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Potential effects of climate change on a Neotropical frog genus: changes in the spatial diversity patterns of *Leptodactylus* (Anura, Leptodactylidae) and implications for their conservation

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Abstract

Climate change and habitat loss are key threats to biodiversity, by acting as controlling factors of species' distributions. In this study, we combined ecological niche modeling with an innovative range-diversity analysis, which simultaneously addresses geographical ranges and species richness, to describe current biodiversity distribution patterns of *Leptodactylus* frogs, and to evaluate their expected changes under climate change scenarios. The genus *Leptodactylus* is distributed across 13.4 million km^2 from Mexico to central Argentina, with overall good-quality presence records and a robust phylogeny. The highest species richness occurred in the Amazonian Forests of Bolivia and Peru, while the lowest species richness was observed in the latitudinal limits of the genus distribution. The range sizes of individual species exhibited a unimodal frequency pattern, with many small ranges and few large ranges. The dispersion field allowed us to identify the Caatinga as a "coldspot," i.e., a site with few species of restricted range size, and the moist forest from Bolivia as a site with many species of medium-size ranges. Under climate change, we expect to observe a general decrease and a geographic displacement of the specific range sizes, but no species extinctions. These patterns imply a decrease in local species richness, which contrasts with a regional increase of biotic heterogeneity.

Keywords Amphibia · Diversity · Ecological niche · Range-diversity plots · Range shift · Species co-occurrence

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1 Introduction

Anthropogenic climate warming is probably the greatest threat in many regions of the world, and significantly increases species extinction risk (Thomas et al. 2004). The expected patterns of climate change vary around the world (Garcia et al. 2014). Instrumental records show temperature rises in Central America, Amazonia, and southern South America during the first decade of the twenty-first century (Harris et al. 2014). Such temperature increase is expected to continue during the twenty-first century in Central and South America; rainfall is also expected to increase in Colombia, Ecuador, Peru, and south-eastern South America, but it is expected to decrease in most of Central America, the Caribbean coast, northern Brazil, Chile, and Patagonia (Christensen et al. 2007).

In a changing climate, species populations are expected to persist where environmental conditions remain adequate (Whittaker 1975). Regional climate change is expected to modify the size and position of species geographic distributions (e.g., Garcia et al. 2014). Since climate change produces species-specific responses (Peterson et al. 2002), the co-occurrence patterns are also likely to be modified, resulting in a reorganization of assemblages (Walther 2010), possibly with associated changes in beta diversity (Whittaker 1972). In the Neotropics, there is a lack of studies linking climate change and spatiotemporal biodiversity patterns, which could derive in ineffective conservation strategies (Brook et al. 2008).

Species range sizes and species richness have traditionally been studied separately (e.g., Farji Brener and Ruggiero 1994; Eeley and Foley 1999). The concept of dispersion field (R) is an attempt to bridge both metrics (Graves and Rahbek 2005). As R is defined as the set of geographic ranges of species occurring in a given site, it is an indicator of the singularity or redundancy of a site to host species, for which it might be informative of the conservation value of a site compared to other sites. Conversely, diversity field (D) is an indicator of species diversity within the geographic range of a particular species (Arita et al. 2008), and it might be important for management when umbrella species are the focus of conservation efforts. Arita et al. (2008, 2012) extended and formalized the R and D concepts from presence-absence matrices (PAMs). Both measures are usually represented in range-diversity (R-D) plots, which are useful to identify sites and species with conservation value (Villalobos et al. 2013), and to predict community rearrangements as a consequence of climate change (Zwiener et al. 2017).

A combination of biodiversity measures with community phylogenetic structure is crucial to develop long-term conservation strategies (Cavender-Bares et al. 2009). The redundancy of genetic information of individual species is associated to phylogenetic distance to other species; thus, the genetic uniqueness of species is not homogeneous (Mouquet et al. 2012). Addressing the phylogenetic signal of the response to environmental changes would highlight certain phylogenetic groups of species that would be especially vulnerable to anthropic pressures and the importance to conserve not only species but genetic diversity (Purvis 2008). However, assessments of the effects of climate change from a phylogenetic perspective are scarce (Peterson et al. 2002; Garcia et al. 2014). In that sense, orienting conservation efforts to groups that are sensitive to climatic change, such as amphibians, becomes a priority.

Amphibians were the first vertebrates to make the transition from aquatic to terrestrial environment, about 360 million years ago (Ridley 2004). They are ectothermic and their development is associated with water availability, which makes them vulnerable to environmental changes (Feder and Burggren 1992). In recent decades, amphibian population declines and extinctions have been reported (see Houlahan et al. 2000; Stuart et al. 2004; Alroy 2015). In a context of rapid climate and land-use changes, amphibians are a conservation priority due to both their strong vulnerability to environmental alterations, and to their restricted mobility (Stuart et al. 2004). Predictions of the effects of climate change on amphibian assemblages are useful to infer threats to their conservation in the future.

The genus *Leptodactylus* Fitzinger 1826 (74 species) is a monophyletic group, endemic to the Neotropical region and the most diverse genus of the Leptodactylidae family (206 spp., Frost 2018). It is distributed in most of the lowlands of South and Central America; its phylogenetic relationships and species distributions are fairly well-known (de Sá et al. 2014). The group presents different reproductive modes, and inhabits different environments throughout the continent, including rainforests, dry forests, savannas, grasslands, and even agriculture and pasture lands (de Sá et al. 2014). Thus, *Leptodactylus* is a good example taxon for analyzing the responses of species distribution to climate change, considering phylogenetic relationships.

In this study, we analyzed the potential consequences of climate change on the diversity and co-occurrence patterns of *Leptodactylus*, using a range-diversity analysis by sites (Arita et al. 2008, 2012). We infer species individual responses to climate change as shifts on their range sizes and geographic position, and we evaluated how species changes impact on biodiversity patterns assessing beta diversity change (i.e., the biota could remain unchanged or become either more heterogeneous or homogeneous, Ochoa-Ochoa et al. 2012). Furthermore, we explore potential diversity changes within protected areas due to their role in conservation efforts. Since closely related species tend to be ecologically similar and react similarly to selection (Freckleton et al. 2002), we analyze the effect of climate change in a phylogenetic context.

