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Climate change shrinks environmental suitability for a viviparous Neotropical skink

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Abstract

Anthropogenic global warming and deforestation are significant drivers of the global biodiversity crisis. Ectothermic and viviparous animals are especially vulnerable since high environmental temperatures can impair embryonic development, but we lack knowledge about these effects upon Neotropical organisms. Here, we estimate how much of the current area with suitable habitats overlaps with protected areas and model the combined effects of climate change and deforestation on the geographic distribution of the viviparous Neotropical lizard *Notomabuya frenata* (Scincidae). This species ranges in Brazil, Argentina, Paraguay, and Bolivia. We use environmental and physiological variables (locomotor performance and hours of activity) to predict suitable present and future areas, considering different scenarios of greenhouse gas emissions and deforestation. The most critical predictors of habitat suitability were isothermality (i.e., the ratio between mean diurnal temperature range and annual temperature range), precipitation during winter, and hours of activity under lower thermal extremes. Still, our models predict a contraction of suitable habitats in all future scenarios and the displacement of these areas towards eastern South America. In addition, protected areas are not enough to ensure suitable habitats for this species. Our findings highlight the vulnerability of tropical and viviparous ectotherms and suggest that even widely distributed species, such as *N. frenata*, may have their conservation compromised shortly due to the low representativeness of their suitable habitats in protected areas combined with the synergistic effects of climate change and deforestation. We stress the need for decision-makers to consider the impact of range shifts in creating protected areas and managing endangered species.

KEYWORDS

biological predictors, climate suitability, deforestation, environmental predictors, geographic distribution, global warming, reptiles, species distribution model

1 | INTRODUCTION

Climate change resulting from anthropogenic greenhouse gas emissions can challenge living organisms worldwide (Parmesan, 2006; Urban, 2015). In response, species can shift their ranges to reach suitable habitats in the future if dispersal is not limited (Araújo et al., 2006; Carvalho et al., 2010; Graham et al., 1996; Tingley et al., 2009). Alternatively, they can adapt to new environmental conditions through evolutionary responses, which can take a long time (Hoffmann & Sgrò, 2011). In this sense, phenotypic plasticity is essential in the face of accelerated climate change, as it allows short-term changes in organisms (Bonamour et al., 2019; Matesanz et al., 2010; Merilä & Hendry, 2014). However, the lack of adjustment can lead to local extinction as suitable habitats for many species are expected to decline due to global warming (Bonino et al., 2015; Minoli & Avila, 2017; Pontes-da-Silva et al., 2018; Sinervo et al., 2010). Moreover, deforestation can increase the consequences of climate change because, in addition to intensifying greenhouse gas emissions, it reduces the availability of suitable habitats and makes it difficult for organisms to disperse due to landscape fragmentation (Powers & Jetz, 2019; Sala et al., 2000; Travis, 2003). Therefore, suitable habitats for species should be effectively represented within protected areas (Corbalán et al., 2011; Dudley, 2008; Novaes e Silva et al., 2014). Thus, to anticipate the challenges of climate change, it is crucial to integrate future climate scenarios with predictions of land use changes and the coverage of protected areas to support appropriate conservation strategies (Hannah et al., 2002).

To investigate the effects of climate change on organisms, species distribution models are a valuable tool (Hannah et al., 2002; Pearson & Dawson, 2003). Some of these models relate environmental predictors to species occurrence records (also called correlative models), often easily accessible from open-access databases (Elith & Leathwick, 2009; Peterson et al., 2015). Despite its high applicability, the complex combination of processes indirectly expressed in their predictions limits the interpretation of their results (Kearney & Porter, 2009; Pearson & Dawson, 2003). Besides, species distribution models can rely on intrinsic biological predictors (also called mechanistic or biophysical models), which increase model accuracy under novel environments and provide an understanding of the biological mechanism behind the response to environmental changes, promoting ecologically interpretable results (Kearney & Porter, 2009; Zurell et al., 2016). However, calibration of these models requires many costly parameters, absent for most organisms (Peterson et al., 2015; Urban et al., 2016). Given the shortcomings of each approach alone, these methods can be seen as complementary by comparing their results or by building hybrid models (Morin & Thuiller, 2009; Talluto et al., 2016).

Species' vulnerability to environmental changes depends on their exposure, sensitivity, resilience, and adaptation potential (Williams et al., 2008). Except for exposure, these factors are determined by intrinsic species characteristics, which can be incorporated as biological predictors in species distribution models (Williams et al., 2008). Among these are physiological (thermal tolerance, locomotor performance), ecological (habitat use, activity time), demographic (population growth, dispersal potential), and evolutionary (genetic variability, gene flow) parameters (reviewed in Urban et al., 2016). Thermal tolerance, that is, the range of temperature the animal can tolerate, is one of the most critical factors for ectotherms since high temperatures may exceed their thermal limits, leading to a reduction in their activity time and compromising survival and reproduction (Huey & Stevenson, 1979; Sinervo et al., 2010). Thus, hours of activity and locomotor performance have often been successfully used in mechanistic and hybrid species distribution models (Pontes-da-Silva et al., 2018; Yuan et al., 2018).

Ectothermic animals are particularly vulnerable to climate change since they depend primarily on heat exchange with the environment to regulate their body temperature (Angilletta et al., 2002; Huey, 1982). This physiological sensitivity may be amplified in tropical species that live in more thermally stable environments and have narrow thermal safety margins, so even slight warming can harm them (Deutsch et al., 2008; Huey et al., 2009). Moreover, small ectotherms, such as lizards, have limited dispersal ability, which makes it difficult for them to reach suitable habitats in the future in the face of accelerated climate change and habitat fragmentation (Spiller et al., 1998; Thomas et al., 2004). Most studies investigating the effects of climate change on reptiles are from temperate-zone species, with critical information gaps for Africa, Asia, and South America, regions that concentrate most of the global reptile richness (Böhm et al., 2016; Winter et al., 2016). Besides, the negative consequences of climate change should be more severe for tropical species because they experience environmental temperatures close to or already at their optimal temperatures (T_{opt}; Deutsch et al., 2008). As T_{opt} of tropical organisms is closer to their critical thermal maximum (CT_{max}), they have narrower thermal safety margin than high latitudes species (Deutsch et al., 2008; Sunday et al., 2011; Tewksbury et al., 2008). Here, we estimate the synergetic effects of climate change and deforestation on the geographic distribution of a viviparous Neotropical lizard, the skink *Notomabuya frenata* (Cope, 1862).

This species occurs in natural habitats in Brazil, Argentina, Bolivia, and Paraguay, primarily in the Atlantic Forest, Cerrado, Chaco, and Pantanal regions (Álvarez et al., 2009; Dirksen & Riva, 1999; Pinto et al., 2017). It is often locally abundant in various microhabitats and has a diverse diet (Linares & Eterovick, 2013; Vrcibradic & Rocha, 1998a).

