Understanding the ecological niche to elucidate spatial strategies of the southernmost *Tupinambis* lizards

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Abstract. Understanding factors that shape ranges of species is central in evolutionary biology. Species distribution models have become important tools to test biogeographical, ecological and evolutionary hypotheses. Moreover, from an ecological and evolutionary perspective, these models help to elucidate the spatial strategies of species at a regional scale. We modelled species distributions of two phylogenetically, geographically and ecologically close *Tupinambis* species (Teiidae) that occupy the southernmost area of the genus distribution in South America. We hypothesized that similarities between these species might have induced spatial strategies at the species level, such as niche differentiation and divergence of distribution patterns at a regional scale. Using logistic regression and MaxEnt we obtained species distribution models that revealed interspecific differences in habitat requirements, such as environmental temperature, precipitation and altitude. Moreover, the models obtained suggest that although the ecological niches of *Tupinambis merianae* and *T. rufescens* are different, these species might co-occur in a large contact zone. We propose that niche plasticity could be the mechanism enabling their co-occurrence. Therefore, the approach used here allowed us to understand the spatial strategies of two *Tupinambis* lizards at a regional scale.

Keywords: environmental factors, evolutionary ecology, niche differentiation, sister species, species distribution modelling, sympatric zone.

Introduction

Species distribution models have become important tools to test biogeographical, ecological and evolutionary hypotheses (Graham et al., 2004). For instance, they have been useful in assessing species niches (Gray et al., 2009; Beaudry et al., 2010; Anadón et al., 2012), determining the environmental factors responsible for the geographical ranges of a species (Di Cola et al., 2008; Di Cola and Chiaraviglio, 2011) and considering questions involving the environmental niches of related taxa (Debandi et al., 2011). Moreover, from an ecological and evolutionary perspective, species distribution models help to elucidate the spatial strate-

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*Corresponding author; e-mail: gabicardozo@yahoo.com.ar gies of species at a regional scale (Luxbacher and Knouft, 2009; Debandi et al., 2011; Di Cola and Chiaraviglio, 2011). Understanding factors that shape species ranges is central in evolutionary biology (Holt, 2003). Niche hypotheses in evolutionary contexts pose significant challenges that could be faced fruitfully using techniques in distributional ecology (Peterson and Holt, 2003).

Phylogenetic and ecological contexts are important to the understanding of the niche of the species (Pawar et al., 2004; Rivera et al., 2011). The genus Tupinambis (Teiidae) comprises seven species. Tupinambis merianae and T. rufescens provide an interesting model system because they are phylogenetically sister species (Fitzgerald et al., 1999; Cabaña et al., 2014). Moreover, they are geographically close, being the southernmost species of the genus in South America. They occur in parallel allopatric zones from approximately 10° to 40°S (T. rufescens occurring more to the west than T. merianae) (Cei, 1993; Colli et al., 1998; Lopes and Abe, 1999; Carvalho et al., 2006) and although these species occur mainly in allopatry, they also co-habit in diverse contact zones (Pe-

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ters and Donoso-Barros, 1986; Fitzgerald et al., 1991; Cei, 1993; Fitzgerald, 1994; Cardozo et al., 2012). Assessing the factors that regulate environmental niches of sister species at a regional scale might contribute to the understanding of the mechanisms that shape intrageneric distribution patterns.

T. merianae and T. rufescens also share morphological and ecological traits. They have similar body size, being the largest lizards of the family Teiidae (Cei, 1993; Colli et al., 1998); they are robust, with big heads (Rieppel, 1980; Cei, 1993). Both species are active foragers (Avila-Pires, 1995) and have an omnivorous diet (Presch, 1973; Williams et al., 1993; Castro and Galletti, 2004). These species overwinter in burrows and emerge during the warm season (Fitzgerald, 1993; Lopes and Abe, 1999). Morphologically similar species are more likely to interact than morphologically dissimilar ones simply because a major portion of the behavioural and ecological activities of animals is associated with morphology (Pianka, 1986; Losos, 1990). Therefore, morphologically and ecologically similar species are thought to share habitat requirements that can hinder their coexistence (Huey, 1974; Huey and Pianka, 1977). However, we hypothesize that morphological similarity between geographically close animal species, such as T. merianae and T. rufescens, might have induced spatial strategies at the species level, such as niche differentiation and divergence of distribution patterns at a regional scale. Accordingly, we expect that the two Tupinambis species have different habitat requirements and consequently, present extended allopatric ranges of distribution.

