tingley et al., 2016; Chiu-Valderrama et al., 2022). These species may also be overlooked on how they will respond to climate change. Furthermore, studies with one or a few species do not elucidate how open-area reptiles will be affected by global climate change. Werneck (2011) and Nori et al. (2016b) suggest that DOF reptiles may be more vulnerable to climate change than forested reptiles. In contrast, Oliveira et al. (2012) suggested that the lizard *Calyptommatus confusionibus* (restricted to sandy soils in the Caatinga) will not be affected and will gain area in a scenario of global climate change, unlike that predicted for the lizard *Mabuya agmosticha* widely distributed in forests.

Given the lack of knowledge about the impact of climate change on psammophilous reptiles in open areas and considering that SDM is a powerful tool to assess these impacts, in this study, we used data on distribution occurrences of 10 species of squamate reptiles (five lizard species and five snake species) endemic to DOF sandy soils to test the hypothesis proposed by Oliveira et al. (2012) that Squamata reptiles will benefit and show a gain in distribution area in the face of climate change scenarios. Specifically, we aimed to (1) predict the potential distribution of the psammophilous squamate species of the DOF in the current climate, (2) identify survey priority areas to sample unknown populations based on model results, (3) estimate the impacts of climate change in two future CO_2 emission scenarios (in 2040 and 2060) on the distribution of the psammophilous squamates endemic to the DOF, and (4) discuss strategies to safeguard the studied species considering prioritization of areas for conservation in a changing world.

2. Material and methods

2.1. Target species and occurrence records

We used occurrence data for ten psammophilous squamate species endemic to the DOF: five gymnophthalmid lizard species and five dipsadid snake species. Among the lizard species, *Vanzosaura multiscutata* (Amaral, 1933) and *Acratosaura mentalis* (Amaral, 1933) are endemic to Brazil and widely distributed in the Caatinga, in northeastern Brazil (Recoder et al., 2014; Uchôa et al., 2022). *Vanzosaura savanicola* Recoder, Werneck, Teixeira Jr, Colli, Sites & Rodrigues (2014) occurs in the northeastern portion of the Brazilian Cerrado, in the states of Bahia, Goiás, Minas Gerais, and Tocantins (Recoder et al., 2014). *Vanzosaura rubricauda* (Boulenger, 1902) is widely distributed in the Argentinean and Bolivian Chaco, the Paraguayan Cerrado, and the Brazilian Cerrado in the states of Goiás, Mato Grosso, and Mato Grosso do Sul (Recoder et al., 2014). *Micrablepharus maximiliani* (Reinhardt and Lütken, 1862) is widely distributed in South America, with records in forested and open areas (Moura et al., 2010).

Among the snake species, *Apostolepis sanctaeritae* Werner, 1924 occurs in the Brazilian Cerrado (states of Bahia, Goiás, Minas Gerais, and Tocantins) and transition areas with the Caatinga (Entiauspe-Neto et al., 2020). *Phalotris matogrossensis* Lema, D'Agostini and Cappelari, 2005 occurs in Paraguay, the western portion of the Brazilian Cerrado, Pantanal, Chiquitano Dry Forests, and Atlantic Forest (Nogueira et al., 2019). *Philodryas psammophidea* Günther, 1872 is distributed throughout the Chaco and western Brazilian Cerrado (Nogueira et al., 2019). *Rodriguesophis iglesiasi* (Gomes, 1915) is endemic to Brazil and distributed in mid to high-altitude areas in western Caatinga and northeastern Cerrado (Guedes et al., 2014a; Nogueira et al., 2019). Lastly, *Xenodon pulcher* (Jan 1813) occurs in the Chaco of Argentina, Brazil, Bolivia, and Paraguay (Nogueira et al., 2019).

We created a database of occurrence records for the target species containing unique localities based on the analysis of specimens in the following biological collections: Coleção Herpetológica da Universidade de Brasília, Coleção Zoológica da Universidade Federal do Piauí, Coleção Zoológica de Referência da Universidade Federal de Mato Grosso do Sul, and Museu de Zoologia da Universidade Federal da Bahia. We complemented our database by including occurrence records obtained in the scientific literature (e.g., Guedes et al., 2014a; Recoder et al., 2014; Nogueira et al., 2019; Uchôa et al., 2022). For this, we included only records that mention vouchered specimens deposited in a scientific collection and identified to species level (Table S1). It worth to mention that four of our target species (*Apostolepis sanctaeritae*, *Vanzosaura rubricauda*, *V. multiscutata*, and *V. savanicola*) recently undergone taxonomic/systematics revisions (Entiauspe-Neto et al., 2020; Recoder et al., 2014, 2020) or distribution revisions (Nogueira et al., 2019; Uchôa et al., 2022) what make a very large number of records from public databases not reliable at this moment to be incorporated in our study due to the risk to include taxonomic or geographical errors (which will require examination of the specimens). Therefore, in order to avoid bias that could compromise the work we opted for not include public databases occurrences in this study.

The geographic coordinates of each specimen in the occurrence database were obtained from gazetteers, scientific publications, or by direct inspection of layers (e.g., boundaries of PAs and municipalities) using the mapping software QGIS v. 3.22 (QGIS Development Team, 2022), Google Earth (https://earth.google.com/web/), and Google Maps (https://www.google.com/maps). Records lacking precise locality data were georeferenced using the municipality centroids. Since the occurrence database based on literature data were mostly constructed by the authors that verified the specimen's identity and locality in biological collections validating the records we used (e.g., TBG is author in Guedes et al., 2014a; Nogueira et al., 2019; Entiauspe-Neto et al., 2020; Uchôa et al., 2022 and DJS is author in Cabral et al., 2022a, 2022b), and the database based on the analysis of specimens in biological collections

took in count the most precise locality data possible of each specimen. We did not perform an automatized data cleaning, geographical coordinates were instead cleaned manually by verification of each occurrence data and by the construction of a map compilation using mapping software QGIS v. 3.22 (QGIS Development Team, 2022). We then used QGIS version 3.22 software (QGIS Development Team, 2022) to make current distribution maps (based on the occurrence database) and geographic distribution model maps of the target species (based on point records and SDM rasters).

For the SDM analyses, we considered only spatially unique occurrences for each species by retaining only one occurrence point in each environmental layer cell (i.e., we eliminated records within ~3 km of each other) (see Aiello-Lammens et al., 2015). All the ten target species of this study are considered having secretive habits (psammophilous) and are difficult to sample in the field (see Böhm et al., 2013; Meiri and Chapple, 2016; Tingley et al., 2016). Since it is known that for secretive reptiles it is necessary to accumulate all data possible along several years to know the approximate range of the species allowing to run reliable species distribution models analyses (see Colli et al., 2016) we did not include the temporal range in our database for SDM analyses.

