Predicting spatial and temporal effects of climate change on the South American lizard genus *Teius* (Squamata: Teiidae)

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Abstract. The consequences of past or future climate change have been studied in many physical and biological systems, and their effects could change the ecology and spatial distribution of suitable areas for a wide variety of organisms. We analyzed the environmental and geographic space of the current suitable area projecting these conditions into Mid-Holocene and 2050 RCP8.5 scenarios to quantify whether climate change would affect the distribution and size of environmental and geographic space for lizard species of the genus *Teius*. The potentially suitable geographic area for the Mid-Holocene was found to be smaller than today for *T. oculatus* (-29.55%) and for *T. teyou* (-6.82%), but for *T. suquiensis* it was inferred as a larger suitable area ($+26\%$). For the future scenario all species showed a decrease in the potentially suitable area compared to the present (*T. oculatus* $= -9.30\%$, *T. teyou* $= -0.79\%$, *T. suquiensis* $= -37.58\%$). The PCA axes that in the environmental space showed a higher contribution for PC1-2 in Mid-Holocene and Present were mostly related to temperature and for PC3 with altitude variables, for the 2050 scenario were temperature for PC1, precipitation for PC2 and altitude-temperature for PC3. The current *Teius*' potentially suitable geographic space results versus the other temporal forecasts, showed specific differences in magnitude changes. This work illustrates how ectothermic organisms might have to face major changes in their environmental and geographic space as a consequence of the effect of climate changes.

Keywords: 2050 scenario, climate, Mid-Holocene, niche modeling, present, reptiles.

Introduction

The ecological niche concept has long been considered to be an important factor determining a species' distribution range and was defined as a set of environmental conditions that maintain each taxon within a certain geographic range, modulated by physiological restrictions under which they can prosper (Grinnell, 1917; James et al., 1984). Numerous works studied this concept in recent decades from the theoretical point of view (Soberón and Peterson, 2005; Peterson et al., 2011) and in general they agree that it includes certain components and they are commonly summarized in the BAM diagram. The BAM framework (Soberón and Peterson,

2005) for a species includes a region with a suitable set of abiotic factors (A) and this represents the geographic expression of the fundamental niche (FN), a region with appropriate biotic interactions (B), a region "accessible" to colonization (M) and a region equivalent to the distribution of the species (P) which is the intersection of the three identified regions (P = A ∩ B ∩ M). The niche concept is commonly separated into two major classes: Grinnellian and Eltonian niches. The Grinnellian niche (Grinnell, 1917; Austin, 2002; Soberón, 2007) is defined mainly by abiotic and non-interactive variables, while biotic interactions and resources define the Eltonian niche (Elton, 1927; Vandermeer, 1972; Leibold, 1995). Usually, these concepts and theoretical frameworks are not taken into account by researchers that model species' niches (Townsend Peterson and Soberón, 2012).

In the past decades, a large number of scientists estimated spatial distributions by calculating and quantifying "environmental" or "ecological" niches (Colwell and Rangel, 2009; Soberón and Nakamura, 2009), mostly through

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mechanistic and correlative models. The analysis of the niche through mechanistic models allows to evaluate a physiological limitation and to project it into the geographic space (Sinervo et al., 2010), while the correlative models perform correlations between several variables and the distribution of the studied organism (Owens et al., 2013). Both types of models have advantages and disadvantages, but correlative models can analyze habitat suitability considering several environmental variables together. Habitat suitability modeling can be subjected to spatial analysis such as area calculation (Di Marco et al., 2016), importance of variables in the geographic distribution (Marino et al., 2011) and interaction of the variables with each other (Hirzel and Le Lay, 2008).

The study of present habitat suitability is an effective method to infer the spatial interactions and shifts of organisms with past and future climate changes (Peterson et al., 2011). Niche modeling analysis is frequently used in research dealing with species distribution to assess geographic ranges within different evolution scenarios (Wiens and Graham, 2005; Warren, Glor and Turelli, 2008); as a tool for biodiversity conservation (Hortal et al., 2015; Jones et al., 2016; Tulloch et al., 2016), or to predict distributions under diverse climate scenarios events (Barrows, 2011; Anderson, 2013). Given the evidence of impact of climate change on biodiversity and on the fate of species' survivorship, there was an eruption of papers focused on this topic, and many scientists made simulation models and predictions based on the climate shift scenarios (e.g., Cane, 2005; Parker, 2010). Several resources, software and algorithms were produced in the last two decades to perform modeling and simulations (Thuiller et al., 2009; Di Cola et al., 2017) using climatic layers (e.g., Lima-Ribeiro et al., 2015) to assess the effect of climate change on species' distribution.