Habitat requirements at a landscape level have been explored for *T. merianae* and *T. rufescens* in allopatric and sympatric zones. These species differ in habitat requirements in allopatric areas, but do not differ in the contact zone, where they are found in sympatry (Cardozo et al., 2012). However, to elucidate the spatial strategies of *T. merianae* and *T. rufescens* from an evolutionary perspective at a regional scale, it is necessary to assess their environmental niches through species distribution models. Comparing species distribution models between related species to identify the environmental factors affecting their occurrence may help to better understand species distribution patterns in contact zones (Scali et al., 2011).

Environmental factors largely limit the niche of Squamata at regional scales (Anadón et al., 2012). Modelling distribution patterns requires the definition of environmental variables relevant for the bioecology of the species (Austin, 2007; Sinclair et al., 2010). Variations in life history traits of a species, such as phenotype of hatchlings (Quintana, 2000) have been related to geographic variation in precipitation. Moreover, environmental temperature might influence diverse behavioural responses (Gifford et al., 2008; Cury de Barros et al., 2010) and trigger reproductive activity in teiid lizards from temperate zones (Cruz et al., 1999). In addition, the spatial pattern of vegetation cover affects thermoregulatory processes in ectotherms (Chiaraviglio, 2006; Cardozo and Chiaraviglio, 2011). Accordingly, Chiarello et al. (2010) hypothesized that vegetation pattern might influence basking of active heliothermic lizards like Tupinambis. Finally, altitude influences life history traits, such as sexual maturity and egg size in lizards (Rohr, 1997; Iraeta et al., 2008). Species distribution models can assess the role of these environmental factors in determining the presence of each species (Di Cola et al., 2008; Debandi et al., 2011; Di Cola and Chiaraviglio, 2011; Anadón et al., 2012).

Overall, the geographical range of a species is a complex expression of its bioecology and evolutionary context. Accordingly, we modelled species distributions of two phylogenetically, geographically and ecologically close *Tupinambis* species that occupy the southernmost area of the genus distribution in South America to understand the spatial strategies that shape their ecological niches and to determine the role of environmental factors on their spatial distributions.

Materials and methods

Species data

The database used included information of the species presence in South America (214 records of T. rufescens and 343 records of T. merianae; fig. 1). Records were gathered from authors' field data and complemented with museum and information from the literature (Coleção SinBiota de Inst FAPESP; Museu de Zoologia/Universidade Estadual de Campinas - ZUEC/REPTEIS; Museu de Zoologia da Universidade de São Paulo (MZUSP); Coleção Herpetológica da Universidade de Brasília; Museum of Comparative Zoology, Marine Science Institute, National Museum of Natural History, Conservation International, MVZ Herp Catalog, and Los Angeles County Museum of Natural History (accessed through GBIF Data Portal, www.gbif.net, 2009-05-30); Database of Administración de Parques Nacionales, Argentina (APN, 2008); published regional herpetological distribution dot maps (Cei, 1986, 1993)). All the distribution data were georeferenced to an 8×8 km resolution of UTM squares; environmental data for each presence record were extracted from the predictor variables described below.