Viviparity has independently evolved many times among squamate reptiles and is often interpreted as a critical adaptation to cold climates (Shine, 2014; Wright et al., 2015). *Notomabuya frenata* is part of a lineage that dispersed from Africa ca. 18 mya and diversified in South America and the Caribbean, so it evolved in warm climates (Hedges & Conn, 2012; Miralles & Carranza, 2010). Thus, viviparity is advantageous for enabling females to control thermal conditions during embryogenesis in cold and warm conditions, enhancing the fitness of offspring (Ji et al., 2007; Shine, 1995). However, despite this control through maternal thermoregulation, the harmful consequences of climate change may be worrying for viviparous species because thermal conditions during gestation can affect embryo viability and offspring phenotype, so high heat exposure can compromise embryonic development and young's performance after birth (Beuchat, 1986; Jara et al., 2019; Lourdais et al., 2004; Shine & Harlow, 1993).

Thus, we aim to estimate (1) the current area with suitable habitats and how much of this area overlaps with protected areas and (2) how climate change and deforestation affect the geographic distribution of the viviparous Neotropical lizard *N. frenata*. Considering that tropical and viviparous organisms are highly vulnerable to climate change and tropical lizards are highly threatened by habitat disturbance (Alroy, 2017), we hypothesize that climate change will reduce the geographical distribution area of this species and that deforestation will exacerbate this threat. Therefore, we expect to test the relative contributions of physiological and environmental predictors in our hybrid models. We hypothesize that the physiological variables will have the most outstanding contribution to the model, as they consider specific traits of the species.

2 | METHODS

2.1 | Environmental variables

We retrieved historical (1970–2000) and future (2041–2060, 2061–2080, and 2081–2100) climatic and elevation data at a 2.5-min resolution from the WorldClim 2.1 database (Fick & Hijmans, 2017). These variables comprised elevation, total monthly precipitation, minimum and maximum monthly temperatures, and 19 derived bioclimatic variables (Hijmans et al., 2005). We cropped rasters to the spatial extent of South America (between 10° and −40° latitude and between −80° and −30° longitude). Regarding the future climate projections, we used two shared socioeconomic pathways (SSP2-4.5 and SSP5-8.5), which estimate how different socioeconomic contexts can lead to different greenhouse gas emission scenarios (Riahi et al., 2017). While SSP2-4.5 has intermediate emissions, SSP5-8.5 has high CO_2 emissions and radiative forcing, so we chose these two pathways because they represent optimistic versus extreme scenarios (Riahi et al., 2017). We used several SSPs to assess the implications of different emissions trajectories for the focal species (Riahi et al., 2017). Besides, we used eight general circulation models (GCMs) to incorporate the uncertainties and biases of the simulated circulations, as these models are based on different spatial resolutions and calculated climate parameters considering different physical processes (Harris et al., 2014; Sofaer et al., 2017; van Ulden & van Oldenborgh, 2006). These uncertainties were reflected in the variation of climatic and physiological predictors and in the projections of suitable habitats, which we estimated separately for each GCM (see Supporting Information).

2.2 | Thermal performance variables

We collected 32 individuals of *N. frenata* using pitfall traps in cerrado sensu stricto and gallery forest habitats at Reserva Ecológica do Instituto Brasileiro de Geografia e Estatística—IBGE (15°56′41″ S, 47°53′07″ W), Distrito Federal, Brazil. It is a protected area within the Cerrado biome in central Brazil, with Aw climate in Köppen's classification (Alvares et al., 2013; Nimer, 1989). In the cerrado *sensu stricto* habitat, we opened the pitfall traps monthly and checked them for 6 days in a row, while in the gallery forest habitat, the traps were always open and checked twice a week. We measured the snout-vent length (with a ruler to the nearest 1 mm) and mass (with a Pesola Micro Line spring scale to the nearest 0.1 g) of all captured individuals.

We brought lizards to the laboratory to collect physiological data. All procedures were approved by the Animal Use Ethics Committee of the University of Brasília (process 33786/2016). We performed all of the following physiological experiments with all 32 individuals collected. First, we estimated the preferred temperature (T_{pref}) of each lizard using a thermal gradient consisting of an MDF plywood terrarium with eight compartments (each 100 × 15 × 30 cm — l × w × h) with a 60-W incandescent lamp at one end and an ice pack on the other, generating a ~20–50°C thermal gradient (Paranjpe et al., 2012).

We recorded lizard body temperature every minute for 1 h with a 36 ga thermocouple (Omega 5SC-TT-T-36-72) taped to their abdomen and connected to a data acquisition module (Omega TC-08 8 Channel Thermocouple USB Data Acquisition Module), using the mean to estimate T_{pref}. We allowed a 5-min acclimatization period in the gradient before recording body temperatures. We observed no impairment of lizard movements during the experiments due to thermometers and considered the lowest and highest temperatures recorded in the T_{pref} experiment as the minimum and maximum voluntary temperatures, respectively.

Then, we estimated thermal performance by inducing lizards to sprint on a track (200 × 30 × 40 cm — l × w × h) at three body temperatures in the following order: voluntary temperature, 5°C below, and 5°C above the room temperature. We performed six sprints per individual, two at each test temperature, and there was a 30-min interval between tests. The "voluntary temperature" was the body temperature at which the individual was at the end of the T_{pref} experiment. As we did not standardize room temperature, we could examine the sprint speed of the species over a range of temperatures to obtain sufficient variation for subsequent regression analyses (Figure S1). We used gel ice packs and incandescent lamps to alter the lizards' body temperature, monitored with an L-K industries Miller & Weber T-6000 Cloacal 0/50°C thermometer. We recorded all runs with a high-speed digital camera (Casio EX-FH25 10.1 MP) at 420 fps and processed videos with Tracker 4.11.0 to obtain the maximum sprint speed for each individual at each temperature.

One hour after the last sprint, we measured the critical thermal minimum (CT_{min}) and maximum (CT_{max}) temperatures with a 1-h interval between them. We always measured CT_{min} before CT_{max}, since the last may be more stressful. We exposed lizards to the sources of heat and cold mentioned above until they lost the righting response, that is, when lizards placed on their dorsum could not flip over to their venter.

We generate a thermal performance curve (Figure S1; Huey & Stevenson, 1979) using a generalized additive mixed model—GAMM (Wood, 2017; Zajitschek et al., 2012). This model used the maximum running speed as the response variable, body temperature as a fixed effect, and snout-vent length (SVL) as a covariate. We included the lizard identification as a random effect. From the thermal performance curve, we estimated thermal performance breadth and optimal temperature for performance (Huey & Stevenson, 1979). As this model estimates the thermal performance based on temperature, we use historical and future biologically relevant temperature data (monthly average minimum and maximum temperatures, and bioclimatic variables related to the minimum and maximum temperatures at specific times of the year—BIO5, BIO6, BIO8, and BIO9) to extrapolate the thermal performance spatially (in South America) and temporally (current and future) using the package MAPINGUARI (Caetano et al., 2019). Thus, we estimated thermal performance for each pixel of the temperature rasters.