2.2. Species distribution modeling analysis

We accessed the 20 environmental variables (19 climatic variables and altitude) available in WorldClim (https://worldclim.org/data/bioclim.html) for the current (1970–2000, at 5-arc min spatial resolution) and future scenarios (2040 and 2060, at 5-arc min spatial resolution; O'Neill et al., 2017). We considered two Shared Socioeconomic Pathway (SSP) scenarios. SSP2-4.5 scenario poses a more optimistic perspective, with socioeconomic development associated with moderate levels of greenhouse gas concentration; while SSP5-8.5 scenario poses a more pessimistic perspective, with low socioeconomic development and high levels of greenhouse gas concentration (O'Neill et al., 2017).

We included altitude as an environmental predictor because for the Neotropical Reptiles it is known that altitude is an important predictor affecting the patterns of distribution of the species (see Guedes et al., 2014b; Azevedo et al., 2020a). Also, elevation can drastically affect the environment, i.e. different elevations under the same latitude may offer different climates, soils, vegetation, evolutionary history (see Azevedo et al., 2020b) as well as consequently different microhabitat conditions and species composition. In addition, high elevation localities may be refugia for species under current and future climate scenarios. Therefore, elevation affects the distribution of species in space and time, also affecting the lineage and diversification.

Information on future climate from the Coupled Model Intercomparison Project 6 (CMIP6) was acquired for two Shared Socioeconomic Pathways (O'Neill et al., 2017): the SSP2-4.5 (optimistic) and SSP5-8.5 (pessimistic). Shared Socioeconomic Pathways (SSPs) are scenarios of projected socioeconomic global changes used to infer greenhouse gas emissions according to various climate policies. These scenarios provide a relatively optimistic and a more pessimistic projection, respectively, in terms of international policy toward environmental sustainability and greenhouse gas emission reduction (Meinshausen et al). For each SSP, the IPCC makes available climate models with distinct parameter inputs and produced from different code chunks. Due to the recent expansion of General Circulation Models (GCMs) availability, such component can be considered a relevant source of uncertainty in the environmental modeling process and may critically affect the robustness of the models (Heikkinen et al., 2006; Qiao et al., 2015; Fajardo et al., 2020; Anjos et al., 2021). To circumvent this limitation, instead of using a dozen GCMs with their respective individual projections, we built an ensemble based on the arithmetic mean of four GCMs, namely BCC-CSM2-MR, CanESM5, CNRM-CM6-1, and MIROC6.

To select the variables to be included in the models, we use the 'usdm' package (Naimi, 2019) to calculate the Variance Inflation Factor (VIF) for each target species and remove variables with multicollinearity problems (VIF >1.8, for species with less than 30 points; VIF >5 for species with more than 30 points). The VIF threshold value varied according to the number of only spatially unique occurrences following Ceron et al. (2021, 2023). The most important variables included in the models were: isothermality (BIO3), important for all species except *Pha. matogrossensis*; mean temperature of the wettest quarter (BIO8), important for seven species, except *V. multiscutata*, *Ap. sanctaeritae*, *R. iglesiasi*; mean diurnal range (BIO2); precipitation of wettest month (BIO13); precipitation seasonality (BIO15); precipitation of warmest quarter (BIO18); and precipitation of coldest quarter (BIO19), important for six species (Table S1). We ran the models in the biomod2 package version 4.0 (Thuiller et al., 2016) considering the algorithms: GLM (Generalised Linear Models; McCullagh and Nelder, 1989), GBM (Generalized Boosting Regression Models; Ridgeway, 1999), RF (Random Forest, Breiman, 2001), GAM (Generalized Additive Models; Hastie and Tibshirani, 1995), CTA (Classification Tree Analysis; Breiman et al., 1984), MARS (Multivariate Adaptive Regression Splines; Friedman, 1991), SRE (Surface Range Envelope; Busby, 1991), FDA (Hastie et al., 1994a), and MAXENT.Phillips (Maximum Entropy Modelling; Phillips et al., 2006). All analyses were performed in the R environment (R Core Team, 2022). The geographic area covered by the models was the Neotropical Cis-Andean region (latitude −90 to −30 and longitude −50 to 15 decimal degrees). All models were estimated using this extent, which avoids overestimated predictions at the same time that allows dispersion, evolving of niche characteristics and comparisons among species (Soberón and Peterson, 2005; Barve et al., 2011; Owens et al., 2019).

We calibrated the models with 80% of the data (randomly selected) and used the remaining 20% for validation (500 pseudo-absences). The individual models were evaluated using two metrics: True Skills

Table 1
Psammophilous squamate reptiles (lizards and snakes) of the Diagonal of Open Formations of South America. List of target species, number of occurrences for each species, domain of distribution of each species; number of records used for modeling considering the retention of a point if there were several points in the same cell of the environmental layer (see details in Material and Methods, and Fig. S1). Acronyms – BC: biological collections, L: literature; CAA: Caatinga, CER: Cerrado, CHA: Chaco.

Species	Total occurrences (BC + L)	Total occurrences for SDM	Domain
Lizards – Gymnophthalmidae			
Acratosaura mentalis	119 (3 + 116)	48	CAA
Micrablepharus maximiliani	812 (0 + 812)	168	CAA, CER, CHA
Vanzosaura multiscutata	681 (3 + 678)	91	CAA
Vanzosaura rubricauda	419 (125 + 294)	54	CER, CHA
Vanzosaura savanicola	219 (7 + 212)	21	CER
Snakes – Dipsadidae			
Apostolepis sanctaeritae	86 (5 + 81)	47	CAA, CER
Phalotris matogrossensis	209 (42 + 167)	82	CER, CHA
Philodryas psammophidea	247 (2 + 245)	170	CER, CHA
Rodriguesophis iglesiasi	53 (10 + 43)	27	CAA, CER
Xenodon pulcher	166 (0 + 166)	121	CHA

Table 2
Impact of climate change on the future distribution of psammophilous squamate reptiles in the Diagonal of Open Formations in South America. Values of area loss and gain and percentage of species range change (SRC) considering the comparison of the current climate with the future optimistic scenarios of 2040 and 2060 (SSP2-4.5) and future pessimistic scenario of 2040 and 2060 (SSP5-8.5). Values were calculated considering the ensemble model for each species (see details in Material and Methods section, and Fig S1–S5 for details). In bold we highlight the biggest values of loss, gain and SRC of each year and scenario. The range loss and gain values are given in pixels, obtained from the BIOMOD_RangeSize function in the biomod2 package.