The abiotic factors can determine regional and local patterns by which communities of organisms are assembled, and the resulting degree of similarity or difference between localities with similar environments (Chase, 2003). Studies on changes of the potential suitable abiotic area for a species have been mostly focused on the geographic space and to a lesser extent in the environmental space (Soberón and Nakamura, 2009; Owens et al., 2013). Ectothermic organisms, and particularly reptiles are susceptible to climate changes (Sinervo et al., 2010; Böhm et al., 2016). Lizards are an optimal study object to test climate change effects, since this group of ectotherm organisms is highly susceptible to climate change (Kubisch et al., 2015) or habitat destruction, because of their reproductive strategies and low dispersal capacity (Zajitschek, Zajitschek and Clobert, 2012). Therefore, the analysis of displacement and contraction of the appropriate climatic-environmental areas for lizard species with little physiological adaptability is a major research goal (Huey et al., 2012; Ceia-Hasse et al., 2014).

In this study, we evaluated the potential effects of climate shifts projected for Mid-Holocene and 2050, in the lizard genus *Teius* using ecological niche modeling (ENM; *sensu* Townsend Peterson and Soberón, 2012), considering the two aspects of Hutchinson's duality: geographic and environmental spaces (*sensu*, Soberón and Nakamura, 2009). The geographic projection of present modeled distributions coupled with comparisons with ∼6000 years ago conditions versus a future medium-term model of 35 years, could provide solid evidence of the niche's shift magnitude in asymmetric time ranges modulated by climate change. The objectives of this study for these taxa were i) to analyze and quantify the current available area with habitat suitability models, and assess potential spatial changes projecting these conditions onto two temporal scenarios: Mid-Holocene (∼6000 years ago) and the 8.5 Representative Concentration Pathway greenhouse gas concentration (RCP8.5) for 2050; and ii) to

evaluate changes in the environmental space through *n*-dimensional hypervolume analysis for the three species, the overall genus, and the three scenarios.

Materials and methods

Studied species and localities data

The genus *Teius* includes three species that geographically range from 40° S in Argentina to Uruguay, Paraguay, and the southeastern region of Brazil and Bolivia at 16°40′S (Cacciali et al., 2016a,b). These species are relatively large and robust (∼144 mm snout-vent), diurnal, carnivorous and oviparous (Cei, 1993). Within this genus, *T. oculatus* and *T. teyou* present a wide distribution in different environments in Argentina, Uruguay, Paraguay and Brazil (Cacciali et al., 2016a). *Teius suquiensis* has a restricted distribution in central Argentina that partially overlaps with the other two taxa (Cabrera and Monguillot, 2007).

We used 1037 georeferenced presence records (*T. oculatus* = 581; *T. suquiensis* = 52; *T. teyou* = 404) from 675 localities. Collection acronyms (Supplementary table S1) used throughout the ms, voucher specimens and detailed localities are according to Cacciali et al. (2016a). Species sampling, observations and collecting events tend to be clustered around accessible areas and roads. This may over-estimate modeling results by including localities that are not spatially independent and do not present environmental variation between them (Dormann et al., 2012). For records with no exact or available geographic locations, we only incorporated them when it was possible to assign approximate coordinates according to the detailed descriptions of locations as they appear in the museums records and literature.

Climate and environmental data

We modeled habitat suitability for each species through a subset of variables selected from the 19 bio-climatic variables for current conditions (∼1950-2000) and included an altitude variable from the data base WorldClim 1.4 – Global Climate (http://www.worldclim.org). We projected current modeled conditions to BCC-CSM1-1 bioclimatic layers (PMIP2, 2009) for the Mid-Holocene scenario (∼6000 years ago) and ACCESS1-0 CMIP5 (2015) layers for modeling 2050 scenarios with RCP8.5 concentrations. The layers for these temporal scenarios were downscaled and calibrated (bias corrected) by their authors through a database using WorldClim 1.4 as baseline 'current' climate (World-Clim – Global Climate Data, 2015). All used layers had a resolution of 30 arc-seconds (∼1 km^2). The Intergovernmental Panel on Climate Change (IPCC) performs simulations of the climate system response to increasing levels of greenhouse gases based on different assumptions about the size of the projected population, technological developments and socio-economic trends. The RCP8.5 scenarios projected relatively large changes based on the most recent observations, which suggested that climate change would be more severe than expected (Meehl et al., 2007; Rahmstorf et al., 2007; Smith et al., 2009).

We estimated the accessible area (M; *sensu* Barve et al., 2011) considering ecological traits, environmental features and potential historical distribution to generate an extent for each taxon. We initially considered the ecoregions as M, but many presence records were located on the edge of these regions, hence we defined M as a minimum convex polygon with an additional spatial buffer of 200 km for each species (following the procedures of Barve et al., 2011; Cooper and Soberón, 2017). Then, we used these extent sizes to clip the environmental layers and generated 5000 random points for each species, and we extracted the pixel values for each bio-climatic variable from these points to use them to create a subset of variables. In order to obtain a representation of both types of climatic variables (Barbet-Massin and Jetz, 2014), we divided them into two groups: 1- precipitation and 2- temperature. We evaluated the number of variables to use implementing an initial Jackknife test (Pearson et al., 2006). Then, for each variable group we performed a Spearman correlation test (threshold selected >0.75) to avoid collinearity (Debandi et al., 2012; Dormann et al., 2013; Kershaw et al., 2013) and additionally a selection criterion with biological significance for the studied species (Rissler and Apodaca, 2007; Debandi et al., 2012; Cacciali et al., 2016a) related to the active months period. We performed all correlation analysis with Ggally 1.0.1 R package (Schloerke et al., 2016).