2 Materials and methods

2.1 Study group

The species of the genus *Leptodactylus* are clustered in four groups: *L. fuscus*, *L. melanonotus*, *L. latrans*, and *L. pentadactylus* (de Sá et al. 2014). The genus is distributed from southern North America to southern South America and the West Indies (de Sá et al. 2014). In South America, *Leptodactylus* species occur mainly towards the east of the Andes, except for Colombia, Ecuador, and Peru, where they occupy both sides of the Andes. Most species occur below 1000 m a.s.l. and few are found above 2000 m a.s.l.

2.2 Presence records

We built a presence-point database for 74 *Leptodactylus* species. We compiled records from 12 herpetological collections, 125 scientific articles, and three online databases. We removed duplicate records and records with outdated taxonomic arrangements (following Frost 2018). To optimize model predictions, we excluded 14 species with less than eight presence records (*L. diedrus*, *L. fallax*, *L. hylodes*, *L. lauramiriamae*, *L. macrosternum*, *L. magistris*, *L. marambaiae*, *L. nesiotus*, *L. oreomantis*, *L. pascoensis*, *L. silvanimbus*, *L. tapiti*, *L. guianensis*, and *L. stenodema*), then, 17,477 records for 60 species were kept (S1). From these, 6992 unique records had useful geographic information and we georeferenced 40% of them because they lacked geographic coordinates. We estimated the uncertainty of the georeferenced points from the collection locality (Wieczorek et al. 2004), keeping only those records with an uncertainty below 5000 m to be consistent with the resolution of the environmental layers. To reduce spatial autocorrelation between presence points, and to avoid over-representation of certain environmental combinations (produced by sampling bias), we spatially filtered them based on a 10 km radius per species, which reduced redundant localities between 0 and 70%. The number of presence records per species used for niche modeling varied between eight and 772 (Table S2a, details of database treatment in S2).

2.3 Estimations of potential geographic distributions

We obtained estimations of the geographical distributions (EGDs) of 60 *Leptodactylus* species through correlative ecological niche modeling protocols (ENM). ENMs link species presence records with local environmental variables to estimate environmental suitability (Soberón and Peterson 2005). We used a simplified approach of the theoretical biotic-abiotic-mobility framework (Soberón and Peterson 2005), considering only abiotic and mobility factors because the biotic component (i.e., biotic interactions) is virtually impossible to spatially quantify thoroughly at regional scales (Peterson et al. 2011). To delineate abiotic components (A), we selected a group of climatic and a group of soil variables since they are associated to the natural history of anurans (Duellman and Trueb 1994; Schalk et al. 2015). Within each group of variables, we used Pearson correlations to detect clusters of correlated variables ($r \geq 0.8$); from each cluster, we kept the variable considered to be more informative to amphibian ecology (Medina et al. 2016). We did not evaluate the correlation between both groups because they are associated to different ecophysiological aspects of amphibians, so we let the modeling algorithm to identify which one was a better predictor without additional restrictions. We kept eight climate variables: annual mean temperature, mean diurnal range (mean of monthly (max temp - min temp)), temperature seasonality (standard deviation *100), max temperature of warmest month, minimum temperature of coldest month, annual precipitation, precipitation of wettest month, precipitation of driest month (Hijmans et al. 2005, through WorldClim); and six upper soil variables: pH index, bulk density, cation-exchange capacity, soil organic carbon, coarse fragments, sand content (Hengl et al. 2014, through ISRIC - WDC Soils). All variables were at a spatial resolution of 2.5′. To delineate the accessibility area (M), we a priori designed a calibration area for each species (Barve et al. 2011) (details of calibration area of ENMs in S2).

We calibrated the ENMs using a maximum entropy method with Maxent v3.3.3 K (Phillips et al. 2006) through the R package ENMGadgets (Barve and Barve 2016). We chose Maxent over other available methods for modeling due to its good performance for presence-only data (Elith et al. 2006; Peterson et al. 2011). To evaluate the models, we used the area under the curve (AUC) of the partial ROC (receiver operating characteristic), which allows the differential weighting of omission and commission errors, and more accurately assesses the quality of the model (Peterson et al. 2008). To obtain binary presence-absence maps, we used a 5th percentile based on the suitability values predicted on the presence records from Maxent as a threshold. This conservative method minimizes the commission error rate (see details in S2).

2.4 Projection on future climate scenarios

To assess the influence of climate change on the range-diversity patterns, we projected the ENMs in 13 global climate models (GCMs) from the IPCC Fifth Assessment Report (Table S2b). We selected two climate scenarios of representative concentration pathways (RCPs) of greenhouse gas concentration: 2.6 (low), and 8.5 (high), for the year 2050 (average 2041–2060), with the same environmental layers and spatial resolution. We acknowledge that some soil variables (e.g., pH and carbon content) are influenced by climate conditions, but there are no conclusive results at the temporal and spatial scales of our study (Singh et al. 2011) thus, current soil variables were kept for future projections. We projected the climate models from the calibration area (mobility component) of each species for an extent between Mexico and South America, and used them to make binary predictions of species distribution using the cut-off threshold described. Final EGDs by species resulted from the strict consensus map based on the multiplication of the 13 binary predictions. These consensuses were cropped to the calibration area of each species, thus avoiding the incorporation of potentially spurious areas produced by extrapolation during model transfer.

2.5 Presence-absence matrices

We summarized species distributions under current and future climate conditions in three presence (1) and absence (0) matrices (PAMs) from the binary EGDs maps of each species using the R package letsR (Vilela and Villalobos 2017) on an equal-area grid of 0.25° × 0.25°. All the PAMs had 60 species, but the number of sites varied due to range contractions or expansions in future climate scenarios: as a result, PAM had 21,508 sites for current climatic conditions, 21,258 sites for RCP 2.6, and 21,376 sites for RCP 8.5.

2.6 Current diversity patterns

We summarized *Leptodactylus* diversity patterns using range and diversity (R-D) plot by sites, following Arita et al. (2008, 2012). This analysis is based on the site species richness (number of species in each site, McIntosh 1967) and the species range sizes (number of sites occupied by each species) obtained from a PAM (Arita et al. 2012). The R-D plot by sites is a scatterplot depicting $\overline{S}^{*}$ vs R (Arita et al. 2012; Soberón and Ceballos 2011), with "$\overline{S}^{*}$" in the ordinate being the proportional species count (respect to the total species number) in each site, and with R, the "dispersion field", in the abscise, expressed as the proportional averages of the range sizes of the species occurring in the sites (proportional per-site range). We used site-based R-D plots to assess whether species-rich and species-poor regions are composed mainly by rare or common (i.e., geographically restricted vs. widely distributed) species. This was used to identify regions with potential importance for conservation. To describe the geographical distribution of these regions, we used the ecoregions sensu Olson et al. (2001) as a reference system.