2.3 | Hours of activity variables

We used data collected at Reserva Ecológica do IBGE (above) and in a gallery forest at Estação Ecológica do Jardim Botânico de Brasília (15°51′12″ S, 47°49′14″ W), Distrito Federal, Brazil. To estimate the hours of activity, we recorded the daily temperature experienced by lizards in the field (operative environmental temperature) and the temperature range in which they are active (Caetano et al., 2020). The latter corresponds to the difference between the minimum and maximum voluntary temperatures. We used data loggers (Onset HOBO Pro v2 2x External Temperature Data Logger U23-003) to estimate the operative environmental temperature with sensors inserted into PVC models of equivalent size and color to *N. frenata* (2.0 cm diameter × 6.0 cm length; brown and gray; Figure S2). We placed the models in microhabitats used by the species: bare ground ($N = 62$), leaf litter, termite mounds ($N = 22$), logs ($N = 33$), trees ($N = 13$), burrows ($N = 22$), and shrubs ($N = 8$). The models were under varying degrees of sunlight exposure among all microhabitats sampled. We deployed data loggers in August 2013, January 2014, and April–July 2014, recording temperatures every minute. In this way, we recorded the temperature variations which animals could experience in each microhabitat. This protocol for estimating operational temperature has been validated for small ectotherms, such as lizards (Pontes-da-Silva et al., 2018; Sinervo et al., 2010). Further, we recorded air temperature every minute at the same time in locations close to the models using 21 data loggers (Onset HOBO Pro v2 Temperature/Relative Humidity Data Logger U23-001-A) placed inside a PVC cover, fixed to a metal pole at 50 cm above the ground. There was no contact between metal poles and data collectors; therefore, there was no interference in the collection of air temperature.

We estimated the daily hours in which the operative temperature in each microhabitat is within the species' voluntary temperature range. We considered the average among microhabitats as the number of hours of activity of *N. frenata*. Then, we built a generalized linear model with Poisson errors relating hours of activity to the maximum daily air temperature recorded in the field (Figure S3). As this model estimates the hours of activity based on air temperature, we use historical and future biologically relevant temperature data (monthly average minimum and maximum temperatures, BIO5, BIO6, BIO8, and BIO9) to extrapolate the hours of activity spatially (in South America) and temporally (current and future) using the package MAPINGUARI (Caetano et al., 2019). Thus, each pixel of the temperature rasters had its estimated value of hours of activity. Similar procedures have been used previously (e.g., Caetano et al., 2020; Kirchhof et al., 2017).

2.4 | Species occurrence records

From the literature and herpetological collections, we obtained 245 occurrence records of *N. frenata*. Then, we removed duplicate records using the DISMO package (Hijmans et al., 2017) to minimize spatial autocorrelation, leaving 200 records. Next, we used the four least collinear environmental variables ($\text{VIF} < 2$) to filter the records using the *EnvSample* function to minimize sampling bias based on environmental heterogeneity (Varela et al., 2014), leaving 130 records.

2.5 | Land cover data

To account for deforested areas, we obtained land cover data at a 0.5 km resolution from Broxton et al. (2014) for the present, based on 10 years (2001–2010) of data from the "5.1 Moderate Resolution Imaging Spectroradiometer (MODIS) Land Cover Type MCD12Q1" collection. We considered 12 classes of land cover as natural vegetations (evergreen needleleaf, evergreen broadleaf, deciduous needleleaf, deciduous broadleaf, mixed forests, closed shrublands, open shrublands, woody savannas, savannas, grasslands, permanent wetlands, and snow/ice) and four classes as deforested (croplands, urban and built up, cropland/natural vegetation, and barren). For the future, we obtained land-use projections at a 1 km resolution made by Li et al. (2017) for 2050 and 2100 under the greenhouse gas emission scenarios B1 and A2. As we considered three future periods in our analyses, we made a linear interpolation between these data to estimate the land use in 2070, using the *interpolate_linear* function of the THINGS package (Baumgartner & Wilson, 2015). We considered three classes of land cover as natural vegetation (water, forest, and grassland) and three as deforested (farmland, urban, and barren). We resampled the present and future land use data to the exact resolution as the climatic/physiological data using the "nearest neighbor" method with the RASTER package (Hijmans et al., 2015).

2.6 | Protected areas data

To assess the effectiveness of protected areas in conserving suitable habitats for *N. frenata*, we obtained protected areas data in Brazil, Argentina, Paraguay, and Bolivia from the World Database on Protected Areas—WDPA (UNEP-WCMC, 2022). We considered all protected areas that overlap the current habitat suitability area for the species, including all International Union for Conservation of Nature and Natural Resources (IUCN) management categories (Dudley, 2008).

2.7 | Habitat suitability modeling

To reduce multicollinearity among spatially correlated variables, which can cause instability in parameter estimation (Dormann et al., 2013), we used a stepwise approach to eliminate highly collinear variables based on the variance inflation factor (VIF) with package USDM (Naimi, 2015). The procedure consisted of calculating VIF for all variables, excluding the one with the highest VIF (> 5), and repeating the procedure until no variables with $\text{VIF} > 5$ remained., Using this procedure, the following variables were retained: BIO2, BIO3, BIO14, BIO15, BIO18, and BIO19; thermal performance based on maximum temperature of the hottest month (BIO5); and hours of activity based on minimum temperature of the coldest month (BIO6) and the average temperature of the wettest quarter (BIO8; Figures S4–S13). Then, we used these nine variables as predictors and the 130 species occurrence records as a response variable to build a model to predict areas of habitat suitability in the present, using package BIOMOD2 (Thuiller et al., 2020). As our data consisted only of presence records and we needed absence records, we generated pseudoabsence records (background) randomly sampled across the study area (Barbet-Massin et al., 2012; VanDerWal et al., 2009). Next, we used 10 algorithms to build the habitat suitability models. Because the number of pseudoabsences can significantly affect model accuracy depending on the algorithm (Barbet-Massin et al., 2012), we used 10,000 pseudoabsences for six algorithms (Generalized Linear Models—GLM, Generalized Additive Models—GAM, Artificial Neural Network—ANN, Surface Range Envelope—SRE, Functional Data Analysis—FDA, Multivariate Adaptive Regression Splines—MARS, and Maximum Entropy—MAXENT.Phillips), and 130 pseudoabsences (= number of presences) for three algorithms (Random Forest—RF, Classification Tree Analysis—CTA, and Generalized Boosting Models—GBM).

We used 75% of the 130 occurrence records to build the models as a training data set and the remaining 25% as a test data set. We repeated this process 10 times. To reduce the uncertainty associated with the choices made for each model (Buisson et al., 2010), we evaluated their quality using the following indexes: KAPPA, TSS, ROC, ACCURACY, BIAS (Allouche et al., 2006; Qiao et al., 2015). Next, we derived an ensemble of the model predictions with TSS ≥ 0.8, weighing their contribution to the set according to the TSS value, using package BIOMOD2 (Thuiller et al., 2020). Then, we calculated predictor importance with the *variables_importance* function of the same package to investigate which type of predictor (environmental or physiological) had the most outstanding contribution to models. This function uses Pearson's correlation between reference predictions (i.e., unchanged values) and the prediction after permuting the investigated variable (Thuiller et al., 2020). Predictor importance is then estimated as 1 − Pearson's correlation, so the lower the correlation, the more significant the influence of the predictor. We repeated this randomization procedure 10 times and averaged the importance values for each variable.