Species	Future optimistic scenario (SSP2-4.5)						Future pessimistic scenario (SSP5-8.5)					
	2040			2060			2040			2060		
	loss	gain	SRC	loss	gain	SRC	loss	gain	SRC	loss	gain	SRC
Ac. mentalis	1517	119		2926	69		1635	161		2855	94	
%	31.32	2.46	−28.86	60.41	1.42	−58.98	33.75	3.32	−30.43	58.94	1.94	−57
Ap. sanctaeritae	804	1356		1218	1126		1052	981		2021	975	
%	10.20	17.20	7	15.45	14.28	−1.17	13.34	12.44	−0.9	25.63	12.36	−13.26
M. maximiliani	908	215		988	30		942	160		1022	23	
%	88.24	20.894	−67.35	96.02	29.15	−93.1	91.55	15.55	−76	99.32	22.35	−97.09
Pha. matogrossensis	2331	2253		4803	0		2523	1935		4160	2827	
%	48.53	−47.12	−1.42	**100**	0	−100	52.53	40.29	−12.24	86.61	58.86	−27.75
Phi. psammophidea	235	2003		346	2815		273	1961		359	3068	
%	1.70	14.50	12.80	2.50	20.38	17.87	1.98	14.19	12.22	2.6	22.21	19.61
R. iglesiasi	447	107		597	0		457	68		565	31	
%	74.87	17.92	−56.95	**100**	0	−100	76.55	11.40	−65.16	94.64	5.19	−89.45
V. multiscutata	596	620		558	2600		643	860		1000	927	
%	8.13	8.46	0.33	7.61	**35.48**	**27.86**	8.77	11.73	2.96	13.64	12.65	−1
V. rubricauda	638	228		982	167		672	148		1168	95	
%	53.3	19.05	−34.25	82.04	13.95	−68.09	56.14	12.36	−43.78	97.58	7.94	−89.64
V. savanicola	461	74		462	11		462	29		462	8	
%	**99.78**	16.02	−83.77	**100**	2.39	−97.62	**100**	6.28	−93.72	**100**	1.73	−98.27
X. pulcher	150	11,126		12,402	2613		159	10,433		170	16,534	
%	0.74	**54.68**	**53.94**	60.95	12.84	−48.11	0.78	**51.27**	**50.49**	0.84	**81.25**	**80.42**

Statistics (TSS) and Area Under the Curve (AUC) of Receiver Operating Characteristics (ROC; Thuiller et al., 2016). Only TSS >0.8 were considered valid. We built consensus models by averaging the individual models with high precision (TSS ≥0.8) (Table 2). A threshold approach implemented in the biomod2 package ("build.clamping.mask = TRUE" and "do.stack = FALSE" arguments; see Thuiller et al., 2016) allowed the transformation of continuous predictions of ensemble models into maps of potential presence versus absence of species.

Using the ensemble model and the 'biomod_RangeSize' function from the biomod2 package, we calculated (by using pixel values) species range change (SRC) and species range loss and gain, comparing the current distribution of each target species with those predicted for future (2040 and 2060) scenarios (Table 2). Thus, we obtained information about lost of suitable areas, new suitable areas, and regions that remained stable for the distribution of each target species (Cobos and Bosch, 2018; Atauchi et al., 2020). To visualize the potential distribution of each target species and access the change in the suitability levels, we prepared individual suitability maps from the raster layers generated in the models (Fig. S1–S5). Finally, we elaborated general suitability maps showing the richness distribution of psammophilous squamates in the DOF for each scenario; we considered the average of the individual models we generated before from binary predictions (see above). For this, we used QGIS v. 3.22 software (QGIS Core QGIS Development Team, 2022), considering the average of the models.

We also calculated stable climate areas for each target species for future climate scenarios (Peterson et al., 2002) by using the package "raster" (Hijmans et al., 2023) performed in the R environment (R Core Team, 2022). We calculated the average of the raster layers of the current distribution and future distribution in the optimistic scenario (4.5, years 2040 and 2060); and average rasters of current distribution and future distribution in the pessimistic scenario (8.5, years 2040 and 2060).

2.3. Edaphic profile

Raxworthy et al. (2003) used data sets of environmental land coverage to demonstrate the ability of niche models to predict the distribution of chameleon species from Madagascar for the current climate. Since we built models for different scenarios, we opted to keep only climatic and altitude data as variables. To achieve our second aim of indicating survey priority areas to sample unexplored psammophilous populations, we evaluated the results of models also considering the edaphic profile of the species. To do this, we collected edaphic information for each species point occurrence (Fig. S8; Tables S2– S5) considering the following variables: (i) soil texture (available from Land Data Assimilation Systems; https://ldas.gsfc.nasa.gov/gldas/soils), (ii) total sand (available from the SoilGrids 2.0 database; Poggio et al., 2021; https://gist.github.com/BlasBenito/2aaf3803174cf053783007f018382d86), and (iii) soil type (following the Soil and Terrain database for Latin America and the Caribbean; Dijkshoorn et al., 2005). We presented these survey priority areas to sample unexplored psammophilous populations on the map through grids (1°) superimposed on the DOF limits.

2.4. Conservation

To discuss strategies to safeguard the target species considering the prioritization of areas for conservation in a changing world, we checked whether the current and future geographic ranges of the target species would be protected by the current limits of the PAs. Thus, we present a conservation perspective by overlapping general maps of potential distribution for current and future scenarios with the strictly PAs in Brazil (following CEM, 2022), Argentina, Bolivia, Paraguay, and Uruguay (following UNEP and IUCN, 2022) (see Fig. S8 and Table S8). Categories considered as strycly PAs for Brazilian domains were Estação Ecológica (ESEC); Monumento Natural (MONA); Parque Nacional (PARNA); Refúgio da Vida Silvestre (REVIS). Categories considered as strycly PAs for the Chaco were I: Reserva Natural Estrita; II: Parque Nacional; III: Monumento Natural; IV: Área de Manejo de Habitat/Espécie.

3. Results

We obtained 3003 occurrences to compose the distribution database of the ten target species. Most occurrence records were obtained from the scientific literature (2806 records, 93.44% of the total), followed by the analysis of specimens from scientific collections (197 records,

6.56%) (Table 1 and Table S1). Lizards accounted for 2242 (74.66%) occurrence records: 812 records for *M. maximiliani*, 681 for *V. multiscutata*, 411 for *V. rubricauda*, 219 for *V. savanicola*, and 119 for *Ac. mentalis*. Snakes accounted for 761 (25.34%) occurrence records: 86 for *Ap. sanctaeritae*, 209 for *Pha. matogrossensis*, 247 for *Phi. psammophidea*, 53 for *R. iglesiasi*, and 166 for *X. pulcher* (Table 1).