The proportional fill of the PAM is estimated as the sum of occurrences in relation to the cells of the matrix, and its inverse is equivalent to the Whittaker's beta diversity index (Whittaker 1960). Consequently, beta diversity is a factor that relates (a) the total number of species with the average species richness by site (Whittaker 1960), and (b) the total number of sites with the average species range sizes (Routledge 1977; Arita et al. 2008). The overall dispersion of the points in the plot depends on the covariance among sites, which is determined by the number of sites sharing species with each individual site (Arita et al. 2008). We describe the 1/beta diversity and the covariance among sites as measures of the potential of species co-occurrence.

2.7 Potential effect of climate change on diversity patterns

To evaluate the effect of climate on *Leptodactylus* diversity, we obtained R-D plots by sites under future climate scenarios. To assess how changes in individual species distributions affect biodiversity patterns, we contrasted the lines of 1/beta diversity and maximum covariance between current and future climate as a summary of the expected trends of the assemblages (Arita et al. 2008). In addition, we evaluated the statistical significance of sites covariance of the R-D plot through randomizations of PAMs for the present and future climate scenarios (details of null models in S2).

At regional scales, we find three possible hypothesis regarding beta diversity: (a) a beta stable hypothesis, in which range sizes remain more or less the same; (b) an homogenization hypothesis, in which decreasing values of beta diversity can be due to an increase of the mean size of the distribution ranges, by extirpation of local populations, invasion of widespread non-native species, range expansion of native generalists, or a combination of these processes (Olden and Poff 2003); and (c) the heterogenization hypothesis, in which increasing values of beta diversity can occur by a decrease in the mean distribution range size due to the incursion of micro-endemic species, or through the net contraction of species ranges (Ochoa-Ochoa et al. 2012).

To visualize diversity patterns, we linked the scatter-plots with a map. In each site, we estimated the difference in $\overline{S}^*$ and R between future and current environmental conditions. We generated categorical maps showing no change, increase under future conditions, and decrease under future conditions. For R, we considered changes as either positive or negative when differences were at least half of the standard deviation of the R value of the current conditions. We performed the calculations and classifications with the "raster" package in R software (Hijmans 2015), and edited the maps in QGis v. 2.18.4 (QGIS Development Team 2017).

To assess the effect of climate change on species assemblages, we contrasted averages and standard deviations of species richness, range sizes, and covariance obtained from current and future projected R-D plot. We compared changes of these metrics between regions defined from the current R-D Plots, and inside protected areas (IUCN categories I–VI and National Parks not categorized, WDPA; downloaded August, 2017. Cambridge, UK: UNEP-WCMC and IUCN. Available at: www.protectedplanet.net).

2.8 Potential effect of climate change on range sizes and geographic shifts

To evaluate the effect of climate on each species, we calculated the range size variation (RSV) (Duan et al. 2016) between current and future conditions. We expressed RSV as a proportion of the current range size:

$$\mathrm{RSV} = \left(n_f - n_p\right)/n_p \times 100$$

Where n is the number of cells, and f and p are the future and present distributions, respectively.

Also, we evaluated the effect of climate on the position of the distributions by quantifying their geographic displacement, through the "O" overlap index (Kou et al. 2011) used for both climate scenarios as:

$$O = n_{\mathrm{f}\cap\mathrm{p}}/n_{\mathrm{f}\cup\mathrm{p}}$$

Where $_{\mathrm{f}}\cap_{\mathrm{p}}$ and $_{\mathrm{f}}\cup_{\mathrm{p}}$ represent the region intersected and combined (sum) between present and future distributions, respectively.

To assess whether the effect of climate change has an aggregate pattern on the phylogeny, we estimated the phylogenetic signal of the RSV and O index. We used the *Leptodactylus* phylogeny proposed by de Sá et al. (2014), with the inclusion of *L. spixi* (following the topology proposed by Pyron and Wiens 2011). Since branch lengths were not available for the species, we used (a) the Abouheif mean (Abouheif 1999; Pavoine et al. 2008), which does not require branch lengths, and (b) Pagel's (1999) λ (Blomberg et al. 2003), which assumes that all branch lengths are 1 (details about the phylogenetic tree and methods to measure phylogenetic signal can be found in S2).

3 Results

3.1 Current diversity pattern

The potential geographic distribution of *Leptodactylus* species spanned from the southern United States to central Argentina, covering an area of approximately 13.4 million km^2 (all the models were significantly different from the null models, Table S2a). The present species geographic ranges varied from 17 sites (cells of ca. 625 km^2) for *L. peritoaktites*, to 10,039 for *L. fuscus* (about 6.25 million km^2), with an average of 1935 sites (ca. 1.2 million km^2) (Fig. 1(a)). The frequency distribution of range sizes showed a unimodal pattern, highly skewed to the right (Fig. 1(b)). Half of the species range sizes (52%) was smaller than 1000