Ecological niche models (ENM)

We generated correlative models of ENM using MaxEnt (3.3.3k version; Phillips, Anderson and Schapire, 2006; Phillips and Dudík, 2008; Elith et al., 2011; Merow, Smith and Silander, 2013, 2016) algorithm, which seeks maximum entropy density through a robust estimation requiring only presence records and has been shown to produce reliable results even with a low number of localities (Pearson et al., 2007; van Proosdij et al., 2016). With this software, we calculated the relationship between the current known distribution of each species and environmental variables, and projected them into the past and future scenarios. We ran MaxEnt using the selected subset for each species of bio-climatic and altitude variables with the default configurations, except for: 10 replicates, 1000 Maximum iterations, "10 percentile training presence logistic threshold" as selected threshold for each average model.

We evaluated the ENMs performance with true skill statistic (TSS) for model's replicates (Allouche, Tsoar and Kadmon, 2006; Lobo, Jiménez-Valverde and Real, 2008) and Area Under the Receiver Operator Curve (further abbreviated to AUC; Phillips, Anderson and Schapire, 2006; Elith et al., 2011) for the averaged models. TSS takes into account both omission and commission errors and success as a result of random guessing, hence this evaluation model is not affected by prevalence and also is not affected by the size of the validation set (Allouche, Tsoar and Kadmon, 2006). The TSS values range from −1 to +1, where +1 indicates perfect agreement and values of zero or less indicate a performance no better than random (Allouche, Tsoar

and Kadmon, 2006). We considered these values as TSS model performance indicators: $< 0.05 - 0.05$ no agreement, $0.06 - 0.39 =$ poor, $0.40 - 0.55 =$ fair, $0.56 - 0.70 =$ good, $0.71 - 0.85 =$ very good, $0.86 - 0.99 =$ excellent, $0.99 - 1 =$ perfect (following Monserud and Leemans, 1992). The AUC is a measure of rank-correlation and high AUC values indicates that sites with high predicted suitability values tend to be areas of known presence and locations, whereas a model with lower prediction values tend to be areas where the species is not known to be present (absent or a random point). A value of 0.5 for AUC means that the model is as good as a random guess. We considered AUC range values to interpret model performance *sensu* Araújo et al. (2005): excellent $\geqslant 0.90$; good $\geqslant 0.80$; fair $\geqslant 0.70$; poor $\geqslant 0.60$; fail $\leqslant 0.50$. Finally, we created binary maps based on the selected threshold on the current average models and projected them to onto the Mid-Holocene and 2050 RCP8.5 scenarios.

Geographic space, spatial analyses and potential effects on adequate areas

We used the suitable habitat from the average output models to quantify the area for each species and scenario. From these surfaces, we calculated impact metric to estimate specific distribution changes of predicted suitable areas and the exposure to climate change per species and for the overall genus. We analyzed the relative exposure to climate change (Recc) between the current surface models (Cm) versus past (Pm) and future models (Fm) as: $Recc = (Pm * 100 / Cm) - 100$ and $Recc = (Fm * 100 / Cm) - 100$ respectively. Thus, high negative relative exposure values indicate that a species decreases the suitable area in that scenario, whereas higher positive values indicate an increase of the suitable area. The estimation and comparison of areas to estimate changes in the different modeling scenarios is a widely implemented method in ENM (e.g., Nori et al., 2013; Nori, Carrasco and Leynaud, 2014; Bonino et al., 2015; Rubio-Salcedo et al., 2016). This might be interpreted as a rigid and conservative estimate of changes from the predicted suitable areas, given that we did not consider areas of recolonization after a potential disappearance of suitable environment. Considering that there is almost no published literature on the spatial ecology of these species, our analyzes were based on the assumption that none of these lizards would be able to disperse to new potentially suitable areas within the time period of the model. These kind of assumptions are commonly associated with forecasting modeling niche techniques (Araújo and Pearson, 2005; Elith and Leathwick, 2009).

We performed all spatial analyses and maps with "raster 2.5-2" (Hijmans, 2017), "maptools 0.8-39" (Bivand and Lewin-Koh, 2018), "sp 1.2-2" (Pebesma and Bivand, 2005), "rgdal 1.1-7" (Bivand, Keitt and Rowlingson, 2018), "geosphere 1.5-1" (Hijmans, 2015), and "rgeos 0.3-17" (Bivand and Rundel, 2018) R packages.