3.1. Species distribution modeling in the current climate

We obtained consensus models of potential distribution with high performance for all species, with TSS ranging from 0.888 to 0.992 and ROC ranging from 0.983 to 0.997 (Table 2). Overall, the potential distributions for the current climate proved to be equivalent to the species occurrence records (Fig. S1), especially for *Ac. mentalis*, *Ap. sanctaeritae*, *R. iglesiasi*, and *V. savanicola*. The exception was *M. maximiliani*, for which the model did not predict its occurrence in forested areas of Brazil (e.g., Amazon rainforest: states of Maranhão, Pará, and Rondônia; Atlantic Forest: states of Rio de Janeiro and Espírito Santo), in some municipalities in northeastern Brazil (Barreirinhas and Santo Amaro, in the state of Maranhão; Caucaia, Fortaleza, and Mungulu, in the state of Ceará), and Paraguay (Paraguarí). For *Phi. psammophidea*, the model also did not coincide with known occurrences in Brazil (municipality of Sorriso, state of Mato Grosso), Bolivia (Carrasco and Tapacari), and Argentina (Corrientes, La Pampa, Mendonza, Neuquén, Santa Fé, Humahuaca, Ledesma, and Tilcara) (Fig. S1 and Table S1). For *V. multiscutata*, the modeling showed low suitability for occurrence records in northeastern Brazil (Parnaíba Delta, state of Piauí; municipality of Cachoeira, state of Bahia; and Pacajus municipality, state of Ceará). For *V. rubricauda*, the model predicted low suitability in the municipality of Serranópolis (state of Goiás, Brazil). Finally, for *X. pulcher*, the SDM showed low suitability in the province of Corrientes (Argentina). On the other hand, the models did not predict the occurrence of *Pha. matogrossensis* in the state of Rio Grande do Sul (Brazil), where the species is known to occur. Considering the current potential distribution, the potential richness of psammophilous squamates in the DOF is distributed (suitability >70%) in northern Argentine Chaco and in transition areas between Caatinga-Cerrado (states of Maranhão, Piauí, Bahia, and Minas Gerais) and Cerrado-Chaco (Paraguay and in the Brazilian states of Mato Grosso and Mato Grosso do Sul) (Fig. 1). The Chaco showed mainly medium suitability areas (30–70%), whereas the Cerrado showed low suitability (<29%) in its northern (state of Maranhão), western (Mato Grosso, Brazil), and southern portions (areas between the states of Goiás, Mato Grosso do Sul, Minas Gerais, and São Paulo; Fig. 1).

3.2. Species distribution modeling under future scenarios

In the optimistic scenario for 2040 (SSP2-4.5), the areas of high suitability for psammophilous squamates (>70%) correspond with the results for the current potential distribution (Fig. 2). The model predicted an increase in areas with medium suitability (30–70%) in the Caatinga, the southern Cerrado, and the Bolivian Chaco, enabling new areas of geographic distribution for the target species in the future (Fig. S2). However, the northern Cerrado remained with low suitability (<29%). In an optimistic 2040, all species showed range loss (0.74%–99.78%), surpassing range gain (2.46–54.68%) (Table 2). *Vanzosaura savanicola* and *M. maximiliani* had the largest area loss (−99.78% and −88.24%, respectively). *Xenodon pulcher* was the species that showed the largest gain in area (54.68%), followed by *Phi. psammophidea* (47.12%) (Table 2). All species showed species range changes (SRC). The largest changes occurred for *V. savanicola* (−83.77%), *M. maximiliani* (−67.35%), *R. iglesiasi* (−56.95%), and *X. pulcher* (53.94%), whereas the smallest changes occurred for *Pha. matogrossensis*

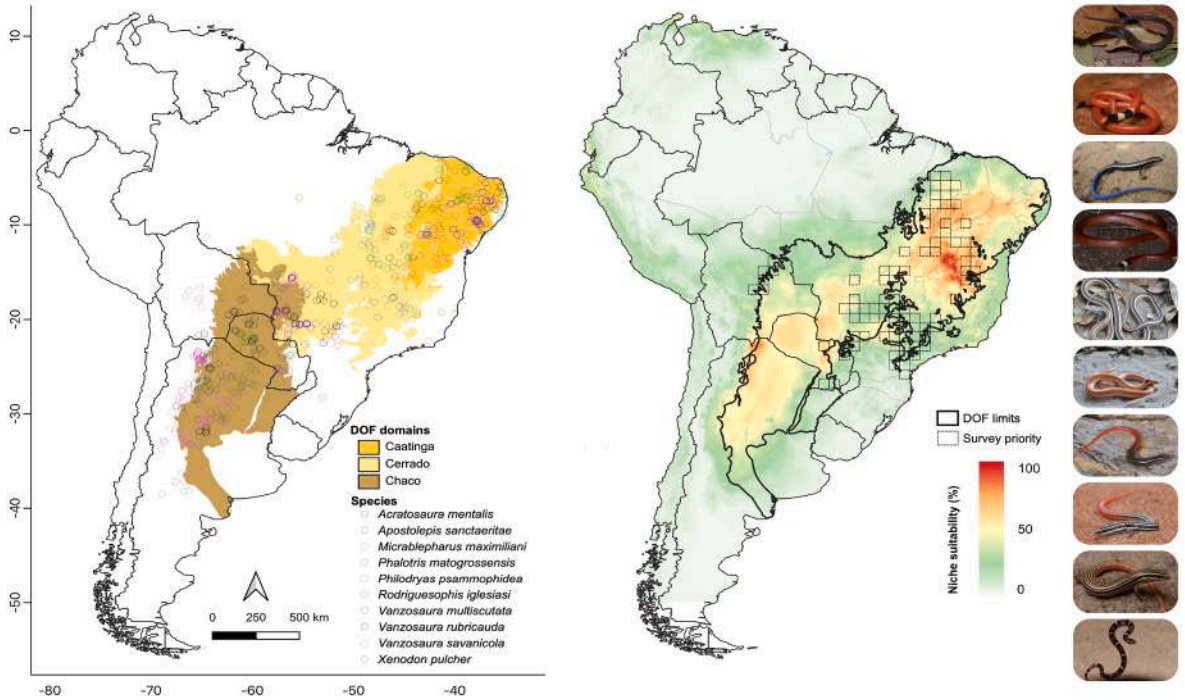

Fig. 1. Distribution of psammophilous squamate reptiles of the Diagonal Open Formations of South America (DOF). Left: Geographic coverage of the Caatinga, Cerrado and Chaco domains of DOF and point occurrences of ten species of Squamata reptiles. Center: General map of the current potential distribution of the Squamata reptiles in the DOF; the grids (1°) superimposed to DOF represent areas for survey priority since they show ≥50% of niche suitability of potential occurrence of Squamata reptiles associated with sandy soils along with appropriate edaphic profile (soil texture, total of sand, and the kind) for these species. Right: Photographies of live specimens of ten target species considered in our study: *Acratosaura mentalis* (Photo credit: Daniel Mesquita), *Apostolepis sanctaeritae* (Photo credit: André Teles), *Micrablepharus maximiliani* (Photo credit: Thaís Guedes), *Phalotris matogrossensis* (Photo credit: Diego Santana), *Philodryas psammophidea* (Photo credit: Davi Pantoja), *Rodriguesophis iglesiasi* (Photo credit: Thaís Guedes), *Vanzosaura multiscutata* (Photo credit: Adrian Garda), *V. rubricauda* (Photo credit: Diego Santana), *V. savanicola* (Photo credit: André Teles), and *Xenodon pulcher* (Photo credit: Hugo Cabral).