We combined the occurrence data of *N. frenata* and the model predictions to calculate an occurrence threshold using the Maximum Sensitivity plus Specificity (maxSSS) method (Liu et al., 2016). The threshold obtained was 0.51, so we considered the pixels with a habitat suitability value above that threshold as presences and those below it as absences. Then, we transformed the habitat suitability predictions into binary surfaces with packages BIOMOD2 and PRESENCEABSENCE (Freeman & Moisen, 2008). Finally, we multiplied the pixel area by the number of presence pixels to obtain the total suitable area for the present, subtracting the deforested areas by 2010 (Broxton et al., 2014).

We implemented a gap analysis to assess the effectiveness of protected areas for *N. frenata*. So, we overlapped the binary presence-absence raster and the polygons of the protected areas and then calculated the number of overlapping pixels with package EXACTEXTRACTR (Baston, 2021). Next, we calculated the pixel area and multiplied it by the number of pixels to calculate the amount (in km^2) and proportion (%) of suitability area within protected areas.

We used the ensemble model to project habitat suitability areas into the future using the same nine predictors we used to build the model. Then, we transformed all projections into binary geographic surfaces and calculated the total area of habitat suitability for the future, disregarding the expected deforestation (Li et al., 2017). For each period considered—2041–2060, 2061–2080, and 2081–2100—we subtracted the projected deforestation for 2050, 2070, and 2100, respectively. Regarding the emission of greenhouse gases, for the projections of habitat suitability in the SSP2-4.5 and SSP5-8.5 scenarios, we used the land use projections for B1 and A2, respectively, due to the greater similarity between them (van Vuuren & Carter, 2014). Finally, we calculated the difference between the current predicted area and future projections to assess gains and losses of suitable habitats for *N. frenata* due to climate change. We conducted all statistical analyses described above in the R environment (R Core Team, 2020).

3 | RESULTS

Regarding the preferred temperature and critical thermals of *N. frenata*, the average T_{pref} for all individuals was 33.53 ± 3.88°C, the average CT_{min} was 14.04 ± 2.87°C, and the average CT_{max} was 41.60 ± 3.37°C. The preferred temperature range, that is, the central 50% of all preferred temperature records (Hertz et al., 1993; Huey et al., 2009), was 28.89–37.40°C. The median of preferred temperature records was 35.60°C. The minimum and maximum voluntary temperatures were 23.90°C and 41.98°C, respectively. The optimal temperature (T_{opt}), that is, the best-performance body temperature, was 31.80°C, closer to CT_{max} than to CT_{min} (Figure S1).

Among the algorithms used to build the model, three had TSS values ≥ 0.8: RF, GBM, and GAM (Table 1). Therefore, we combined their predictions to estimate the current habitat suitability area for *N. frenata* and project it into the future. Isothermality (BIO3) made the most outstanding contribution to the model, followed by precipitation of the coldest quarter (BIO19) and hours of activity based on the minimum temperature of the coldest month (BIO6; Figures 1 and S14).

We observed changes in the three physiological variables in the future compared to the present (Figure 2). In 2080–2100, in both greenhouse gas emissions scenarios, the thermal performance based on the maximum temperature of the warmest month (BIO5) tends to decrease, while both hours of activity based on the minimum temperature of the coldest month (BIO6) and the average temperature of the wettest quarter (BIO8) tended to increase.

Excluding areas deforested between 2001 and 2010, we estimated the currently suitable area at 3,686,948 km^2 (Figure 3). However, our gap analysis showed that only 159,209.6 km^2 of suitable areas lie within protected areas, corresponding to only 4.32% of the total area (Figure 3).

We obtained 48 projections for the future forecasts, 16 for each period (2041–2060, 2061–2080, and 2081–2100; Figures S15–S17). Although the results showed substantial variation due to the combination of SSPs, GCMs, years, and deforestation, suitable areas decreased in the future in all projections, suggesting a negative effect of climate change on the species (Table S1).

TABLE 1 Quality of the algorithms for building the ensemble model considering five evaluation metrics.

Algorithm	Accuracy	BIAS	KAPPA	ROC	TSS
RF	0.92351	0.99628	0.84683	0.96614	0.84683[a]
GBM	0.91751	0.99659	0.83487	0.96327	0.83487[a]
GAM	0.98700	0.88518	0.36179	0.94180	0.82212[a]
MARS	0.98745	0.90887	0.35430	0.94313	0.78697
MAXENT.Phillips	0.99290	0.99038	0.69088	0.89907	0.76401
CTA	0.86909	0.91824	0.73818	0.87893	0.73818
GLM	0.98723	0.71190	0.26180	0.90627	0.73554
ANN	0.98700	0.20593	0.19801	0.89671	0.73542
FDA	0.98829	0.97427	0.36526	0.92838	0.73490
SRE	0.98974	0.65031	0.58703	0.80912	0.61831

Abbreviations: ANN, Artificial Neural Network; CTA, Classification Tree Analysis; FDA, Functional Data Analysis; GAM, Generalized Additive Models; GBM, Generalized Boosting Models; GLM, Generalized Linear Models; MARS, Multivariate Adaptive Regression Splines; MAXENT.Phillips, Maximum Entropy; RF, Random Forest; SRE, Surface Range Envelope.

[a] The models that have been combined (TSS ≥ 0.8).