Predictor variables

Predictors should be selected based on the bioecological processes thought to influence the biota (Austin, 2007). Due to their importance in the life history of Squamata species, we selected the following predictor variables: I). Vegetation biomass measured by the Normalized Difference Vegetation Index (NDVI), which is a derivate of the photosynthetically active biomass and represents greenness. At a regional scale NDVI has been used to characterize tropical forest types (Vadrevu et al., 2007), to differentiate between active vegetation and areas devoted to crops or uncovered soil (Dedios, 2006) and to evidence land cover changes (Paruelo et al., 2004; Cardozo and Chiaraviglio, 2008). II). Environmental temperature measured by the Land Surface Temperature (LST). The thermal environment is especially important for ectotherms in order to control their internal body temperature (Row and Blouin-Demers, 2006; Sabo, 2003). Both NDVI and LST were derived from the Advanced Very High Resolution Radiometer (AVHRR) on-board the National Oceanic and Atmospheric Administration's (NOAA) polarorbiting meteorological satellites. These data are monthly averaged products derived from satellite images from the period 1982 to 2000 with a pixel size of 8 km \times 8 km. III). Precipitation, which has been frequently addressed as responsible for the distribution patterns exhibited by many reptile species (Brito et al., 1999; Guisan and Hofer, 2003). Precipitation data corresponded to a 1960-1990 monthly total precipitation series with a pixel size of $1 \text{ km} \times 1 \text{ km}$ obtained from WorldClim (Hijmans et al., 2005). Differences in the temporal ranges between NDVI-LST and Precipitation are due to the different sources of datasets: NDVI and LST data are obtained from satellite data and are not available before 1982, whereas Precipitation data are obtained from interpolations from meteorological stations using the thin-plate smoothing spline algorithm implemented in ANUSPLIN (Hutchinson, 2004). Due to the low number of meteorological stations for South America we decided to



Figure 1. Maps of the study area indicating the presence records of *Tupinambis rufescens* (left) and *Tupinambis merianae* (right) in South America.

use a greater period for Precipitation data than for NDVI-LST data. IV). The topographic variable used was Altitude (ALT), which was also obtained from WorldClim (Hijmans et al., 2005) with a pixel size of 1 km \times 1 km. Such composites of NDVI, LST, precipitation and topographic data have been shown to be effective data inputs for large-scale predictions of reptile species distributions (Guisan and Hofer, 2003; Di Cola et al., 2008; Brito et al., 2011; Di Cola and Chiaraviglio, 2011).

Environmental data were georeferenced to a latitudelongitude coordinate system and were resampled to adjust the pixel size to 8 km \times 8 km. ENVI 4.1 software (System Research) was used in all data analyses. Resulting data layers had 714 \times 1063 pixels and covered the area of South America between 13° and 56°S and 33° and 82°W.

We used the summarized NDVI, LST and precipitation time series obtained from a Principal Components Analysis (PCA) performed by Di Cola et al. (2008) to determine the predominant patterns of variance in the environmental variables and to produce uncorrelated data sets (Eastman and Fulk, 1993; Jensen, 2005). We selected as predictor variables the first two principal components of each environmental variable because they accounted for most of the total variance of each series (supplementary table S1).

PCA is an attractive statistical tool to summarize information from time series images because it decomposes the series into a sequence of spatial and temporal components. Typically, the first component indicates the characteristic value of the variable, whereas subsequent components represent change elements of decreasing magnitude. In an image series, coarse spatial variation is typically explained by the first principal component. Finer-scale spatial patterns and temporal changes are captured by the second and higher order components. To characterize the temporal pattern of the second principal components, Di Cola et al. (2008) correlated them with the original environmental variables of the monthly average series. The period from October to March was considered the wet season, from April to September, the dry season. The second component of precipitation (PRE2) was negatively correlated with precipitation of the wet season months. The second components of NDVI and temperature (NDVI2 and TEMP2) were positively correlated with the corresponding environmental variables of the dry season months. Here we illustrated the relationships between the original variables of the monthly average series and the principal components through PCA biplots (fig. 2). The PCA was conducted using R Core Team (2013).