Environmental space and n-dimensional hypervolumes

We evaluated changes in the environmental space for each of the species considering visualization results and metrics between the *n*-dimensional hypervolumes obtained from the geographic suitable outcome area for each of the model's scenarios. The environmental space state is a complex system that involves interactions for more than two variables and can be described as a *n*-dimensional cloud of points or a *n*-dimensional hypervolume (Soberón, Osorio-Olvera and Peterson, 2017). If these environmental space conditions are disturbed, this might lead to changes in the values of these variables and, as a result, to a different *n*-dimensional hypervolume; hence the comparison of two or more hypervolumes could provide an assessment of the magnitude of changes that the ecosystem suffered, such as shifts from the initial state (Blonder et al., 2014). In order to do this, we followed the "framework to study ecosystem stability in face of environmental changes using *n*-dimensional hypervolumes" (*sensu*, Barros et al., 2016). Within this framework, we calculated three metrics to made hypervolumes comparisons: 1 – the proportion of overlap between pre and post perturbation hypervolumes will reflect overall differences between the two corresponding states, 2 – the distance between the centroids of the pre and post perturbation hypervolumes will reflect how much mean values of the ecosystem components have departed from their pre perturbation levels (changes in mean values) and 3 – the contribution of the variables to each retained component.

To accomplish these analyses, we randomly sampled points ($=$ number of localities $* 10$) from each of the species' suitable area, and we used these random points to extract the information from the sum of the individual layers employed in MaxEnt for each taxon. Then, all this environmental information for each species was compiled and we performed a Principal Component Analysis (PCA) per scenario, to quantify the ecological multivariate space from the variables that determine the geographic models, and explore how these spaces interacted among the three taxa through time. To improve the visualization of the points, we incorporated gridded ellipses including 95% of the observations for each factor level. We used "The Scree Test" and "Proportion of Variance Accounted For" criteria and components that explain a minimum of $\sim 10\%$ of the variation (O'Rourke and Hatcher, 2013), to decide how many PCA axes we had to consider for this analysis. For these given dimensions, we evaluated the variables' contributions with the function "fviz_contrib". This function calculates any row/column with a contribution above the reference threshold, under which it could be considered as an important variable in contributing to the *n*-dimensions taken into account (Kassambara and Mundt, 2017). We compared the hypervolumes implementing the algorithm "hypervolume_distance" which calculates the Euclidean distance between two hypervolumes centroids (Blonder, 2015). This algorithm calculates the distance between two hypervolumes either defined as the Euclidean distance between centroids or as the minimum Euclidean distance between the random points comprising either hypervolume (*sensu* Blonder, 2015).

We performed all environmental space analyses with "FactoMineR 1.34" (Lê, Josse, and Husson, 2008), "factoextra 1.0.4.999" (Kassambara and Mundt, 2017), "hypervolume 1.4.1" (Blonder, 2015), "car 2.1-4" (Fox and Weisberg, 2011), "ade4 1.7-5" (Dray and Dufour, 2007), and "rgl 0.96.0" (Adler and Murdoch, 2017) R packages.

Results

ENM, spatial analyses and potential temporal shifts in suitable areas

Considering the bio-climatic correlation analysis outcome, we selected altitude and these environmental variables for each species: *Teius oculatus*: bio1 (annual mean temperature), bio3 (Isothermality = (bio2 / bio7 ∗ 100), bio5 (maximum temperature of warmest month), bio7 (temperature annual range = bio5–bio6), bio9 (mean temperature of driest quarter), bio17 (precipitation of driest quarter), bio18 (precipitation of warmest quarter); *T. suquiensis*: bio2 (mean diurnal range = (mean of monthly (maximum temp − minimum temp)), bio3, bio4 (temperature seasonality = (standard deviation ∗ 100)), bio5, bio6 (minimum temperature of coldest month), bio15 (precipitation of seasonality = (coefficient of variation)), bio18; *T. teyou*: bio2, bio3, bio4, bio5, bio15, bio17, bio18. The replicates performance through TSS indicated models fitted above "fair" or "good", with relatively high values for most of the replicates in the three species (supplementary material fig. S1). The average test AUC for replicate runs for *Teius oculatus* was 0.763 (±0.028 SD), 0.922 (±0.043 SD) for *T. suquiensis*, and 0.797 (±0.028 SD) for *T. teyou*.

The suitable climate area in Present scenario was 748,911.98 km^2 for *Teius oculatus*, 104,209.16 km^2 for *T. suquiensis* and 926,690.31 km^2 for *T. teyou* (fig. 1). The Recc for *T. oculatus* Mid-Holocene scenario suitable area showed a reduction of 29.55% and 9.30% for 2050 RCP8.5 (fig. 1); but *T. teyou* Recc presented a moderate decrease in both past and future scenarios with a reduction of 6.82% and 0.79% respectively (table 1, fig. 1). The Mid-Holocene models Recc for *T. suquiensis* indicated a 26% higher suitable area than the Present scenario and a reduction of 37.58% for 2050 RCP8.5 (table 1, fig. 1). All species did not show future considerable differences in changes of latitude or longitude (fig. 1). The relative ex-posure to climate change (Recc) for different scenarios and suitable area shifts for *Teius* are detailed in table 1.