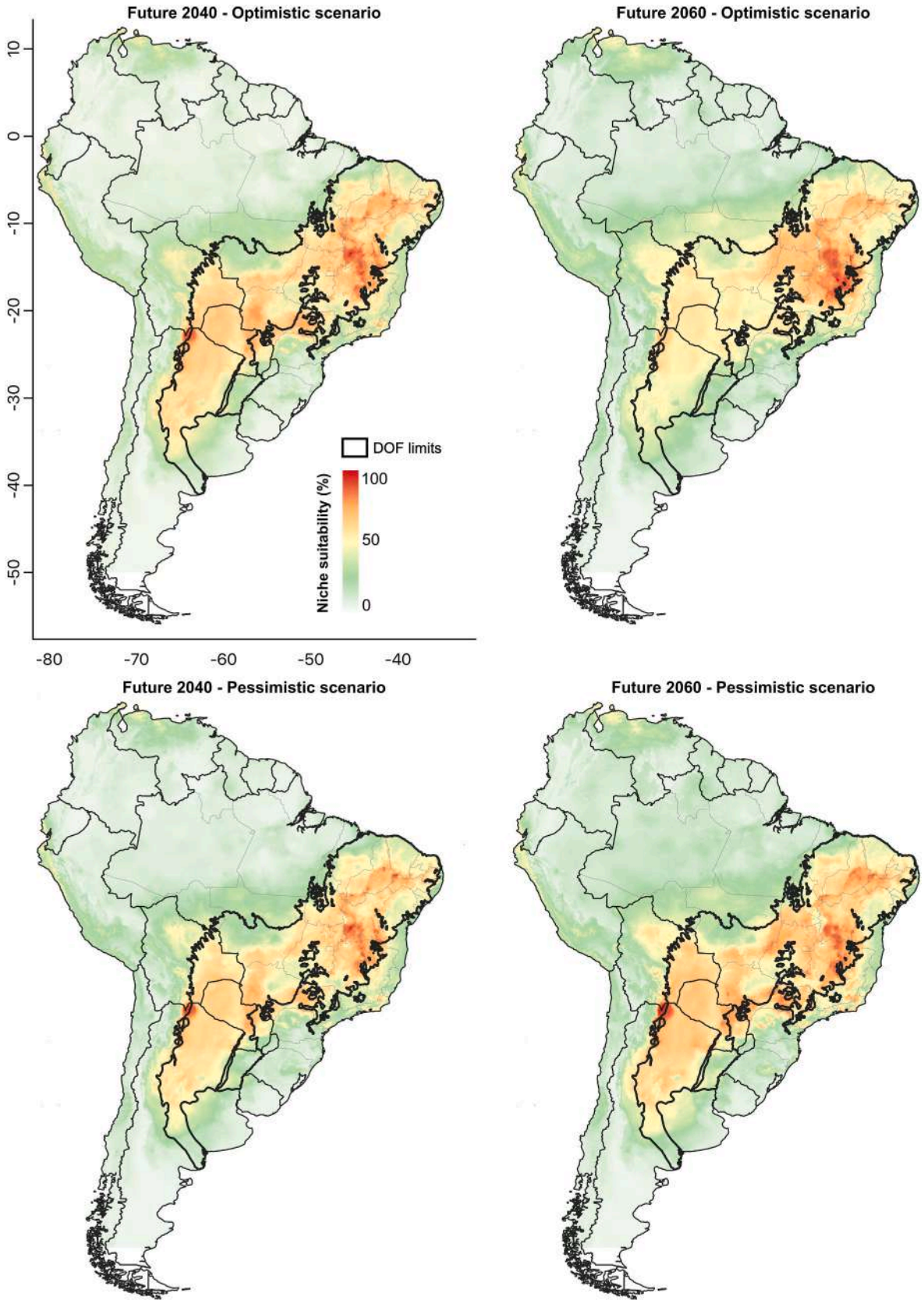

Fig. 2. General maps of the future potential distribution of psammophilous squamate reptiles of the Diagonal of Open Formations of South America. Future 2040 optimistic scenario refers to SSP2-4.5; future 2060 optimistic scenario refers to SSP2-4.5; future 2040 pessimistic scenario refers to SSP5-8.5; future 2060 pessimistic scenario refers to SSP5-8.5. Gradient colors represent suitability levels of the ensemble models.

and *V. multiscutata* (−1.42% and 0.33%, respectively (Table 2 and Fig. S2).

In the optimistic scenario for 2060 (SSP2-4.5), the psammophilous squamates of the DOF were predicted to occur (suitability >70%) in the Caatinga-Cerrado transition area and the central-eastern portion of the Brazilian Cerrado (states of Goiás and Tocantins) (Fig. 2). The Cerrado-Chaco transition and northern Argentinean Chaco lost suitability (30–70%) compared to the results obtained for the current potential distribution (suitability >70%), indicating a contraction of the geographic distribution of the target species. We detected area loss for all species, ranging from 2.50 to 100% (Table 2). *Vanzosaura savanicola*, *Pha. matogrossensis*, and *R. iglesiasi* were predicted to lose their total area (−100%). *Vanzosaura rubricauda*, *X. pulcher*, and *Ac. mentalis* were predicted to lose more than half of their ranges (−82.04%, −60.95%, and −60.41%, respectively) (Table 2). We detected area gain for eight species, except for *Pha. matogrossensis* and *R. iglesiasi*; the gain ranged from 1.42% to 35.48%. *Vanzosaura multiscutata* was predicted to have the largest gain (35.48%). We detected SRC changes for all species. The largest SRC changes will occur for *Pha. matogrossensis* and *R. iglesiasi* (−100% for both species), followed by *V. savanicola* (−97.62%) and *M. maximiliani* (−93.1%) (Table 2).

In the pessimistic scenario for 2040, we observed changes in the suitability of the species compared to the current potential distribution. Under this scenario, the psammophilous squamates of the DOF were predicted to occur (suitability >70%) in the Caatinga, Chaco, and Cerrado (except in areas that showed low suitability in the current climate) (Fig. 2). Portions of the Caatinga (except southern Ceará, Paraíba, and Pernambuco) and Cerrado (between the states of Goiás and Mato Grosso do Sul) showed medium suitability (30–70%). However, the Cerrado areas with low suitability in the current climate remained with low suitability (<29%) in the 2040 pessimistic scenario. We detected loss of area for all species (Table 2). The loss ranged from 0.78% to 100% and was larger than the area gain for the period (3.32% and 51.27%). *Vanzosaura savanicola* was predicted to lose its total area (−100%), whereas *M. maximiliani* and *R. iglesiasi* were predicted to lose 91.55% and 76.55% of their area, respectively. *Vanzosaura rubricauda* and *Pha. matogrossensis* will also show substantial losses (56.14% and 52.53%, respectively) (Table 2). *Xenodon pulcher* was predicted to have the most substantial gain (51.27%), followed by *Pha. matogrossensis* (40.29%). We detected SRC changes for all species. *Vanzosaura savanicola* (−93.72%), *M. maximiliani* (−76%), *R. iglesiasi* (−65.16%), and *X. pulcher* (50.49%) will have the largest SRC changes (Table 2 and Fig. S4).