To generate the final environmental data set, we built a composite image with the first and second components of the PCA of each environmental factor plus a single altitude layer. All variables were standardized before analysis with the relativization by maximum method (Noy-Meir et al., 1975).

Predictive distribution models

To minimize statistical uncertainties associated with species distribution models we used two modelling techniques: logistic regression and MaxEnt (Guisan and Zimmermann, 2000; Pearce and Ferrier, 2000; Phillips et al., 2006; Phillips



Figure 2. Principal component Analysis (PCA) biplots showing the relationships between original environmental monthly variables and first and second components. NDVI: Normalized Vegetation Index. LST: Land surface temperature. PRE: Precipitation. PC1: first component of the PCA. PC2: second component of the PCA.

and Dudík, 2008). We used the same data sets (presence records and environmental predictors) in both methods. Logistic regression has been frequently used to analyze the effects of one or several independent variables over a dichotomous (presence/absence) variable along environmental gradients (Brito et al., 1999; Di Cola et al., 2008). Presence-absence data are likely to contain samples that span the environmental gradients of interest, yielding reliable model fitting (Wintle et al., 2005). These models perform very well; therefore, they are increasingly used when only presence data are available by creating artificial absence data (usually called pseudo-absences or background data) (Barbet-Masin et al., 2012). We selected random pseudo-absences from outside the buffer area of 8 km around the original presence point data. The distance buffer threshold selected exceeded the ecological range reported for Tupinambis: Cardozo et al. (2012) considered buffer areas of 2-km radius as zones potentially used by individuals which is, in turn, twice the area reported for other Tupinambis spp. (Mendoza and Noss, 2003; Winck, 2007). The number of pseudo-absence data was the same as the presence data. We ran 100 replicates of the logistic regression with a random seed variable as a function of the replicate number. At each run, we randomly set aside 20% of the training set for validation. The importance of the environmental variables to the presence of Tupinambis species was analyzed according to the magnitude of the coefficients of each independent variable. The logistic regression analysis was conducted using R Core Team (2013).

MaxEnt method, which is based on the maximumentropy approach to model species habitat, has been found to perform best among many modelling methods (Ortega-Huerta and Peterson, 2008). MaxEnt estimates the probability distribution for the occurrence of a species based on environmental constraints (Phillips et al., 2006). We used the freely available MaxEnt software, version 3.3.3k (http:// www.cs.princeton.edu/~schapire/maxent/). We randomly set aside 25% of the training set for validation. Other userspecified parameters were set to their default values: convergence threshold 10-5, maximum iterations 500, regularization multiplier 1 and maximum number of background points 10 000, replicated run type (subsample), output format (logistic), and "auto features" activated. We ran 100 replicates with a random seed.

We evaluated the predictive capacity of each model (Pearce and Ferrier, 2000; Luck, 2002). We plotted pairwise sensitivity values and their equivalent (1-specificity) in a ROC (Receiver Operator Characteristic) plot for each model to obtain the area under the ROC function (AUC) (Fielding and Bell, 1997), which was interpreted according to Lobo et al. (2008).

The probable area of occurrence of each *Tupinambis* species was obtained from both modelling techniques (logistic regression and MaxEnt). Since probability is continuous, we split the probable area of occurrence into suitable and unsuitable grid cells by setting a threshold; thus, dichotomous presence-absence maps for each species were generated. Thresholds can be chosen to optimize map accuracy, as judged by one of several criteria (Freeman and Moisen, 2008). In the logistic regression models we used

the cut-off point that produced the most correct classification rate of presences and absences. Similarly, in MaxEnt models we used the cut-off value of equal training sensitivity and specificity. Although other thresholds are commonly used (Phillips et al., 2006), we applied this conservative cutoff value because it performs better than other commonly used thresholds (Liu et al., 2005). The threshold used places equal weight on presences and absences, thus minimizing the difference between sensitivity and specificity (Negga, 2007; Lobo et al., 2008). To evaluate potential sympatry, presence-absence maps were overlapped to estimate the extent of contact zones between the species.