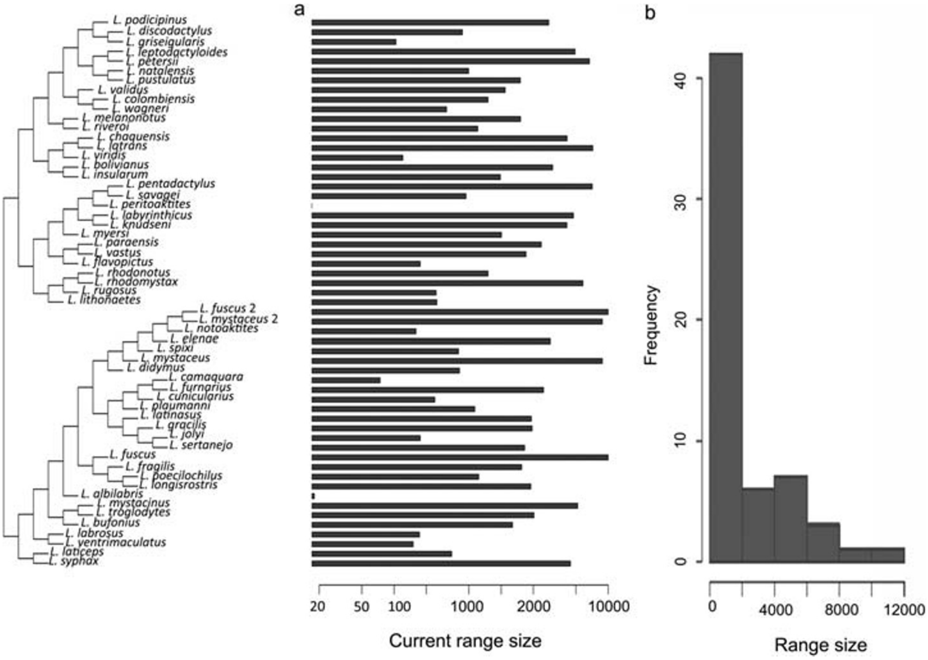

Fig. 1 Geographic range size of *Leptodactylus* species. (a) Range size under current climate conditions, expressed as number of sites where species are present. *L. rhodomerus* (71 sites), *L. caatingae* (788 sites), *L. turimiquensis* (25 sites), *L. cupreus* (68 sites), and *L. sabanensis* (83 sites) are not shown in the graph because they were not included in the phylogeny of de Sá et al. (2014). (b) Species range size frequency distribution (expressed as number of sites)

sites, 18% was between 1000 and 2000 sites, and 30% was above 2000 sites (i.e., more than 1.25 million km^2).

Sites with the highest richness were found in tropical and Subtropical Moist Broadleaf Forests (Bolivian Southwest Amazon Forest, Madeira-Tapajos Moist Forest, Alto Paraná Atlantic Forest, and Serra do Mar Coastal Forest); Tropical Savannas (Guyana region of the Guianan Highlands); Subtropical Dry Broadleaf Forests (Humid Chaco); and Tropical and Subtropical Savannas (Cerrado). Sites with the lowest richness occurred towards the latitudinal limits of the species distribution (Mexico, Central America, and Central Argentina) and in tropical lands (the Amazon basin and the Caatinga). Most of the sites harbored between one and eight species, with an average of five species per site. Sites with the highest richness harbored 15 species.

3.2 R-D plot per sites

Four types of sites that represent categories of interest for conservation were found (Fig. 2(a–e)): (A) regions with low R and $\overline{S}^*$ (blue sites); (B) regions with medium R and $\overline{S}^*$ (orange sites); (C) regions with medium R and high $\overline{S}^*$ (red sites); (D) regions with high R and low $\overline{S}^*$ (green sites) (see Fig. S4 for a simplified version of RD plots and interpretation of the regions identified within them according to the dispersion of points). Sites with the lowest co-occurrence (blue and green dots) harbored, on average, two species (average proportional richness = 0.03; Fig. 2(D)). Of these sites, those that harbored species with the smallest range size (blue dots) had an average range size of 1290 sites (average proportional range = 0.06; Fig. 2(c)). Sites harboring species with the largest ranges had an average range size of 7528 sites (green dots; average proportional range = 0.35; Fig. 2(c)). Sites with the highest co-occurrence harbored between eight and 11 species (orange dots, average proportional richness = 0.14; red dots, average proportional richness = 0.19; Fig. 2(D)). These regions housed species with average range sizes of 4947 sites (average proportional range size = 0.23; Fig. 2(C)).

Different types of sites were geographically clustered (Fig. 2(B)): sites A were found mainly in Central and South America, towards the West of the Andes, and in the Caatinga; sites D and B occurred mainly in the lowlands of South America, with sites D being concentrated at higher latitudes; and sites C occurred in Bolivia. Sites A had a negative covariation with the remaining sites (Fig. 2(E)), i.e., they shared few species (mean covariance of −0.001). On the other hand, sites B, C, and D showed a positive covariation, and regions C had the highest covariance (mean covariance of 0.027).

3.3 Potential effect of climate change on diversity patterns

The diversity patterns of *Leptodactylus* varied between current and future climatic scenarios. Future distributions projected a decrease in the maximum covariance, D, n, R, and $\overline{S}^*$, and an increase in the Whittaker's beta index from 11.11 today to 14.90 and 14.35 for RCP 2.6 and 8.5, respectively (Fig. 3, Table S3a). The general pattern of sites' covariance of the R-D plot was significantly different from the null model, which assumes that the covariance pattern can be explained solely by the number of sites and species occurrences and not by the particular spatial pattern of the projected species' distributions (details of null models in S2).

The proportional species richness ($\overline{S}^*$) and the dispersion field expressed as proportional per-site range (R) were projected to decrease in most sites (Fig. 4, S5). R decreased between