In the pessimistic scenario for 2060 (SSP5-8.5), the distribution of the psammophilous squamates of the DOF is high (suitability >70%) in the Caatinga (southern Ceará, Paraíba, and Pernambuco), the Caatinga-Cerrado transition areas, the Cerrado (except in the northern portion of the states of Maranhão and Mato Grosso and the portion between the states of Goiás and Mato Grosso do Sul), the Cerrado-Chaco, and Chaco transition area (Fig. 2). Portions of the Caatinga (except southern Ceará, Paraíba, and Pernambuco) and Cerrado (between the states of Goiás and Mato Grosso do Sul) showed medium suitability (30–70%). As in the other scenarios, the Cerrado portions in the north of the Brazilian states of Maranhão and Mato Grosso showed low suitability (<29%) for the distribution of the studied diversity. Area loss for all species ranged from 0.84 to 100% (Table 2), which surpassed the area gain for the period (1.73% and 81.25%). *Vanzosaura savanicola* (−100%), *M. maximiliani* (−99.32%), and V. *rubricauda* (−97.58%) were predicted to have the most substantial area losses (>50%) (Table 2). The largest area gains were predicted for *X. pulcher* (81.25%) and *Pha. matogrossensis* (58.86%). We detected SRC changes for all species. The most significant changes were detected for *Vanzosaura savanicola* (−98.27%), *M. maximiliani* (−97.09%), *V. rubricauda* (−89.64%), *R. iglesiasi* (−89.45%), *Ac. mentalis* (−57%), and *X. pulcher* (80.41%) (Table 2; Table S1 and Fig. S5).

The areas of climate stability for the target species in the future climate scenarios (Fig. S6 and S7) were equivalent to our results of areas of high suitability (suitability >70%) for both scenarios. The transition areas between the Caatinga and Cerrado domains and the north of the Argentine Chaco proved to be the most stable (stability> 70%) for the potential distribution of species in both the optimistic and pessimistic scenarios).

3.3. Edaphic profile

The DOF psammophilous squamates occurred in 18 soil classes (Fig. S8), with records of all species in Cambisol, Ferralsol, and Leptsol. Regarding soil texture, DOF psammophilous squamates occurred in categories 3 to 12 (mean = 7.1), composed of 17–82% sand. All species were recorded in clay-silty loam soil texture (58% sand); only *M. maximiliani* was recorded in silt loam soil texture (17% sand). Regarding total sand, the DOF psammophilous squamates occur in soils with 1.9–77.6g of sand per kilogram of soil (mean = 52.4g/kg). The edaphic profile for each target species is shown in Tables S2-S4.

Considering the edaphic profile of the target species and the results obtained for the current potential occurrence, we identified survey priority areas (i.e., no occurrence points for the target species) in the following regions: northern Cerrado (southern portion of the states of Maranhão and Piauí), southern Cerrado (comprising the Brazilian states of Minas Gerais, São Paulo, Paraná, and Mato Grosso do Sul), northern Chaco (Santa Cruz, in Bolivia), Atlantic Forest (southern Bahia and mid-western Espírito Santo), Pampas (midwestern region of the states of Paraná and Rio Grande do Sul, Brazil), northwestern Argentina, and northern Bolivia (Fig. 1).

In each scenario, the areas with the greatest species richness are coincident. Thus, in all scenarios, except for an optimistic 2060, the transition areas between the Caatinga and Cerrado domains and the north of the Argentine Chaco present a greater richness of psammophilous reptiles. In optimistic 2060, the areas with the greatest species richness are the Caatinga (western and southern portion) and the central-eastern Cerrado (see Fig. 2).

3.4. Conservation

There are 138 PAs throughout the DOF (Fig. 3), but only 18 currently protect the potential richness of squamates studied here (Fig. S9 and Table S8). In the current potential distribution, 59 PAs (42.75%) show medium suitability (30–70%), and two PAs (1.44%) show high suitability (>70%) for the potential occurrence of the richness pattern (Fig. 3). We identified eight species, all except *A. sanctaeritae* and *Pha. matogrossensis*, showing occurrences points inside the limits of medium and high suitability PAs. In the optimistic scenario for 2040, we detected 63 PAs (45.5%) with medium suitability and only one (0.73%) with high suitability. In the optimistic scenario for 2060, we detected 56 PAs (40.58%) with medium suitability and three PAs (2.17%) with high suitability (>70%). In a pessimistic scenario for 2040, we detected 62 PAs (44.93%) with medium suitability and eight (5.8%) with high suitability. In the pessimistic scenario for 2060, we detected 68 PAs (49.28%) with medium suitability and eight PAs (5.8%) with high suitability for protecting the target species (Fig. S8 and Table S8).

4. Discussion

Using a detailed database of occurrences with environmental and climatic data, we demonstrate that the SDM is a powerful tool for predicting species distribution and recognizing the impacts of climate change on the psammophilous squamates of the DOF. The potential distribution models for the current climate scenario coincided with the occurrence records of the target species. However, the models added areas where some species may occur but have not yet been recorded (e.g., *Ac. mentalis* in the Brazilian state of Maranhão and *M. maximiliani* in the Argentine Chaco domain). Moreover, the model highlighted areas