Results

The analyses performed allowed us to determine: general spatial and temporal habitat requirements of both *T. rufescens* and *T. merianae*; relative importance of habitat requirements for the presence of both species; differences in spatial and temporal habitat requirements between species; probable area of occurrence of each *Tupinambis* species and potential sympatric area, and accuracy of the models obtained.

The species distribution models obtained by both logistic regression and MaxEnt showed that spatial and temporal patterns of precipitation, vegetation and temperature, as well as altitude, explain the distribution of *T. rufescens* and *T. merianae* (table 1 and fig. 3). Considering the coefficients of logistic regression models and the response curves of MaxEnt models for the

Table 1. Variables included in the logistic regressionmodels and their coefficients for *Tupinambis rufescens*and *Tupinambis merianae*. Abbreviations: NDVI1, NDVI2,TEMP1, TEMP2, PRE1 and PRE2 indicate the first and sec-ond components obtained in the Principal Component Anal-yses of each environmental series.

Variable	Percentage of variance explained	T. rufescens model	T. merianae model
NDVI1	86.6	18.79	15.85
NDVI2	7.9	-4.95	-3.48
TEMP1	79.1	23.03	-18.74
TEMP2	17.6	-13.37	-14.05
PRE1	55.3	-420.73	-154.58
PRE2	31.5	-10.80	-11.55
ALT		-2.93	-12.06
Constant		366.69	168.01



Figure 3. Response curves for each environmental variable in MaxEnt models of (a) *Tupinambis rufescens* and (b) *Tupinambis merianae*. Percentages values in parentheses indicate the contribution of the variables to the model of each species.

spatial patterns of the environmental variables (first principal components), we characterized the zones of South America where *T. rufescens* and *T. merianae* would occur. Both species were positively associated with NDVI and thus, would be present in zones with abundant vegetation biomass; in turn, as both species were negatively associated with PRE1, they would occur in dry areas. In addition, species vary in their temperature requirements according to the logistic regression models. The response curves of MaxEnt models showed that both species were associated with high values of TEMP1, but *T. merianae* was also associated with low values of TEMP1.

Considering the temporal pattern of environmental variables (second principal components), we observed that both *T. rufescens* and

T. merianae were negatively associated with PRE2, according to the logistic regression models (table 1). In MaxEnt models the range of both species was located in low values of PRE2 axis (fig. 3). Therefore, considering that PRE2 is, in turn, negatively correlated with precipitation of the wet season (fig. 2 and table S1), the species would occupy areas of abundant precipitation from October to March. Moreover, T. rufescens and T. merianae were negatively related to NDVI2 and TEMP2, according to the logistic regression models (table 1). In Max-Ent models the species' range is located in low values of the axes of NDVI2 and TEMP2 (in comparison with NDVI1 and TEMP1) (fig. 3). Therefore, considering that NDVI2 and TEMP2 are positively correlated with the corresponding monthly variables of the dry season (fig. 2 and supplementary table S1), the species would occupy areas with scarce vegetation and low temperature from April to September.

The relative importance of the environmental variables in explaining the presence of *Tupinambis* species was analyzed according to the magnitude of their coefficients in the logistic regression models: *Tupinambis rufescens* and *T. merianae* were mainly dependent on PRE1, TEMP1 and NDVI1 (table 1). According to MaxEnt models, the variable that highly contributed to the presence of the species was TEMP2, followed by PRE1, PRE2 and TEMP1 (fig. 3). According to a Jackknife test, the environmental variables with highest gain when used in isolation were PRE1 for *T. rufescens* and TEMP2 for *T. merianae*.