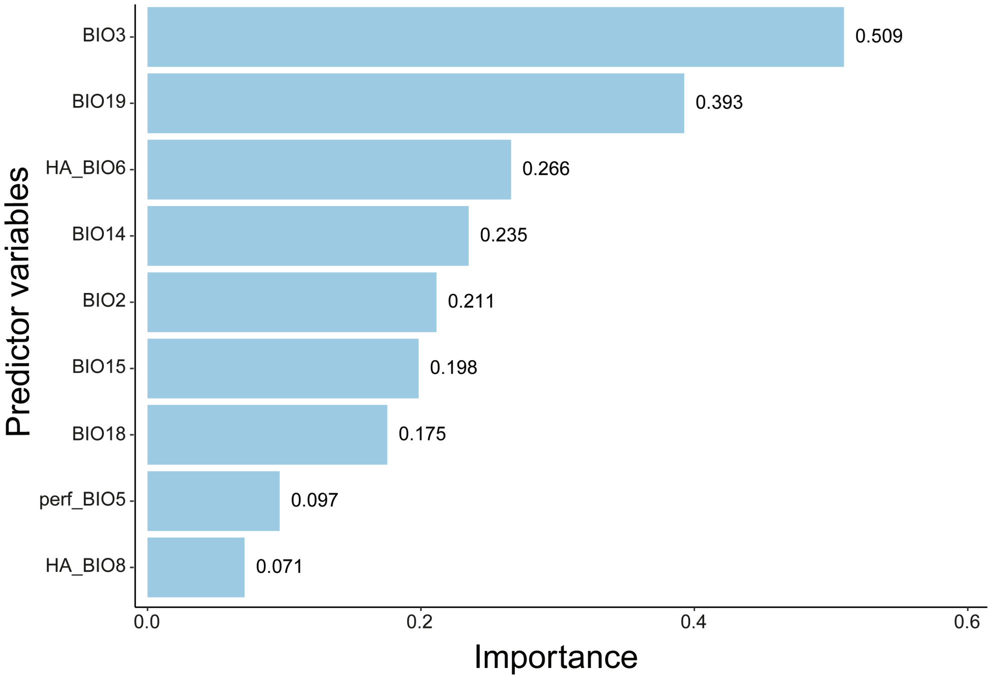

FIGURE 1 Importance of the predictor variables for the *Notomabuya frenata* distribution model. The numbers indicate the proportion of contribution, calculated by 1 − Pearson's correlation between reference prediction (i.e., with unchanged values) and the prediction with the investigated variable randomly permuted. In the figure, BIO3, isothermality; BIO19, precipitation of the coldest quarter; HA_BIO6, species' hours of activity based on the minimum temperature of the coldest month; BIO14, precipitation of the driest month; BIO2, mean diurnal range; BIO15, precipitation seasonality (coefficient of variation); BIO18, precipitation of the warmest quarter; perf_BIO5, thermal performance of the species based on the maximum temperature of the hottest month; HA_BIO8, species' hours of activity based on the mean temperature of the wettest quarter.

Based on the SSP2-4.5 scenario and its deforestation projection, we estimated the average contraction in suitable habitats at 38.16% for 2041–2060, 54.35% for 2061–2080, and 58.50% for 2081–2100 (Figure 4 and Table S1). Based on the SSP5-8.5 scenario and its respective deforestation, the average reduction was estimated at 55.54% for 2041–2060, 79.94% for 2061–2080, and 89.66% for 2081–2100. Among the GCMs, the maximum reduction was projected with CanESM5 in the SSP5-8.5 scenario, with 86.33% for 2041–2060, 95.15% for 2061–2080, and 99.17% for 2081–2100.

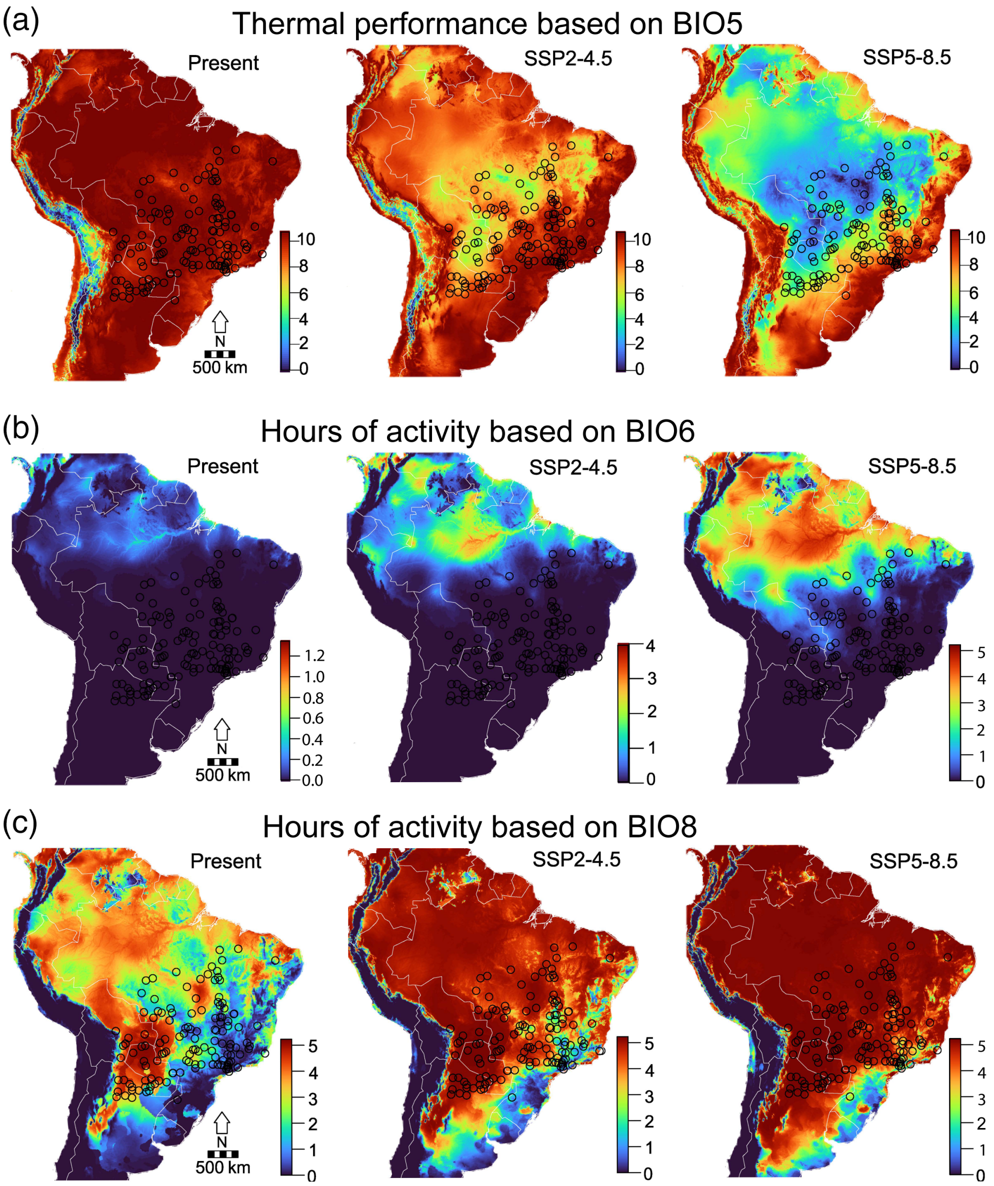

FIGURE 2 Physiological variables of *Notomabuya frenata* in the present and projected for the future (2081–2100) in two shared socioeconomic pathways (SSP2-4.5 and SSP5-8.5), considering eight general circulation models (GCMs). The physiological variables are (a) thermal performance based on the maximum temperature of the warmest month (BIO5); (b) hours of activity based on the minimum temperature of the coldest month (BIO6), and (c) hours of activity based on the average temperature of the wettest quarter (BIO8). The closer to red, the higher the thermal performance and more hours of activity. The points are the occurrence records of the species used in our analyses.