Environmental space

We observed changes in the environmental space for all the studied species. Principal component analysis indicated that most of the hypervolume variation could be explained by the first three components for the 3 studied scenarios. The first three axes accounted for all scenarios a variance over 86% of the variation for each temporal scenario (table 2). The variables that most contributed in Mid-Holocene and Present were BIO6, BIO7 and BIO 4 for PC1; BIO17, BIO1, BIO15 and BIO5 for PC2; and BIO3, BIO5, and altitude for PC3. For the 2050 scenario the variables with higher contribution for PC1 were BIO7, BIO9, BIO4, BIO6; for PC2 BIO, BIO17, BIO15; and altitude, BIO5 for PC3 (fig. 2). The hypervolume distances from the Present scenario to the Mid-Holocene were 67.80 for *T. oculatus*, 95.67 for *T. teyou*, and 275.57 for *T. suquiensis*. The hypervolume distances from the Present scenario to the 2050 were 309.10 for *T. oculatus*, 442.67 for *T. teyou*, and 248.07 for *T. suquiensis*. These changes in the ellipses for each of the analyzed angles (fig. 3) were moderate between the Mid-Holocene and the Present scenario. On the other hand, the ellipses of the Present and 2050 scenarios showed considerable changes between them, especially for *T. teyou* and *T. suquiensis* (fig. 3).

Discussion

We found strong support for Grinnellian niche shifts in the past and future scenarios for *Teius* species. The geographic space from an ENM does not exclusively rely on abiotic variables and, on the contrary there are several factors that determine it (Peterson et al., 2005; Soberón and Peterson, 2005). Despite this, the Grinnellian niche is a good approach to study the relationship between climatic changes
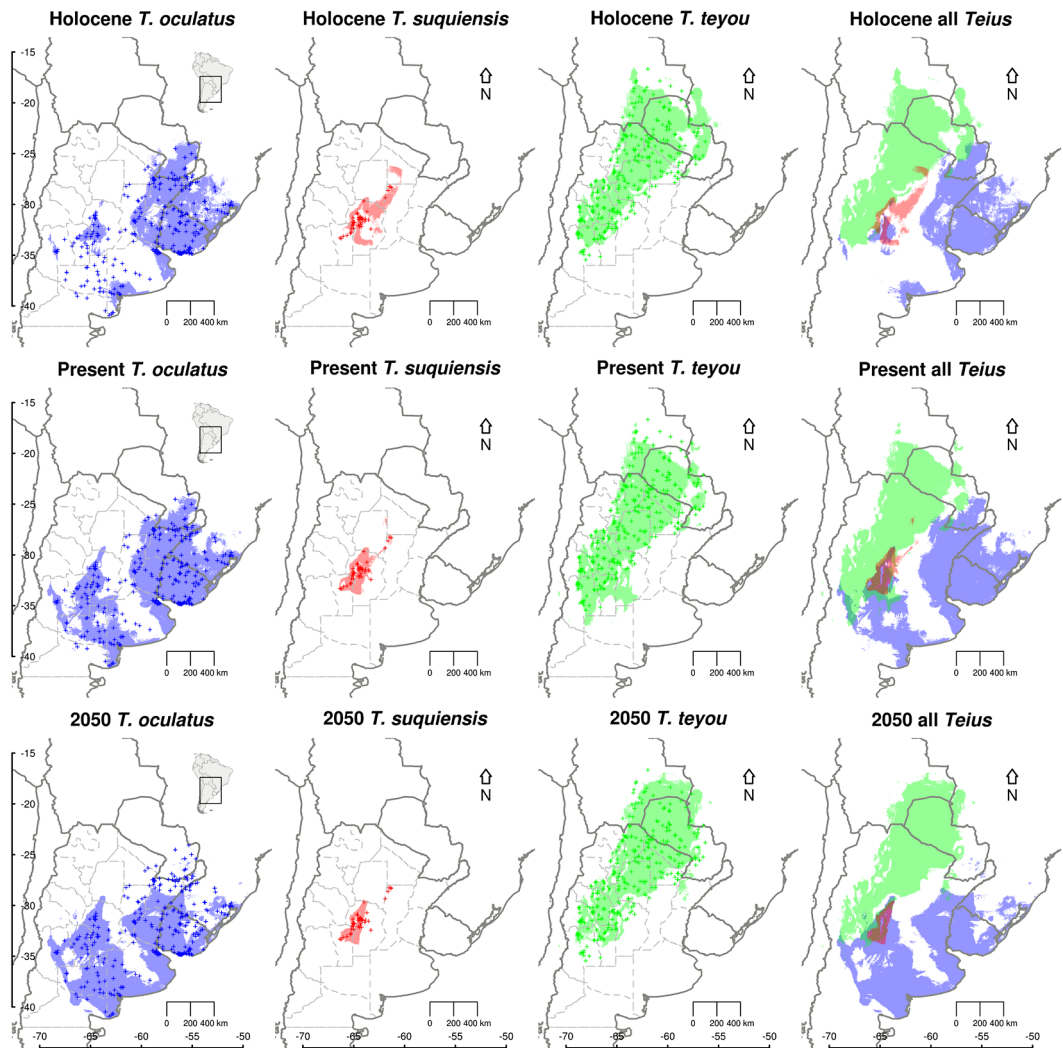
Figure 1. Area models for suitability habitat from the averaged replications output. *Teius oculatus* in blue, *T. suquiensis* in red, *T. teyou* in green and all the genus. Projection: WGS84, coordinate system: EPSG 4326. Crosses represent localities from each species.