The models also allowed us to determine differences in spatial patterns of habitat requirements between species. In the logistic regression models (table 1) we observed that species differed in the sign of coefficient for TEMP1; *T. rufescens* would be distributed in warmer areas than *T. merianae*. Although the sign of the coefficients of PRE1 and ALT did not differ between species, the magnitude of these coefficients indicates that *T. rufescens* would occupy drier and higher areas than those used by T. merianae. The response curves of MaxEnt models also showed differences in the spatial habitat requirements between species (fig. 3): considering TEMP1, both species were associated specifically with warm environments, but T. merianae would also occur in a greater variety of conditions, reaching colder environments. In addition, although both species occupied a similar range for PRE1, T. merianae would also occur in wetter areas than T. rufescens. Considering topography, species shared an intermediate range of ALT, but T. rufescens would reach high altitudes (presence data ranged from 100 to 1600 m a.s.l.), whereas T. merianae would occupy low altitude areas (presence data ranged from 0 to 1000 m a.s.l.) (fig. 3). In addition, MaxEnt models showed that although both species were similarly associated with NDVI1, T. rufescens would be also present in environments with intermediate or low vegetal biomass, whereas T. merianae would reach environments with high vegetation density (fig. 2).

We did not find differences in temporal patterns of habitat requirements between species. In the logistic regression models, neither the sign of coefficients for PRE2, TEMP2 and NDVI2 nor the correspondent confidence intervals differed between species. The response curves obtained in MaxEnt models also showed similarity for second principal components. Some differences can be indicated only for TEMP2: during the dry season *T. rufescens* would occur in a wider range of thermal environments (reaching colder environments) than *T. merianae* (fig. 3).

Model accuracy assessment indicated high modelling performance (AUC values: 0.91 for the *T. rufescens* model and of 0.88 for the *T. merianae* model in logistic regression, and 0.94 for the *T. rufescens* model and 0.92 for *T. merianae* model in MaxEnt). Habitat-suitability areas of both *Tupinambis* species were predicted by logistic regression and MaxEnt models (fig. 4). Logistic regression maps predicted a presence area that exceeded the known southern and western limits of the distribution of



Figure 4. Predictive distribution maps of *Tupinambis rufescens* (left) and *Tupinambis merianae* (right) in (A) MaxEnt models and (B) Logistic regression models. In MaxEnt models, the equal training sensitivity and specificity threshold rule was 0.26 for *T. rufescens* and 0.34 for *T. merianae*. In logistic regression models, the cut-off points that produced the most correct classification rate of presences and absences were 0.70 for *T. rufescens* and 0.77 for *T. merianae*.

T. merianae; and a larger presence area at the south and east limits of the distribution of *T. rufescens* than the maps generated by MaxEnt models. The overlap area corresponded to 72% and 82% of the distribution area of *T. merianae* and *T. rufescens*, respectively, in logistic regression models; and to 29.01% and 43.39% of the distribution area of *T. merianae* and *T. rufescens*, respectively, in MaxEnt models.

Discussion

The species distribution models obtained showed that temperature, precipitation, vegetal biomass and altitude shape the ecological niche of both *Tupinambis* species. However, the differences found in the distribution models between species support the hypothesis that although *T. merianae* and *T. rufescens* are phylogenetically, geographically and ecologically close species, their distribution patterns might be the result of habitat niche differentiation in some requirements, such as environmental temperature, precipitation and altitude. The results also provide evidence that although the ecological niches are different, these species might cooccur in a large contact zone. Therefore, the approach used here allowed us to understand the spatial strategies of *Tupinambis* lizards in the southernmost area of the genus distribution in South America.

According to the results obtained, three major issues merit analysis: importance of environmental factors as spatial and temporal constraints of the ecological niches of *T. rufescens* and *T. merianae*; contribution of environmen-



Figure 4. (Continued.)

tal factors to the differentiation of the species niches; probable area of occurrence of *Tupinambis* species and potential mechanisms involved in sympatric areas.