As for the geographic location of suitable habitats for *N. frenata* in the future, its expansion was concentrated in small regions in northeastern Brazil and northern Argentina (Figure 5). Contrarily, its contraction occurred in large areas of central Brazil, eastern Bolivia, and northern and western Paraguay.

4 | DISCUSSION

Isothermality (BIO3), precipitation of the coldest quarter (BIO19), and hours of activity based on the minimum temperature of the coldest month were the three predictors of the most outstanding contribution to the distribution model of *N. frenata*. Thus, environmental variables had a more significant contribution, contradicting our initial hypothesis that physiological variables would be more critical. We found that only 4.32% of the currently suitable areas are within protected areas. Furthermore, all projections show that suitable areas will decrease shortly, corroborating our hypothesis that climate change and deforestation may cause a drastic reduction in the potential range.

4.1 | Contribution of predictor variables

The importance of predictor variables should be interpreted with caution since their indirect—rather than direct—effects may be responsible for limiting the species distribution. The most important predictor of habitat suitability was isothermality (BIO3), i.e., the ratio between the mean diurnal temperature range and the annual temperature range. The distribution of *N. frenata* is

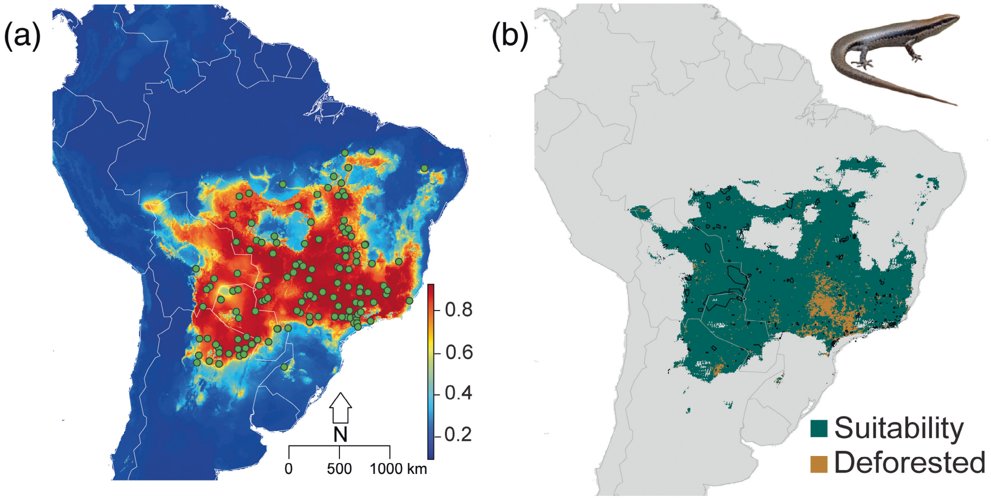

FIGURE 3 Predicted area of habitat suitability for *Notomabuya frenata* at present (3,686,948 km^2). In (a), the closer to red, the greater the habitat suitability of the site for the species. The green points are the occurrence records of the species used in our analyses. In (b), the binary image is represented, where green indicates the area of habitat suitability for the species and brown represents the deforested area between 2001 and 2010. The black polygons represent the boundaries of protected areas.

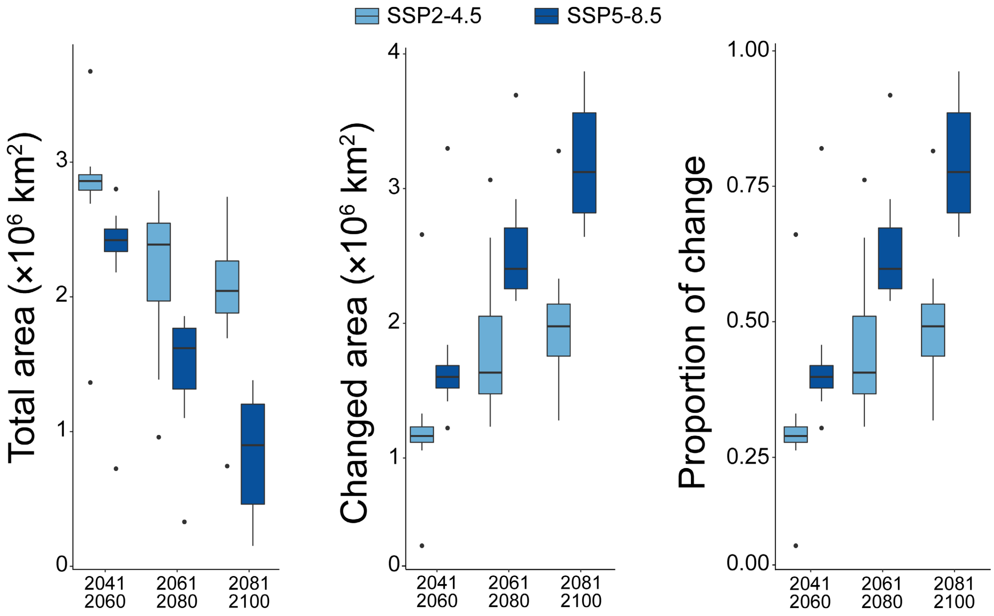

FIGURE 4 Area of habitat suitability for *Notomabuya frenata* projected for 2041–2060, 2061–2080, and 2081–2100 for two shared socioeconomic pathways (SSP2-4.5 and SSP5-8.5), considering eight general circulation models (GCMs). The values in the graph represent (a) the total suitable area in the future, subtracting the projected deforestation for 2050, 2070, and 2100, respectively; (b) the changing suitable area (reduced in all cases) between current and future, subtracting current and projected deforestation, respectively, and (c) proportion of the change shown in (b).

associated with areas of intermediate to high isothermality, mainly in the portion corresponding to the Cerrado biome. This greater thermal stability may be reflected in the high diversity of viviparous skinks in central Brazil, harboring at least four often sympatric species (Hedges & Conn, 2012). Although we have not tested these parameters, the importance of isothermality for *N. frenata* may be related to the influence of incubation temperature variability in increasing gestation duration and reducing offspring locomotor performance, as observed in other viviparous lizards (Ji et al., 2007; Ma et al., 2018). This finding suggests that the distribution of *N. frenata* is mainly limited by the thermal stability of the environment, which can influence thermoregulation behavior, life history patterns, and phenotypic plasticity (Clarke & Zani, 2012; Ma et al., 2018; Noble et al., 2018). This