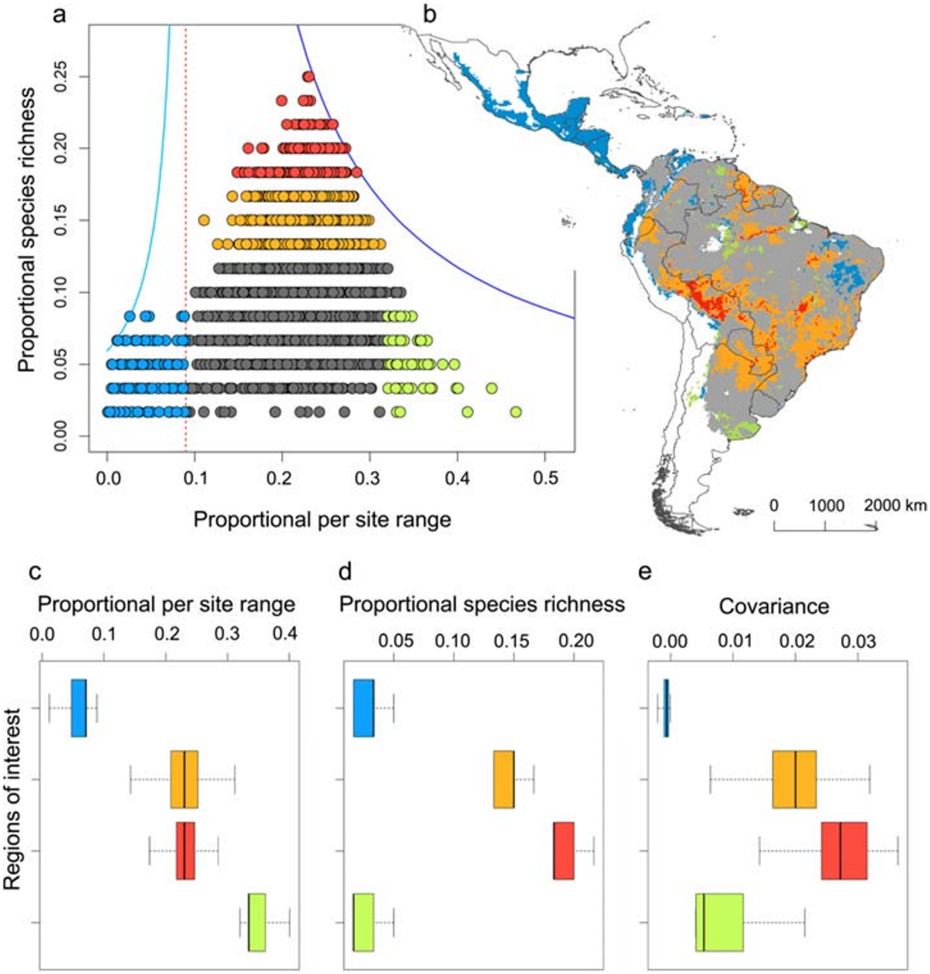

Fig. 2 *Leptodactylus* diversity patterns by regions of interest. Blue, orange, red, and green colors denote different regions of interest according to their proportional richness and proportional per site–range values (range sizes). Blue (sites A): low proportional per-site range, low proportional richness; orange (sites B): medium proportional per-site range, medium proportional richness; red (sites C): medium proportional per-site range, maximum proportional richness; green (sites D): large proportional per-site range, low proportional richness. (a) R-D plots by sites. (b) Proportional species richness maps. (c–d) Boxplot of regions of interest by proportional per-site range, proportional species richness, and covariance, respectively

0.026 (564 sites) and 0.38 (8136 sites), for the RCP 2.6 scenario, and between 0.026 (564 sites) and 0.43 (9104 sites), for the RCP 8.5 scenario. Since the estimated median range size of *Leptodactylus* was 1277 sites, decreases of R would vary up to 6 and 7 times for the RCP 2.6 and 8.5 scenarios, respectively, compared to the median range size. The decrease in $\overline{S}^*$ varied between 1 and 9 species for the RCP 2.6 scenario, and 1–11 species for the RCP 8.5 scenario. In southern Mexico and Central America, *Leptodactylus* diversity patterns did not change drastically. In South America, we projected a matrix of sites with declining richness and

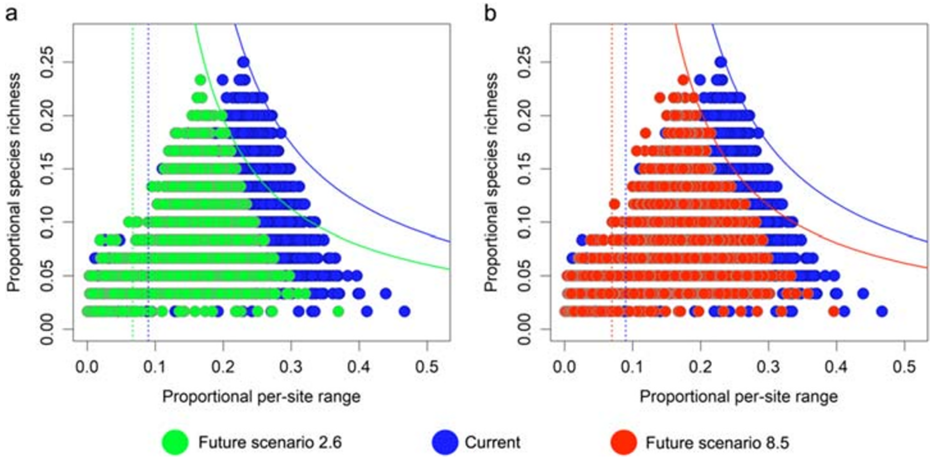

Fig. 3 Graphical comparison of the range-diversity patterns under current and future climate conditions through R-D plot by sites. The inverse of beta is represented by dotted lines, and the maximum covariance is represented by solid lines. (a) R-D plot by sites for current conditions and for RCP 2.6 future climate scenario. (b) R-D plot by sites for current conditions and for RCP 8.5 future climate scenario. Blue, green, and red colors represent current climate conditions, RCP 2.6 and RCP 8.5 future scenarios, respectively

species range sizes, surrounding patches with no change or with increases in such attributes. Sites with decreasing richness were more frequent in the RCP 8.5 scenario.

In some regions, $\overline{S}^*$ and R increased under both climate scenarios. In the case of $\overline{S}^*$, such increase varied between 1 and 4 species for the RCP 2.6 scenario, occurring in the transitional zones between the Cerrado and the Caatinga, in Mato Grosso Seasonal forests, in Maranhao Babacu moist forests, Tocantins Pindaré, Guianan Piedemont, and lowland forests, Purus-Madeira, Bolivian Yungas, grasslands of the Humid Pampas, and the Uruguayan savanna (Fig. S5 a–c). In the RCP 8.5 scenario, such increase varied between 1 and 6 species occurring in Japurá-Solimoes-Negro and Monte Alegre Varzeá, Colombian, and Venezuelan Llanos (Fig. 4(a–c)). The increase in R varied between 0.026 (564 sites) for both scenarios, 0.23 (5061 sites) for RCP 2.6, and 0.36 (7760 sites) for the RCP 8.5 scenario. Under the RCP 2.6 scenario, the increase corresponded to moist forests of Brazil, such as Maranhao Babaçu, Xingú-Tocantins-Araguaia, Juruá-Purus, and the Colombian and Venezuelan Llanos (Fig. S5 d–f). Under the RCP 8.5 scenario, the increase corresponded to the Argentine Dry Chaco and Humid Pampas, Bahia interior forests of the Atlantic forest, and central regions of the Cerrado (Fig. 4(d–f)).

Future climate conditions are projected to affect $\overline{S}^*$, R and average covariance in almost all the regions of interest (Fig. 5(a–c)). Sites B and C (red and orange; Fig. 2(a, b)) showed a decrease of $\overline{S}^*$, R, and average covariance. Sites A (blue; Fig. 2(a, b)), did not show changes in their diversity patterns under future scenarios. Sites D (green regions; Fig. 2(a, b)) showed a decrease on average R and average covariance, but did not show changes in $\overline{S}^*$. Sites within protected areas showed a similar trend to the regional pattern, with decreases on average $\overline{S}^*$, R and covariance (Fig. S6).