The main spatial patterns of environmental variables that constrain the probability of presence for T. rufescens and T. merianae are PRE1 and TEMP1, indicating that the spatial variation of precipitation and environmental temperature determines the distribution areas of these lizards in South America. Brandt and Navas (2011) stated that rain patterns may influence not only distribution but also lizard life history variation at regional scales; their data suggest that patterns of precipitation may exert an indirect effect on clutch size in Tropidurines, perhaps via effects on primary production. According to TEMP1 in MaxEnt models, Tupinambis rufescens and T. merianae were associated with warm areas. Minimum temperatures might have

a limiting role in their environmental niche as it does for other ectothermic species (Boretto and Ibargüengoytía, 2009; Anadón et al., 2012). Environmental temperature influences key processes in *Tupinambis* spp., such as basking in males before territorial demarcation for reproduction and basking in females; the latter determines the critical temperatures reached in nests because females transfer heat from basking to the eggs through body contact (Manes et al., 2003; Winck and Cechin, 2008). Mass and volume of *Tupinambis* spp. eggs would also be regulated by environmental temperature (Yanosky and Mercolli, 1995; Andrews et al., 2000; Quintana, 2001).

The spatial pattern of vegetation biomass (NDVI1) had a low contribution to the species niches according to MaxEnt models; however, both species were positively related to vegetation biomass (table 1 and fig. 3). Distribution of Squamata fauna in South America is generally closely related to vegetation features (Nogueira et al., 2009) because vegetation might regulate ecological processes (Cardozo et al., 2007; Cardozo and Chiaraviglio, 2011). For instance, Cardozo et al. (2007) demonstrated that dispersal of ectotherms is influenced by vegetation loss, and Cardozo and Chiaraviglio (2008 and 2011) showed phenotypic plasticity in lifehistory traits in relation to landscape vegetation changes. Indeed, although the potential distribution areas can be climatically favourable, vegetation cover would be a limiting factor for species presence (Opdam and Wascher, 2004; Chiarello et al., 2010; Fouquet et al., 2010). Accordingly, at a landscape scale, Cardozo et al. (2012) observed that although T. rufescens and T. merianae differed in vegetation habitat requirements in allopatry, both species selected areas with a great proportion of forest and shrublands.

Moreover, according to the contribution of the variables in MaxEnt models, the ecological niches of both Tupinambis species were strongly constrained by seasonal patterns of climatic variables (TEMP2 and PRE2). Considering the logistic regression models, the presences of T. rufescens and T. merianae were negatively related to these variables. Hence, taking into account the relationship of TEMP2 and PRE2 with the original climatic variables (fig. 2 and table S1), the species would be associated with areas of low temperature in winter and high precipitation in summer. Accordingly, the environments that these lizards inhabit, like the South American Gran Chaco, are seasonal ecosystems: rainfall is below 1600 mm/year, with at least 5-6 months receiving less than 100 mm and with vegetation being mostly deciduous during the dry season (Pennington et al., 2000). Coincidently, annual activity patterns of both Tupinambis species present seasonal bioecological features, such as hibernation (Donadío and Gallardo, 1984; Milsom et al., 2008) and cyclic reproduction (Mercolli and Yanosky, 1990; Noriega et al., 1996). Indeed, S. Lanfri et al.

mating and egg laying in *T. rufescens* and *T. merianae* are restricted to the beginning of the wet season, when environmental temperature increases (Fitzgerald et al., 1993). Thus, yearlings find suitable thermal environments and vegetation cover during the summer (Deeming, 2004).