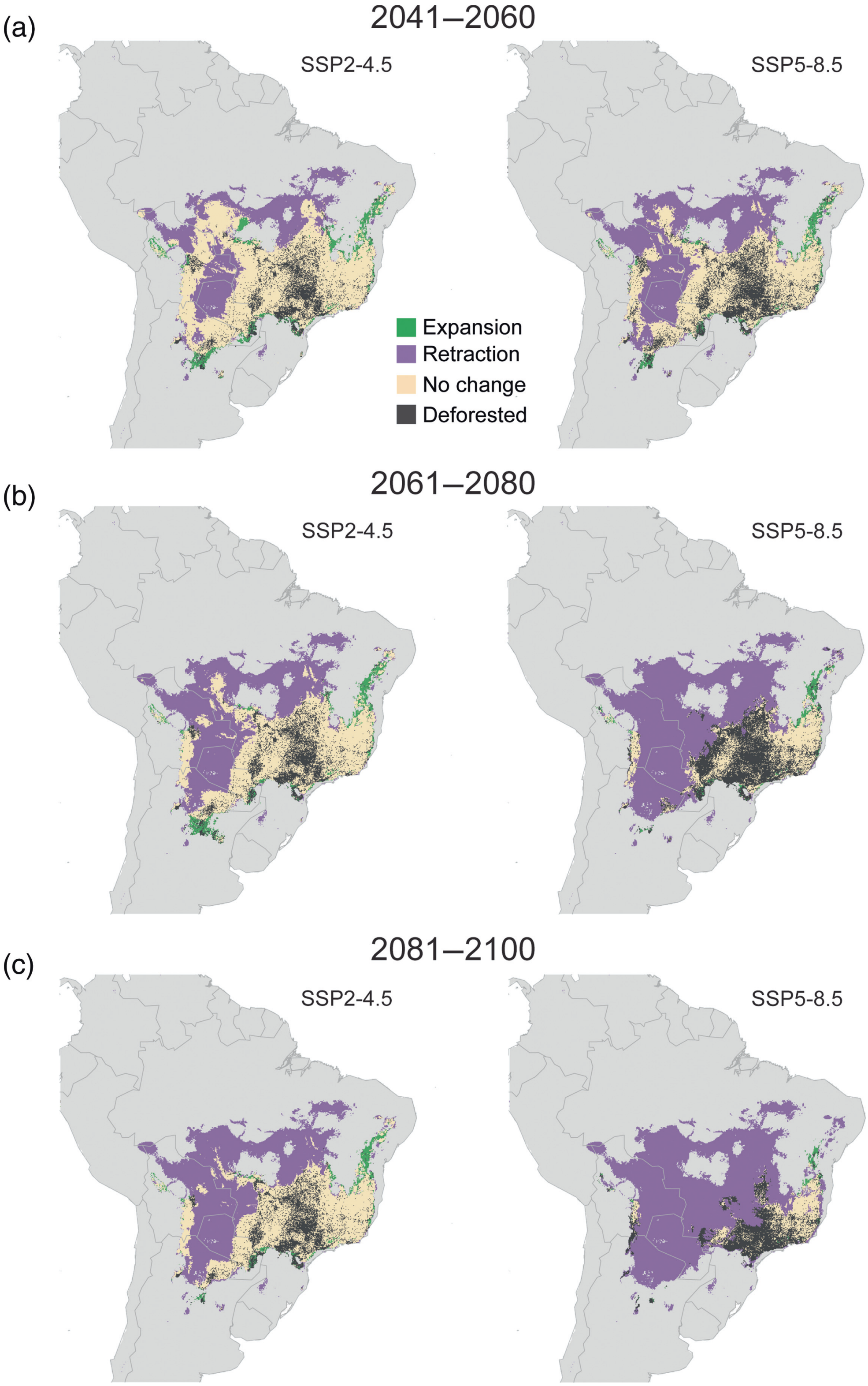

FIGURE 5 Geographic location of the average expansion (green) and contraction (purple) of the suitable habitats for *Notomabuya frenata* in (a) 2041–2060, (b) 2061–2080, and (c) 2081–2100. In the figure, the suitable habitats that were not altered between the present and the future are represented in beige, while the deforested area projected for 2050, 2070, and 2100 is represented in black.

variable also has a dominant effect on the distribution of other tropical organisms, such as plants, mammals, and other lizards (Huang et al., 2021; Santos et al., 2014; Varela et al., 2009).

The precipitation of the coldest quarter (BIO19) was second in importance for predicting the habitat suitability for *N. frenata*. Its distribution is mainly concentrated in areas with low or no precipitation in winter, as in the Cerrado and northern Chaco (Figure S14; Reboita et al., 2010). Thus, the range of this species seems to be strongly associated with regions of Aw climate in Köppen's classification, characterized by a dry winter (Peel et al., 2007). In this scenario, viviparity can be advantageous to buffer environmental fluctuations, ensure good hydric conditions for embryonic development, and avoid eggs' desiccation risk if they are deposited on dry soils (Shine & Brown, 2008). In addition, hatchlings usually occur between the end of the dry season and the beginning of the rainy season, coinciding with the increase in insect abundance in the Cerrado, which is the main component of the species' diet (Pinheiro et al., 2002; Vrcibradic & Rocha, 1998a, 1998b). Thus, the importance of precipitation in determining the distribution of *N. frenata* seems to be related to intrinsic traits that configure adaptive advantages to the seasonality of water and food. Previous studies also show precipitation as a determining predictor for the distribution of reptiles, including lizards that occur in Brazil (Bradie & Leung, 2017; Caetano et al., 2020; Winck et al., 2014).

Physiological variables also contributed to the species distribution model of *N. frenata*. Hours of activity based on the minimum temperature of the coldest month (BIO6) was the third most relevant predictor. This finding indicates that climatic extremes limit activity time, shaping the geographic distribution. However, unlike other lizard species, the distribution of *N. frenata* appears to be influenced by lower thermal extremes, which reduce the time of activity (Figure S14; Medina et al., 2016; Monasterio et al., 2013).

Physiological performance should be significantly affected in the future. In 2080–2100, in both greenhouse gas emissions scenarios, the thermal performance based on the maximum temperature of the warmest month (BIO5) tends to decrease mainly north and west of the species' current distribution. This performance reaches zero in some places in central Brazil, indicating that climate change can lead to temperatures that exceed the thermal limits of activity of the species. This reduced thermal performance and the occurrence of body temperatures that exceed the critical thermal maximum in the future have already been estimated for other lizards (e.g., Buckley et al., 2015; Gilbert & Miles, 2017). Thus, species will depend on their ability to maximize physiological performance at higher temperatures to ensure their persistence under changing climates (Logan et al., 2014). In contrast, both hours of activity based on the minimum temperature of the coldest month (BIO6) and the average temperature of the wettest quarter (BIO8) tended to increase in 2080–2100. While the first increased only in the north, the second increased throughout the species' current distribution area. These alterations indicate that climate change may influence the physiological parameters of species along their geographic distribution differently.

However, the physiological predictors used in this work are based on only one site since local adaptations can promote intraspecific variations in the thermal physiology of ectotherms (Bozinovic et al., 2011; Herrando-Pérez et al., 2019; Pontes-da-Silva et al., 2018). Consequently, the importance of variables may vary across the distribution, and model predictions far away from the sampled locality are less precise. This stems from the challenge of obtaining ecophysiological data for sufficient sites for comprehensive coverage due to wide distribution and time and resource constraints (Peterson et al., 2015; Urban et al., 2016).