Table 1. Spatial analysis performed on output models for each time scenario. References: % relative exposure to climate change (Recc) from present area.

Scenarios	Area (km²)							
	Teius	*%*	*T. oculatus*	*%*	*T. suquiensis*	*%*	*T. teyou*	*%*
Mid-Holocene	1,7174,23.23	−12.48	748,911.98	−29.55	104,209.16	26.00	926,690.31	−6.82
Present	1,962,427.11	–	1,063,106.79	–	82,708.09	–	994,568.05	–
2050	1,892,090.42	−3.58	964,195.47	−9.30	51,624.04	−37.58	986,697.77	−0.79
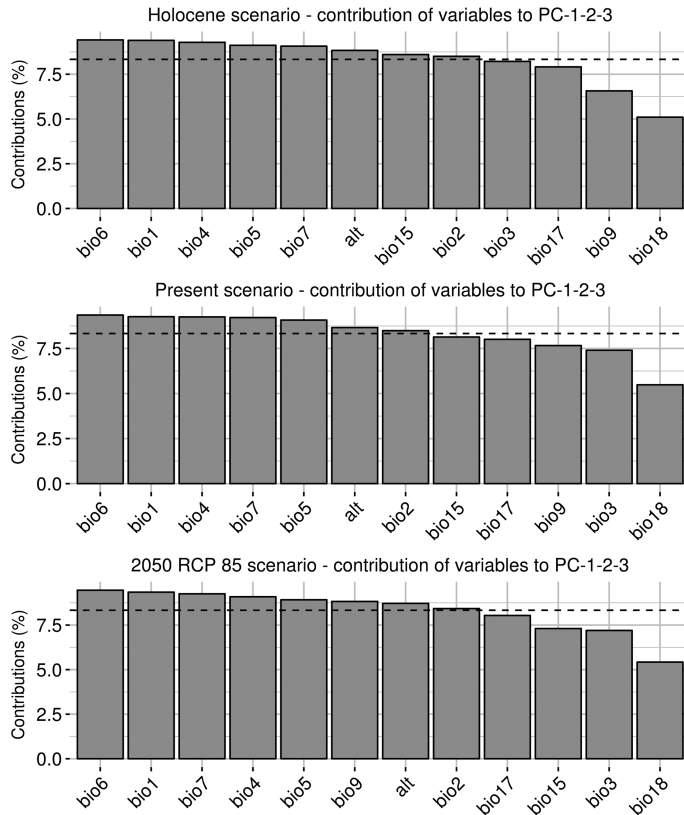
Figure 2. Barplot of variables contribution for the multivariate environmental space. Reference: dashed line corresponds to the expected value if the contribution where uniform between the considered dimensions.

Table 2. Principal Component Analysis of the environmental space for each temporal scenario.

Axis	Eigenvalue	Variance %	Cumulative Variance %
Holocene			
PC 1	5.62	46.80	46.80
PC 2	3.62	30.20	77.00
PC 3	1.11	9.21	86.21
Present			
PC 1	6.10	50.84	50.84
PC 2	3.16	26.34	77.18
PC 3	1.24	10.36	87.55
Future			
PC 1	6.13	51.07	51.07
PC 2	3.19	26.59	77.66
PC 3	1.15	9.56	87.23

and areas suitable for the species' presence without introducing biases of non-climatic aspects (Larson, Olden and Usio, 2010; Chalghaf et al., 2016). Our results, in congruence with other published works related to climate change in lizards (Ballesteros-Barrera, Martínez-Meyer and Gadsden, 2007; Kaliontzopoulou et al., 2008; Winck, Almeida-Santos and Rocha, 2014) and amphibians (Lemes, Melo and Loyola, 2014; Zank et al., 2014; Vasconcelos and Do Nascimento, 2016), showed a general tendency toward smaller potentially adequate habitat in the past scenario (Fontanella et al., 2012; Sillero and Carretero, 2013; Breitman et al., 2015) and also a reduction in a span of decades to the future (Araújo, Thuiller and Pearson, 2006; Bonino et al., 2015; Minoli and Avila, 2017).