Although the ecological niches of T. rufescens and T. merianae share some features, we found marked differences in their habitat requirements. Environmental factors might have different effects on the differentiation of distributions of related species (Scali et al., 2011). In fact, we found that the spatial patterns of climatic variables (PRE1 and TEMP1) were the main factors that lead to niche differentiation between species. According to the models obtained T. rufescens would be present at drier and warmer sites than those occupied by T. merianae. These species-specific habitat requirements might be related to speciesspecific life history traits. For example, hydric conditions during incubation strongly influence the phenotypic traits of neonates in Squamata (Brown and Shine, 2005). Egg incubation of T. merianae and T. rufescens occurs during the wet season and is dependent on seasonal precipitation (Quintana, 2000); however, humidity requirements for incubation would differ between species, since T. rufescens is associated with drier biogeographic regions than T. merianae (Andrade et al., 2004; Werneck and Colli, 2006). As for the temperature pattern, we observed yearlings of T. rufescens spending more time basking than those of T. merianae (Cardozo, unpublished data), which suggests that newborns of these species might also differ in thermal requirements. Therefore, the models obtained suggest that spatial patterns of precipitation and temperature are the main environmental factors determining interspecific differences in spatial distribution of the species at a regional scale.

In other model systems of squamate species, altitude was the variable that best separated species distributions (Scali et al., 2011). Ac-



Figure 5. Potential sympatric area according to MaxEnt models (left) and logistic regression models (right).

cordingly, considering the results obtained by both procedures, we also noted that altitude contributes to differentiation of the ecological niche of the species: T. merianae should occur in low altitude habitats, whereas T. rufescens should reach higher-altitude habitats. Tupinambis rufescens should occupy not only high but also warm areas, because decreasing temperatures might affect performance, such as timing of hatching, clutch size, body size, sexual maturity and fecundity (Luddecke, 1997). In oviparous lizards, the thermal quality of the environments suitable for thermoregulation could constrain distribution (Medina et al., 2009). Navas (2003) indicated that differences in ecophysiological plasticity influence the ability of different taxa to extend the altitudinal distribution. The possibility of differences in physiological plasticity, which could allow closely related Tupinambis species to exploit the altitudinal gradient differently, should be explored.

As Peterson and Holt (2003) stated, variations in species-environment relationships might be the result of niche evolution. They postulated that variations in species distribution models suggest the occurrence of variations in ecological niches of species. High model accuracy assessment obtained by AUC, which has been traditionally used to evaluate model performance but is here interpreted according to Lobo et al. (2008), would reinforce the hypothesis that the species of our model system present species-specific habitat requirements. The real value of AUC is that it provides a measure of the degree to which a species is restricted to a part of the range of environmental variables. A high AUC value indicates that the species has a restricted distribution across the range of predictor conditions. Therefore, although morphological similarity among species induces niche similarity (Pianka, 1986; Losos, 1990), the high model accuracy assessments obtained suggest

that species have specialized habitat requirements differing in several features of their ecological niches.

Finally, although the species distribution models obtained show that T. rufescens and T. merianae have differentiated their niches at a regional scale, the potential sympatry maps generated (fig. 5) indicate a large potential overlap in the distribution range of the species. Here, we noted that prediction maps for T. merianae and T. rufescens overfit the density area of presences, underestimating the presences farther north than 20°S latitude (fig. 1). Moreover, logistic regression maps overpredict the actual distribution of both Tupinambis mainly at the southern limit, possibly due to the number of pseudoabsences used (Barbet-Masin et al., 2012). Therefore, the resulting maps might be underestimating the northern distribution of both species and thus, the potential northern area of sympatry. Mechanisms underlying the occurrence of these sympatric areas are interesting future research lines. Accordinlgy, Cardozo et al. (2012) have recently shown that niche plasticity in Tupinambis could be operating at a landscape level, allowing the occurrence of overlap areas; for instance, T. rufescens strikingly modifies landscape habitat use between allopatric and sympatric areas. Peterson and Holt (2003), in the context of species distribution modelling, also suggest that geographical variations within a species may arise from phenotypic plasticity. In our study, assessment of the ecological niche contributed to our understanding of the spatial strategies of the species at a regional scale. However, future studies should consider niche plasticity at a regional level. The combination of information provided by satellite imagery and distribution models are a useful tool to explore modifications of the species niche in contact zones, which have long been recognized as natural laboratories of evolution.

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