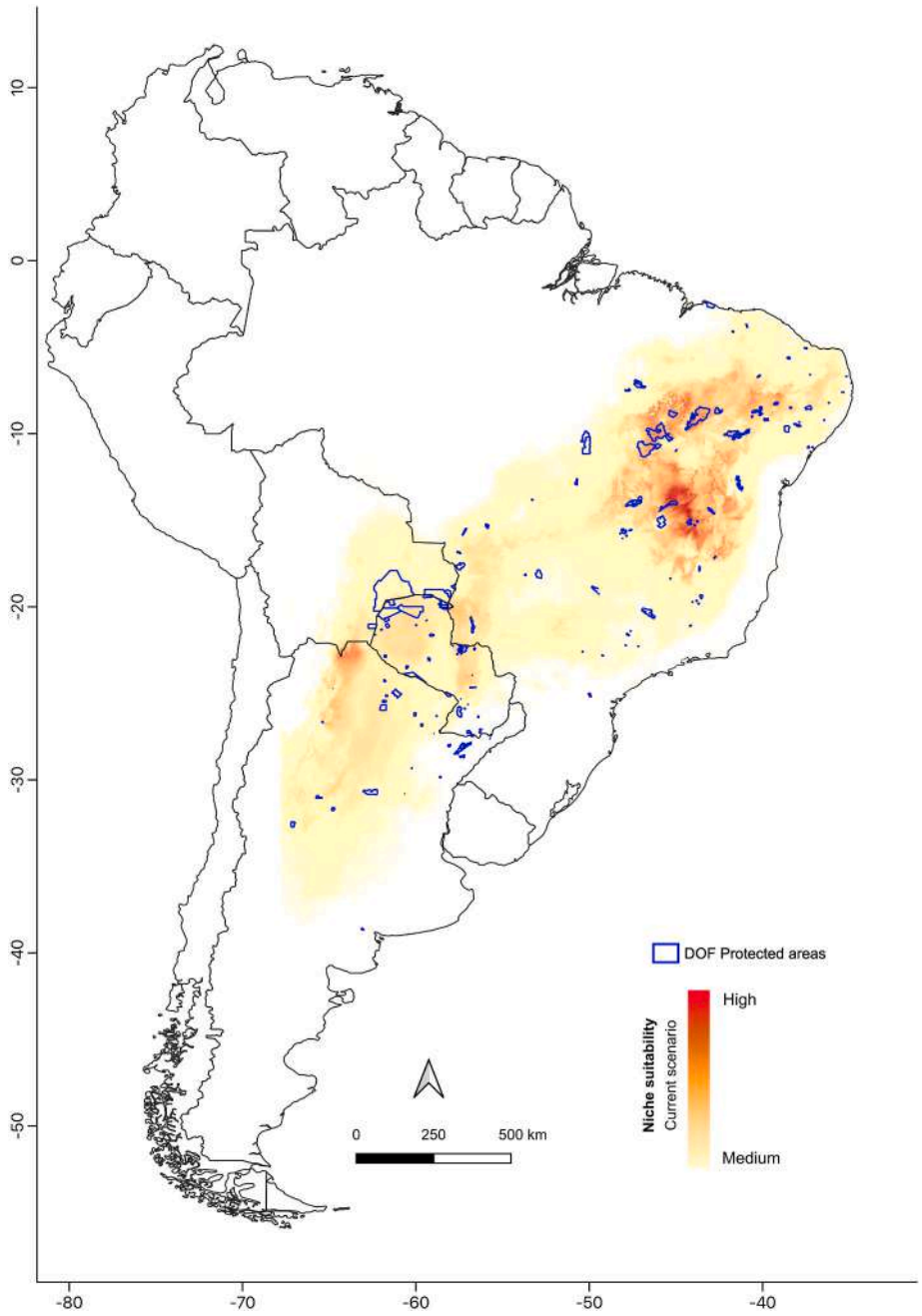

Fig. 3. Map of conservation of the current potential distribution of the psammophilous squamate reptiles in the DOF. General map of potential distribution show medium (30–70%) and high (>70%) niche suitability for the current climate. Strictly protected areas (PAs) are from CEM (2022) for Brazil limits and from UNEP and IUCN (2022) for Argentina, Bolivia, Paraguay and Uruguay limits.

where the species occur, but the models was not able to recover (e.g., *Pha. matogrossensis* in the state of Rio Grande do Sul, Brazil; *Phi. psammophidea* in Neuquén, Argentina). Nevertheless, the models were robust enough to represent the target species' known range.

The potential richness distribution map shows areas with high potential for the occurrence of psammophilous squamates (Fig. 1). The northern and southern portions of the Brazilian Cerrado and northern Bolivian Chaco show habitat suitability and edaphic profile that allow the occurrence of populations of the psammophilous squamates studied here and indicate the possible occurrence of other psammophilous species (including new taxa) endemic to the DOF (Fig. 1). Except for *M. maximiliani* and *Pha. matogrossensis*, all other species studied are endemic to the DOF, with occurrence records in one or two domains. One example is *Ap. sanctaeritae*, endemic to the Caatinga and Cerrado (Entiauspe-Neto et al., 2020). The potential distribution areas of psammophilous squamates may also indicate regions of high endemism still unknown in the DOF, such as the São Francisco River Dunes (Bahia state, Brazil), which became extremely relevant for the conservation of the Caatinga in the late 1990s after the discovery of several unique species (Rodrigues, 2003). We recommend field collection expeditions in areas the survey priority areas (Fig. 1) with a high potential richness of psammophilous squamates.

Raxworthy et al. (2003) used species' presence data and environmental and climatic variables to model the distribution of chameleon species in Madagascar. Their study recorded seven new species and revealed new areas of endemism, thus contributing to identifying regional endemism of reptiles and expanding conservation areas in Madagascar. Moreover, Raxworthy et al. (2003) highlighted SDM as an

important tool for biodiversity conservation in the face of anthropogenic impacts. Using the same methodology, we predicted the potential distribution of the psammophilous squamate species of the DOF in the current climate and we estimated the impacts of climate change in two future CO2 emission scenarios (in 2040 and 2060) on the distribution of the psammophilous squamates endemic to the DOF. For this purpose, we did not include anything related to niche evolution/niche conservatism since that it is out of our goal to include evolution in short-time (Peterson et al., 1999, 2018). Using the same methodology, we found that all species studied here occur in Cambisol, Ferralsol, and Leptsol soils with clay-silty loam soil texture. Changes in the profile of these soils may modify the distribution of squamates in current and future climate scenarios (Lara-Reséndiz et al., 2021).

In general, temperature and precipitation (BIO 2, BIO3 and BIO8; see topic 2.2 and Table 1) were the environmental variables that best explained the distribution of the psammophilous squamates of the DOF. These variables interfere with reptile distribution and metabolic and reproductive performance (Meiri et al., 2013; Ceron et al., 2021). Isothermality, the mean diurnal temperature range relative to the annual temperature range, was the most important variable for all species except *Phi. psammophidea*. Isothermality also explained the distribution of the snakes *Lygophis flavifrenatus* and *L. paucidens* in Cerrado and Chaco, two of the DOF domains (Ceron et al., 2021).

The potential distribution models for future scenarios (2040 and 2060) warn of climate change's effect on reducing and modifying the home range of the psammophilous squamates of the DOF by changing the niche conditions currently available. Climate change is predicted to shift the suitability of the richness patterns of our target species, reducing the potential geographic ranges of most species, contributing to the loss of known populations and areas of endemism in the DOF under future climate scenarios. Our results may be a proxy for other reptile species and lineages with similar habits (e.g., amphisbaenians) regarding lack of knowledge and vulnerability to climate change and associated threats. At least for psammophilous reptiles, our data do not support the hypothesis proposed by Oliveira et al. (2012) that squamates will benefit and gain distribution ranges in the face of climate change scenarios. Moreover, our data provide evidence for the suggestions made by Werneck (2011) and Nori et al. (2016b) that reptiles from South American open areas may be more vulnerable to climate change than forested reptiles. Although we studied a select group of squamates, our results corroborate previous research indicating the prevalence of negative effects of climate change in Squamata (e.g., Meiri et al., 2013; Lourenço-de-Moraes et al., 2019; Lara-Reséndiz et al., 2021).