Although the studied genus inhabits environments from a wide geographic space, our findings supported the hypothesis that the suitable area changes as the result of exposure to climate change (Vera-Escalona et al., 2012; Minoli
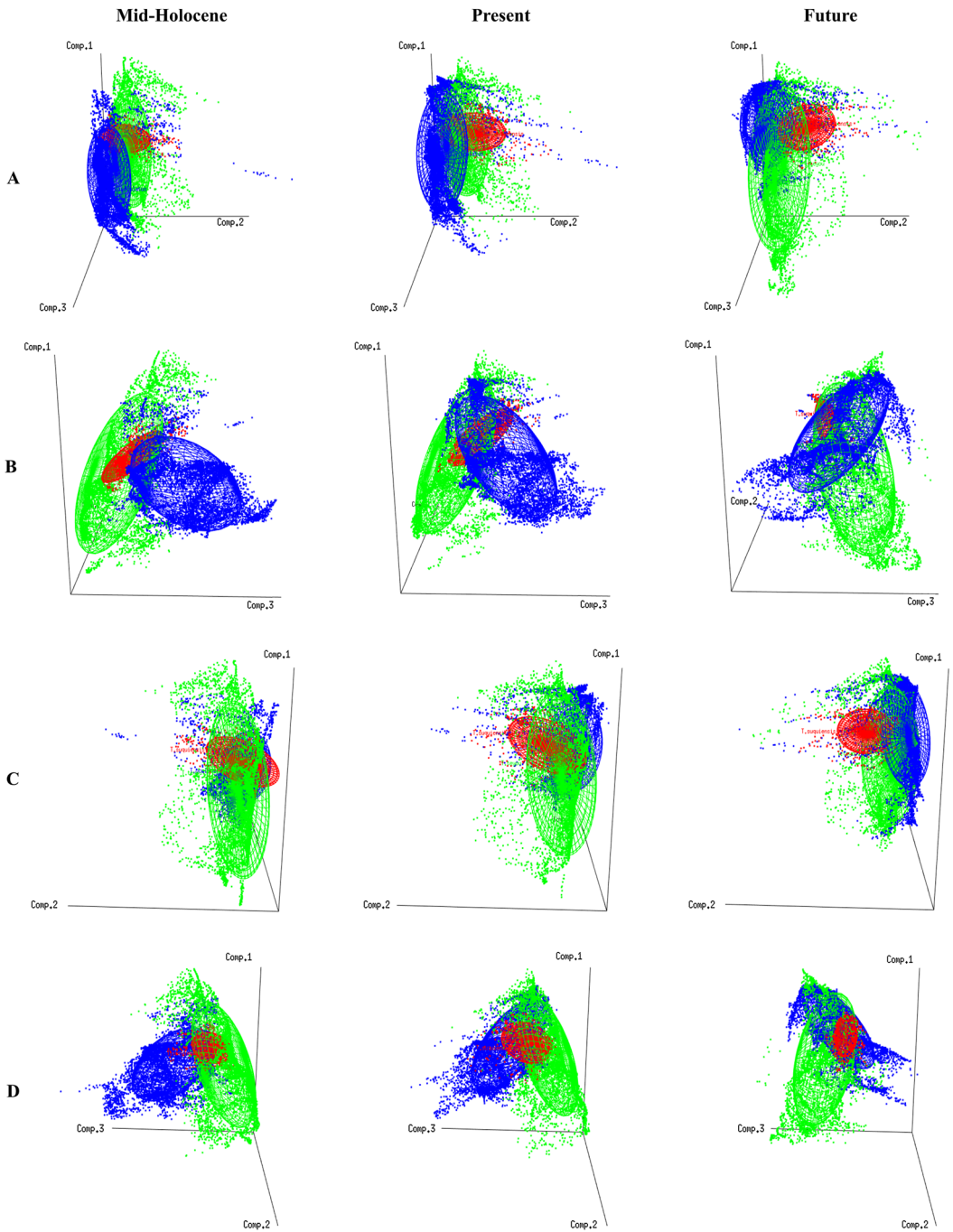
Figure 3. Changes of the environmental space in a multivariate context from the *Teius* studied scenarios. References: (A) environmental space in a 0° degree view; (B) environmental space in a 37° degree view; (C) environmental space in a 74° degree view; (D) environmental space in a 111° degree view. Colors: blue: *T. oculatus*; green: *T. teyou* and red: *T. suquiensis*.

and Avila, 2017). Comparing the spatial forecasts among the studied species, *T. teyou* and *T. oculatus* showed less reduction of their potential future area than *T. suquiensis*, which presented high Recc values resulting in a major reduction of the potential future area. In addition, these findings support the theoretical framework that states that each species has its own niche area (Medina, Ponssa and Aráoz, 2016) and magnitude of response to potential changes in their Grinnellian niche (Colwell and Rangel, 2009; Soberón and Nakamura, 2009). Although the differences between results may be due to possible sampling bias (Syfert, Smith and Coomes, 2013), we tried to diminish this geographic bias by using different information sources to include all the available locations for the genus.