Models based on environmental predictors deal with species'-realized niche, inferring the environmental requirements for their occurrence, and models based on biological predictors deal with species' fundamental niche, modeling distribution based on knowledge of their physiology (Morin & Thuiller, 2009; Peterson et al., 2015). Thus, the use of hours of activity and thermal performance enables a more detailed identification of the processes that can limit species distributions because these variables are closely linked to vital organism processes, such as feeding, considering the foraging time; survival, through the escape of predators, and reproduction, through the meeting of partners (Irschick & Losos, 1998; Robson & Miles, 2000).

4.2 | Protected areas

We estimated the currently suitable area for *N. frenata* at 3,686,948 km^2, but only 4.32% of this total is within protected areas, corresponding to 159,209.6 km^2. Therefore, the protected areas are insufficient to provide suitable habitats for this species. This finding is worrying because, in addition to this species being harmed by climate change, it is threatened by changes in the landscape, such as deforestation for agriculture and pasture, mining, road construction, and fires (Ribeiro-Júnior & Amaral, 2016). This result can be more disturbing given that all types of IUCN-protected areas were considered; therefore, some allow different levels of human use (Dudley, 2008).

As there are few protected areas, several South American species have a tiny portion of their distribution protected, such as Chaco reptiles in several countries (Bax & Francesconi, 2019), Paraguayan reptiles (Cacciali et al., 2015), lizards endemic to the Cerrado (Novaes e Silva et al., 2014), and Amazonian lizards (Ribeiro-Júnior & Amaral, 2016), for example. Like us, Ribeiro-Júnior and Amaral (2016) observed a low proportion of the *N. frenata* distribution within protected areas, but specifically for the Brazilian Amazonia in their work. In addition, the authors highlighted that 52% of the Amazonian range of this species had been deforested, as it coincides with the “arc of deforestation” (Ribeiro-Júnior & Amaral, 2016).

4.3 | Climate change and geographic distribution

Our models predicted an extensive contraction of suitable habitats in all scenarios, indicating that climate change will severely impair *N. frenata*. The most significant area reduction was predicted for the last two decades of the 21st century under the most pessimistic scenario of greenhouse gas emissions, when an average increase of 4°C in the temperature of South America is estimated (Magrin et al., 2014). This result highlights the importance of mitigating these emissions to avoid drastic changes in the planet's temperature and guarantee biodiversity's future (Warren et al., 2013).

In this sense, our results add to other studies that project a contraction in the future geographic distribution of lizards from tropical regions (Berriozabal-Islas et al., 2018; Pontes-da-Silva et al., 2018), reinforcing the concept that species from lower latitudes have high vulnerability to climate change (Tewksbury et al., 2008). Additionally, our results reinforce that the T_{opt} of tropical organisms is closer to its CT_{max} than its CT_{min}, reducing its thermal safety margin (Deutsch et al., 2008; Sunday et al., 2011; Tewksbury et al., 2008). In addition, this study shows one more viviparous lizard that is potentially vulnerable to climate change, as has been discussed in other works (Jara et al., 2019; Pincheira-Donoso et al., 2013).

The models identified changes in the geographic location of areas of suitable habitats for *N. frenata* in the future. A dominant pattern is a cumulative reduction in the suitable area with increased greenhouse gas emissions. We found that suitable habitats are restricted to southeastern and parts of southern and northeastern Brazil, coinciding with Atlantic Forest areas (Ewers & Banks-Leite, 2013). However, this is also the most degraded biome in Brazil, with about 12% of its original area remaining (Ribeiro et al., 2009), which threatens the availability of areas for *N. frenata*. In addition, if the species reaches these suitable habitats, this colonization can result in competition with native species of the region, which often leads to changes in the ecological balance of that site (Ricciardi & Simberloff, 2009). Migrating species tend to have a competitive advantage over those already in the area since even if they compete on equal terms for food resources, new species have a marginally lower predation risk, which may lead to decreased abundance of resident species (Fryxell & Sinclair, 1988).

Our results should be interpreted with caution since model building has some limitations. Among these is the risk of converting continuous habitat suitability values into binary presence-absence maps because it can limit results with a wide range of variation to just two different probabilities of occurrence (Lawson et al., 2013). Additionally, a limitation is an uncertainty associated with using pseudo-absences rather than verified absences because the former may indicate unsuitable or suitable but unoccupied habitats (Gu & Swihart, 2004). However, obtaining verified absence data is very difficult and expensive (Mackenzie & Royle, 2005). Another possible limitation is the use of climate predictors and land use data based on mathematical models, as they simulate environmental conditions but cannot guarantee exact predictions, especially for the future (Harris et al., 2014; Weaver et al., 2012).

4.4 | Land-use changes

We found that changes in land use should amplify the effects of climate change upon *N. frenata*, reducing the areas available for survival and maintenance. This finding reinforces the threat of synergistic effects of climate and landscape changes on biodiversity (Sala et al., 2000; Travis, 2003). There is a strong interaction among them because while the climate is the primary determinant of vegetation structure, deforestation exacerbates the effects of climate change (Hahmann & Dickinson, 1997; Zhang et al., 1996).

The four countries that make up the distribution of the species accounted for 80% of all deforestation in South America and the Caribbean between 2001 and 2010 (Aide et al., 2013). In the Chaco areas of northern Argentina, 1.4 million hectares were deforested between 1972 and 2007 (Gasparri & Grau, 2009). More than 50% of the Cerrado has been converted and fragmented to create farming areas (Klink & Machado, 2005; Sano et al., 2008). Thus, even if our models predict small expansions of suitable habitats for *N. frenata* in the future, the reach of these sites will be hampered not only by the limited capacity of the lizards to disperse but by the loss and fragmentation of habitats (Thomas et al., 2004). This result highlights the relevance of considering land use in climate change studies to have more realistic predictions of organisms' responses.

4.5 | Overview and recommendations

In summary, our work indicates that environmental variables significantly contributed to the distribution model of *N. frenata*. However, environmental and physiological predictors proved essential in estimating the effect of climate change on suitable areas. Our modeling approach is still scarce for species from the Neotropical region. In addition, temperature variability, precipitation during winter, and lower thermal extremes are among the main limitations for the distribution of this and other species. Moreover, we found low effectiveness of protected areas in conserving sites with current areas of high habitat suitability for *N. frenata*. Finally, our findings indicate that climate change and its effects on physiological parameters may cause a drastic reduction in the species' potential range, stressing the high vulnerability of tropical and viviparous lizards to local extinctions. Considering projected deforestation for the future showed that the suitable habitats are much smaller than projected, indicating how the growing land-use change can exacerbate the threat of climate change to biodiversity. Our work suggests that widely distributed species, such as *N. frenata*, may have their conservation compromised soon due to the low representativeness of their habitat suitability in protected areas combined with changes in climate and landscape. Therefore, we highlight the need for decision-makers to consider this and other works in creating protected areas and other conservation projects.

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DATA AVAILABILITY STATEMENT

The datasets and code files are on Dryad: https://doi.org/10.5061/dryad.6djh9w156

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