3.4 Potential effect of climate change on range sizes and geographic shifts

On average, range sizes are projected to decrease by 21% ($VRS_{8.5} = -20.63 \pm SD = 27.94$) and 26% ($VRS_{2.6} = -25.55 \pm SD\ 20.19$) under future climate scenarios

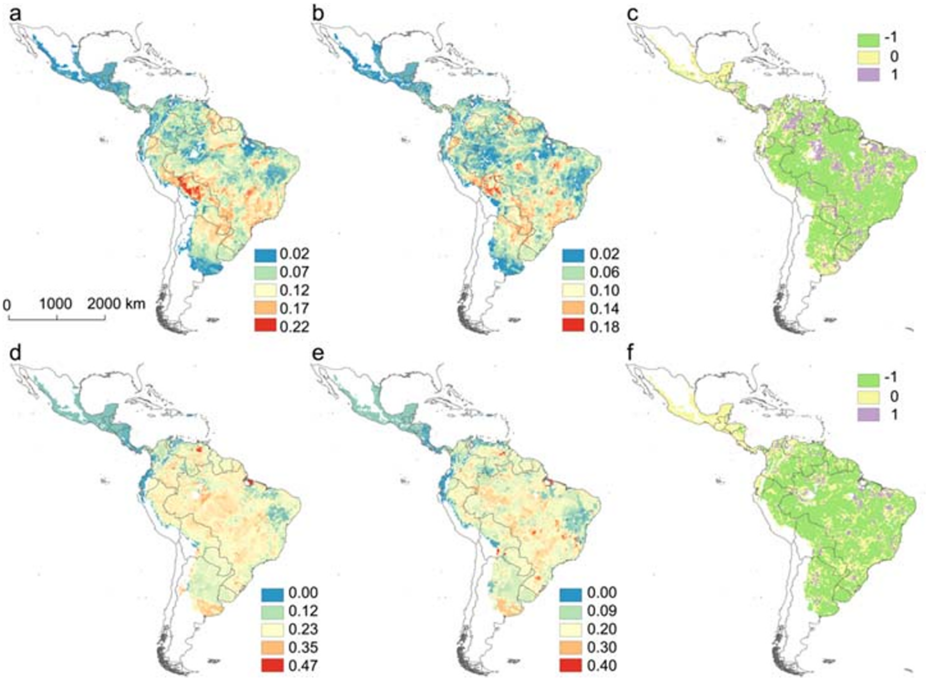

Fig. 4 Species richness and range size comparison between current and future climate conditions (RCP 8.5). (a) Proportional species richness under current climate conditions. (b) Proportional species richness under the RCP 8.5 future climate scenario. (c) Reclassification of proportional species richness by site based on species gain, loss, or absence of change, resulting from the difference between RCP 8.5 future climate scenario and current climate conditions. (d) Proportional per-site range under current climate conditions. (e) Proportional per-site range under the RCP 8.5 future climate scenario. (f) Reclassification of proportional per-site range by site based on range size gain, loss, or absence of change, resulting from the difference between current climate conditions and the RCP 8.5 future climate scenario. Green (− 1), yellow (0), and purple colors (1) show, loss, absence of change, and gain values, respectively

(Fig. 6(a–c)). The geographic shift of *Leptodactylus* distributions was approximately 34% in the low-emission scenario ($O_{2.6} = 0.66 \pm$ SD 0.11) and 43% in the high-emission scenario ($O_{8.5} = 0.57 \pm$ SD 0.14) (Fig. 6(c)). The overlap of species ranges under lower and higher emissions was not statistically significant (Fig. 6(d)). We did not find any phylogenetic signal of the effect of climate change in *Leptodactylus* (Table S3b).

4 Discussion

According to our results, the current distributional and diversity patterns of *Leptodactylus* would be prone to spatial reorganization as a consequence of climate change. *Leptodactylus*' potential distributions show geographic shifts, with decreasing local species richness and range size, but no species extinction. Regionally, a decrease in the range sizes and in the association among sites occurs, which would imply an increase of biotic heterogeneity in the Neotropical lowlands, even within protected areas.

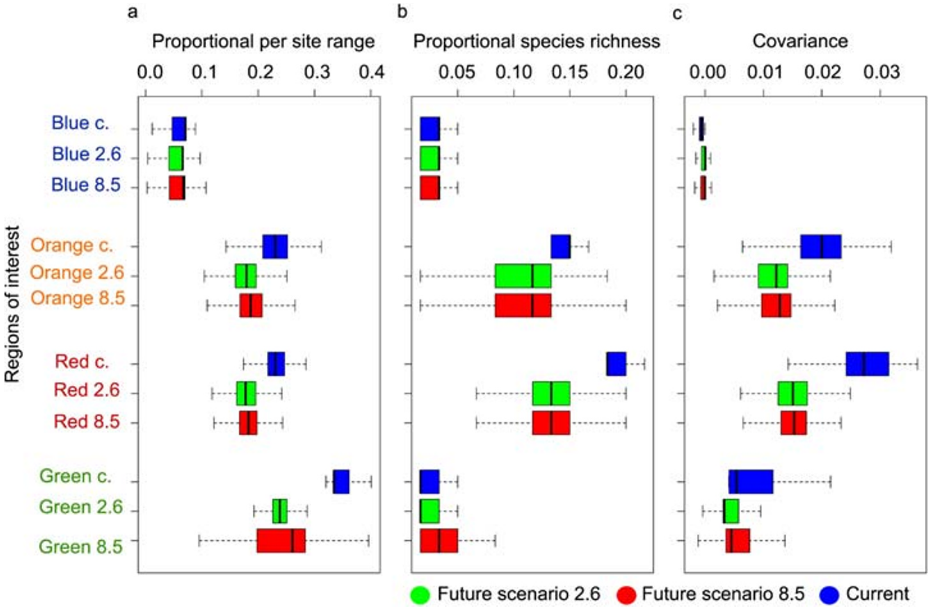

Fig. 5 Boxplot of diversity range parameters under current and future climate conditions, and by regions of interest. Regions of interest are shown in the left side of the plot. c, current climatic conditions; 2.6 = RCP 2.6 future climate scenario, 8.5 = RCP 8.5 future climate scenario. Blue, green, and red colors of the boxes represent current climate conditions, RCP 2.6, and RCP 8.5 future scenarios, respectively