The pessimistic scenario for 2060 was predicted to have the greatest impact on DOF psammophilous squamates. This scenario resulted in the largest range losses for the studied species (Table 2 and Fig. S3). This scenario predicts (1) extinction (i.e., total loss of geographic range) of *R. iglesiasi* and *Pha. matogrossensis*, (2) >80% reduction of habitat suitability for *M. maximiliani* and *V. savanicola*, and (3) range losses of 50–80% for *Ac. mentalis* and *V. rubricauda*. Our results confirm the prediction made by Meiri et al. (2013) that high temperatures caused by climate change will influence the ecology and evolution of lizards including *M. maximiliani;* but oppose prediction of Sinervo et al. (2010) that this species is not threatened. The IUCN categorizes our target species as Least Concern (IUCN, 2022). This categorization occurs partly because the IUCN often disregards climate change as an extinction threat criterion in their assessments, which underestimates the impacts of climate change and associated threats (Trull et al., 2017). The loss of species due to climate change may be greater than predicted, which will ultimately contribute to the ecological imbalance of many natural environments and the loss of ecosystem services (Prieto-Torres et al., 2022).

The impacts of climate change on the distribution of reptiles depend on their dispersal ability (which is usually limited), adaptation to fragmented areas, and biotic factors such as interactions among species (overlooked in this work, but relevant) (Andrade-Díaz et al., 2019). The current potential distributions recovered may not correspond to the expansion of species' geographic range to swaths of natural open areas since it will depend of the edaphic conditions. Kind and texture of the soil contribute to explaining the higher richness of fossorial snakes in open environments of the Chaco than in forested areas, as suitable soil benefits species displacement, protection, and feeding (Cabral et al., 2022a). The transition areas between the Caatinga and Cerrado domains and the north of the Argentine Chaco remained stable for potential distribution of psammophilous squamate reptiles (Fig. S6 and S7) in all scenarios and were identified as areas with greater suitability (suitability >70%) for the potential distribution of the species in most scenarios). We confirm the prediction by Hidasi-Neto et al. (2022) about the North of the Cerrado, at least its transition zone with the Caatinga, of being considered stable areas that could be a refuge for other vertebrates, in addition to birds, in the current climate scenario.

We detected SRC gain for *Phi. psammophidea* in all scenarios, which may be explained by its generalist distribution (Nogueira et al., 2019). We identified range loss for *X. pulcher* only in the pessimistic scenario for 2060, but SRC gain (>50%) in the other scenarios, confirming a prediction made previously for the species (Andrade-Díaz et al., 2019). The potential distribution areas of these species present the same edaphic profile as the current distribution (e.g., Chaco in the central-eastern portion of Bolivia, Santa Cruz department), indicating that the soil is suitable for the occurrence of the species, not being an impediment to their occurrence in climate change scenarios. Other potential areas show only climatic suitability (e.g., Caatinga of the western portion of Pernambuco state, Brazil).

The extent of PAs is small compared to the territorial extent of the DOF. The DOF protection rate corresponds to less than 2% for the Caatinga (Rodrigues, 2003; Guedes et al., 2014b), 10% for the Cerrado, and 9% for the Chaco (Nori et al., 2016a). Our study demonstrates that future climatic conditions may decrease the effectiveness of current areas in protecting the diversity of psammophilous squamates because less than 16% of the PAs in the Caatinga and Cerrado have suitability for their occurrence in future climatic scenarios (Table S8). This scenario resembles that observed for snakes from the Atlantic Forest (Lourenço-de-Moraes et al., 2019) and the Argentinean Dry Chaco (Andrade-Díaz et al., 2019). In contrast, Chaco's PAs (85.08–97.02%) will show suitability for psammophilous squamates of the DOF (Table S8). Prieto-Torres et al. (2022) found an increased distribution of 56 almost-restricted and endemic Chaco vertebrates (including 12 reptile species) in future climatic scenarios (2040 and 2060). However, after combining the future climatic models with agriculture-linked activities, they observed a narrower range of species distribution and the need to expand PAs by 5.6% to ensure the representativeness of the species of conservation concern.

Our study, considering a broader geographic area, corroborates Hidasi-Neto et al. (2022) that state a homogenization in the species richness of birds and mammals of the Cerrado is expected by the year 2100; and Moura et al. (2023) that by 2060 the climate change will affect the distribution of plants, promoting a homogenization of 40% of their plant assemblages in the Caatinga. Such changes in plants, birds and mammals for these open landscapes (Caatinga end Cerrado) tend to promote a snowball effect biodiversity loss along these DOF regions including fossorial species (Lara-Reséndiz et al., 2021; Moura et al., 2023).

In Brazil, the creation of new Protected Areas is mainly based in look at strategic areas and connectivities allowing protection of those species already included in any threatened category through the National Action Plan (PAN) for the Conservation of Threatened Species by Ministry of the Environment of the Brazilian Federal Government. However, until the last elaboration of the Reptile Brazilian Red List (following International Union for Conservation of Nature and Natural Resources guidelines) no data on climate change was considered (TBG pers. Comm.). In the last six years, 27 protected areas were created along the DOF, a positive aspect for the conservation of reptiles. However, we

reinforce that, even though protection areas designated for the conservation of other taxa can benefit Squamata (Cox et al., 2022), it is necessary that reptiles be included in decisions about expanding and creating new protection areas.

Using psammophilous squamates of the DOF, our study demonstrates that predictive distribution modeling using species occurrences associated with environmental layers provides crucial data to understand the current distribution pattern of species and, consequently, identify the spatial pattern of richness. Our study also indicates potential occurrence areas for the psammophilous squamates of the DOF that still need to be sampled and represent a survey priority for future inventories. There is, therefore, potential to discover new spots rich in endemic reptiles in the DOF or even species with habits similar to those of the target species, including new taxa (see Raxworthy et al., 2003). Still overlooked in conservation planning and assessment of species conservation status, predictions for future scenarios provide important indications about the loss of relevant species of the DOF (some of them endemic) and should be urgently incorporated in conservation planning in a changing world.

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CRediT authorship contribution statement

Júlia S. Oliveira: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. **Diego J. Santana:** Conceptualization, Data curation, Funding acquisition, Investigation, Validation, Visualization, Writing – review & editing. **Davi L. Pantoja:** Conceptualization, Data curation, Investigation, Validation, Visualization, Writing – review & editing. **Karoline Ceron:** Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – review & editing. **Thaís B. Guedes:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data are available in the supplementary material section

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.jaridenv.2023.105117.

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