Spatial barriers in reptiles (Sahlean et al., 2014) and potential changes in the distribution of suitable areas and their inter-species overlaps (Barbosa et al., 2012), have been extensively documented and related to hypotheses about hybridization events as a consequence of this phenomenon (Ahmadzadeh et al., 2013; Engler et al., 2013). The most important finding in the geographic context, was the change in the potential suitable habitat for *T. suquiensis*, which currently has a broader distribution range that the one projected in the future, and smaller than the past. This parthenogenetic species showed significant changes in both geographically and ecological space with a noticeable tendency towards the reduction of adequate area through temporal scenarios (fig. 1, supplementary material figs. S2, S3 and S4). Our results support that this species showed the greatest decrease of potentially suitable areas for the future, and even the suitable northern area for the present model would disappear in the future scenario.

The unisexual species could have a hybrid and recent origin, perhaps within ten thousands of years (Moritz et al., 1992). The majority of unisexual taxa are expected to have shorter persistence than sexual ones, and they usually colonize and occupy ecotone habitats

faster than their sexually reproducing relatives (Pough et al., 2015). Considering that multiple factors (e.g., anthropic changes, such as oil extraction, cultivated soils, dams, desertification) could play a decisive role increasing the effects of potential contractions of the species' suitable areas (Bastos, Araújo and Silva, 2005; Nori et al., 2013), new field surveys are needed in this species' geographic range, which is inferred as lost in the 2050 scenarios.

The limited knowledge on the *Teius*' species dispersion or fossil records combined with the great fragmentation and degradation of their environments (Pelegrin et al., 2009, 2013; Pelegrin and Bucher, 2012), lead us to think that some of the suitable climate spaces predicted in our results for temporal scenarios remain may not be occupied (Araújo and New, 2007; Colwell and Rangel, 2009). Despite this, past or future impacts of climate change remain uncertain due the effects of biotic and abiotic interactions, and uncertain dispersal events (Townsend Peterson, Papeş and Soberón, 2016), the robustness of the models presented here were supported by the definition of the segment (i.e., Grinnellian) of the studied niche (Soberón, Osorio-Olvera and Peterson, 2017). The use of open algorithms should contribute to future improvements in their calculations (Phillips et al., 2017). ENM generation can undergo future changes or improvements in several ways, such as description of new species (Romero et al., 2014), evaluation of hybrid zones (Engler et al., 2013), new data with absences (Brotons et al., 2004) and/or new biotic information (Tanner et al., 2017). The limitations of not using biotic and dispersion variables in our models might be mitigated and still provide accurate forecasts of changes in suitable geographic and climate spaces, with more dense sampling of species presence, as well as better methods. Both will improve the certainty of model predictions of the segmented (Grinnellian) niche (Radosavljevic and Anderson, 2014).

In the last two decades several authors have done review works of ENM concepts (Soberón

and Nakamura, 2009; McInerny and Etienne, 2012a,b,c; Rangel and Loyola, 2012; Townsend Peterson and Soberón, 2012), listing advantages and disadvantages of correlative, mechanistic and process-oriented models (Rangel and Loyola, 2012). Moreover, some authors propose blurry boundaries among these approaches (Dormann et al., 2012), and consider that these three approaches overlap and interconnect (e.g., correlational niche estimates being used in process-oriented approaches). The main advantage of using correlative models that we implemented here, is that they analyze a wider range of dimensions that define the niche of the study object (not just one variable; as usual in mechanistic models), but the biggest disadvantage is that they are not able to evaluate physiological thresholds as mechanistic models (Townsend Peterson, Papeş and Soberón, 2016). Until present, there have been numerous publications that use ENM as a tool to predict temporal changes in the distribution of suitable environments in the geographic space and projected them onto other scenarios (Schwartz, 2012; Lemes, Melo and Loyola, 2014; Ruete and Leynaud, 2015; Allen and Lendemer, 2016; Jones et al., 2016). However, the future challenge in these studies should be to perform methods or analyses with very detailed explanations in order to be repeatable in both geographical and ecological space to also obtain quantified results on how and how much the climate change affects species' distribution.

The information provided in this work highlights the importance of potential distribution in the geographic and ecological space as tools to better understand the processes linked to recent species contractions and expansions at the regional and local context. The information provided here also allows adding testable data for the use of some species as proxies for climatic changes in the past and in the future. Moreover, understanding the processes that are behind this kind of phenomenon in such a wide area of South America is essential to understand biota changes through time in this subcontinent.

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