4.1 Current diversity patterns

In *Leptodactylus*, the highest and lowest species richness occur in ecoregions of the Tropical and Subtropical Moist Broadleaf Forests biome. In the Guiana Shield, central Amazonia, and the Amazon delta, there are few presence records, which might reflect reduced species richness, or be a result of methodological issues, for example, areas with underrepresentation either in the selected collections or exhibiting collection gaps. Although the EGDs obtained from ENMs are robust to deal with biased collection efforts, they cannot deal with an absolute lack of records. The analyses of species future distribution are only slightly affected by these issues, since their results and implications should only be considered in comparative terms. Moreover, an analysis about genetic distances among anuran populations of Amazonia and Guiana suggested that many cryptic species may remain undescribed, and therefore, species richness could be underestimated in those regions (Fouquet et al. 2007). We acknowledge that ENM is sensitive to species miss-identification. Also, the use of a single taxon as indicator of total species richness is problematic, since there might be little congruence among distributions of different taxonomic assemblages (Bilton et al. 2006), due to species distributions being controlled by specific factors (e.g., physiological or historical), which might not reflect general patterns. In sum, different processes could be influencing the spatial diversity patterns of *Leptodactylus* genus.

Leptodactylus richness patterns are consistent with their evolutionary history (Heyer 1975; Fouquet et al. 2013). Heyer (1975) hypothesized that Leptodactylinae originated in the Amazonian and Southeast Brazil forests, spreading secondarily to South-American savannas, and subsequently to the West Indies, Central America, and Mexico. This hypothesis is

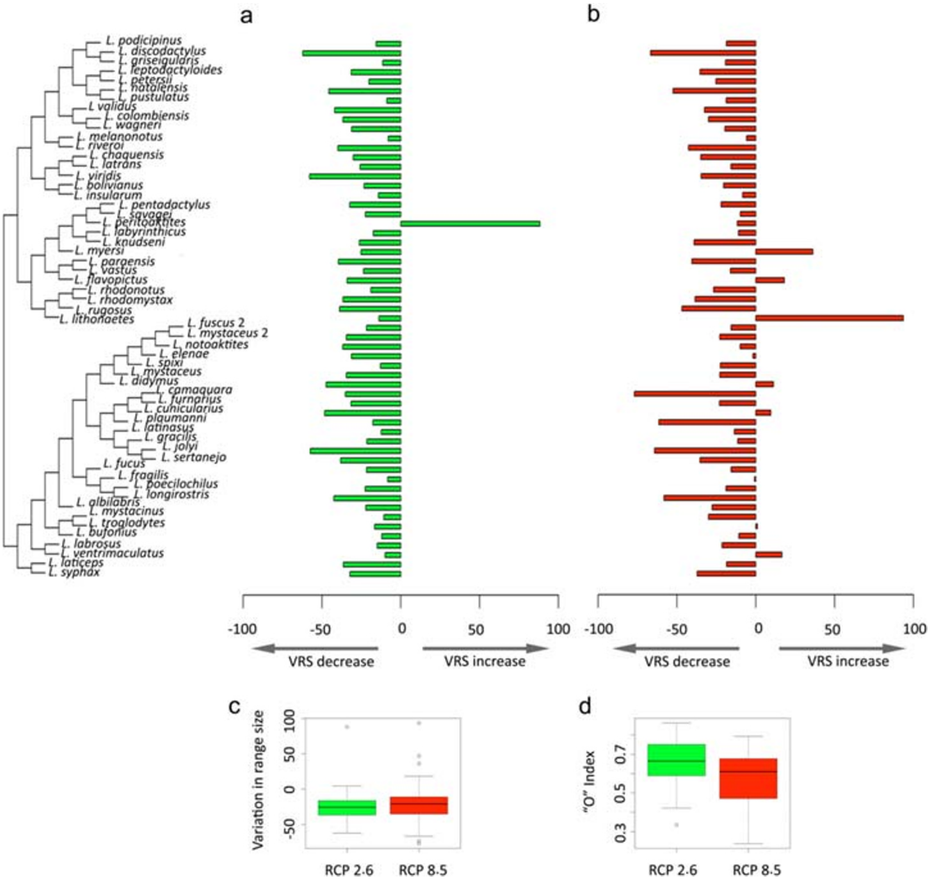

Fig. 6 Range size variation (RSV) of *Leptodactylus* species. (a, b) RSV expressed as percentage: positive and negative values represent range size increase and decrease, respectively. (c) Boxplot of RSV by future climate scenario. (d) Boxplot of overlap index "O" by future climate scenario. Green and red colors represent the RCP 2.6 and 8.5 future climate scenarios, respectively

supported by recent biogeographic and paleoclimatic analyses (Fouquet et al. 2013). The highest *Leptodactylus* species richness coincides with regions that have been characterized by high environmental diversity, e.g., moist forests of Bolivia and Monte Alegre Varzeá (WWF 2017). The hypothesis of habitat heterogeneity could explain this pattern, i.e., habitats with high environmental diversity can host species with diverse requirements, thus increasing species richness (Kerr and Packer 1997). Other factors, such as species physiological tolerance or density-dependent processes (e.g., competition, disease, herbivory, interspecific gene flow, facilitation, mutualism) (Cavender-Bares et al. 2009), can explain the observed richness patterns. Thus further analyses addressing the role of these factors are much needed.

Regions with high species richness are known as biodiversity "hotspots" (Myers 1988), and they are widely used to establish conservation objectives. Hotspots usually host species with small ranges (i.e., endemisms). By contrast, "coldspots" (i.e., sites with low number of species) are usually not considered as conservation targets, even when they might host species with restricted ranges (Kareiva and Marvier 2003). The R-D plot by sites showed that regions of maximum *Leptodactylus* richness host species with medium range sizes; thus, no strict

Leptodactylus “hotspots” were identified. Studies have already provided evidence suggesting little spatial congruence between species richness and rarity/endemism (e.g., Ceballos and Ehrlich 2006), and between different taxonomic assemblages (Kareiva and Marvier 2003). On the other hand, the R-D plots by sites showed regions with low species richness hosting *Leptodactylus* species with small range sizes, which could be categorized as “coldspot” regions. Most of them, except for the Caatinga, have been classified as hotspots based on plants and vertebrates, namely the Tropical Andes, Chocó and Darién forests, Mesoamerica, and the Caribbean (Myers et al. 2000). Consequently, the prioritization of hotspots for conservation implies the protection of most of the *Leptodactylus* “coldspots” (Mittermeier et al. 1998; Myers et al. 2000). The Caatinga ecoregion exhibits low species richness and site covariance with the rest of the assemblage, harboring *L. caatingae*, *L. troglodytes*, and *L. vastus*. We propose to consider the Caatinga as a “coldspot” for *Leptodactylus* due its evolutionary relevance since it houses species belonging to two *Leptodactylus* clades (de Sá et al. 2014), which represents the evolution of two reproductive modes for amphibians (Heyer 1969).

4.2 Potential effect of climate change on diversity patterns

The increase of beta diversity values projected for 2050 agrees with the heterogenization (i.e., biotic differentiation) hypothesis. This implies an increase of *Leptodactylus* heterogeneity, which is mainly explained by the reduction of species’ range sizes under future climate conditions. One of the ecological mechanisms of biotic homogenization/differentiation proposed by Olden and Poff (2003) posits that local extinctions of coexisting species increase biotic differentiation at the beginning of the process, up to a threshold. Once that threshold is passed, range contractions increase the likelihood of species complete extinction, and biota tends to homogenization. *Leptodactylus* could be undergoing the beginning of such process, since species ranges are projected to shrink only by 24% of their current area. In Mexican amphibians, increases in biota heterogeneity in the earliest period analyzed (2000–2020) were followed by biotic homogenization (2020–2050 and 2050–2080 periods); thus, the point-to-point analysis (from 2000 to 2080) seemed to support the counter-intuitive hypothesis of a stable beta (Ochoa-Ochoa et al. 2012). Recently, a biotic homogenization pattern has been projected for 2050 and 2080 in the woody Atlantic Forests (Zwiener et al. 2017). In that sense, climate change might be a driver of biodiversity spatiotemporal changes, implying both biotic homogenization and heterogenization in the Neotropical region.

While we projected a heterogenization process at a regional scale, in some areas, the opposite pattern would likely to occur. The biodiversity change patterns in contact areas between the Cerrado and the Caatinga, and the Cerrado and the Amazonia varied in relation to the remaining areas, since range expansions of co-occurring species were projected in these areas, which suggest the homogenization of *Leptodactylus* species. Such increase of similarity for the taxon in these ecotonal regions is a wake-up call, and is especially relevant since these regions are conservation priorities due to their biotic complexity (Smith et al. 2001).

The projected contraction of species ranges, which increases biota heterogeneity, would be likely to occur in lowlands below 1500 m a.s.l., encompassing the altitudinal distribution range of the genus (de Sá et al. 2014). This pattern has also been predicted for bird assemblages in mountainous systems, where steep environmental gradients determine the adaptation of species to changes with minor spatial shifts (Peterson 2003). Given similar changes in temperature, the horizontal adaptive shift of species ranges is expected to be greater in flat lands, and the probability of successful adaptation by migrations should be lower (Peterson 2003). Nevertheless, our analysis does not consider species movement capacity or land-use change, which would likely produce species extinction or greater range reductions; therefore, these parameters under future climate conditions would be underestimated. Although *Leptodactylus* can tolerate anthropogenic disturbances (de Sá et al. 2014), deforestation implies a loss of habitat for forest habitat specialist species (e.g., *L. laticeps* in the Dry Chaco; Medina et al. 2016).

4.3 Potential effect of climate change on range sizes and geographic shifts

Reductions in species geographic ranges usually precede species extinctions (e.g., Peterson et al. 2002). In *Leptodactylus* species with small range sizes (median range size = 121 sites), like *L. camaquara*, *L. cupreus*, *L. discodactylus*, *L. jolyi*, and *L. viridis*, an increased extinction risk might occur due to the lack of stability across their suitable environmental envelopes. We projected drastic range size reductions and significant range shifts under climate scenarios for these species. The IUCN categorizes them as data deficient, with unknown population trends (Barreto Nascimento et al. 2004; Silvano and Pimenta 2004; Giaretta 2010; IUCN SSC 2010). This lack of research about threatened species exacerbates the uncertainty regarding extinction risk, which is increased by land-use change. *Leptodactylus camaquara, L. cupreus*, *L. jolyi, L. natalensis*, and *L. viridis* are distributed in the Atlantic Forest, one of the most threatened biodiversity hotspots (Bellard et al. 2014). In this region, range contractions for approximately 350 amphibian species have been predicted by 2050, as a consequence of climate change (Lemes et al. 2014). More recently, 37 out of 512 species were predicted to become extinct by 2050 and 2070 in the Atlantic Forest (Vasconcelos et al. 2018). In the Dry Chaco, where the genus *Leptodactylus* is the most diverse among anurans (Medina et al. 2016), a considerable proportion of extant birds and mammals are predicted to become extinct due to past landscape transformation, and the long-term unviability of their present populations, i.e., a high “extinction debt” (Semper-Pascual et al. 2018). This highlights the urgent need of performing similar studies for other anuran assemblages.

Under both climate change scenarios, projected range size variations were similar, but the displacement was higher in RCP 8.5. Thus, if high greenhouse gas emissions continue, the effect would be greater on geographical displacement than on range size. This would constitute an increased threat for the less vagile species, such as amphibians, for which a geographical displacement of environmental conditions would imply range contraction. This alarming situation was projected for *L. discodactylus*, *L. riveroi*, *L. camaquara*, *L. didymus*, *L. jolyi*, *L. longirostris*, and *L. leptodactyloides.*

In *Leptodactylus*, neither the decrease nor the increase of geographic ranges or the degree of geographic displacement due to climate change showed an association with phylogenetic structure. This prevents increased loss of evolutionary history when extinctions occur (Thuiller et al. 2011). In that sense, a low phylogenetic signal against climate change has also been reported in European plants, birds, and mammals (Thuiller et al. 2011).

The range-diversity analysis, which considers both species diversity (richness) and distribution (range sizes), is useful for the prioritization of conservation areas (Villalobos et al. 2013). The dispersion field patterns allowed us to determine “coldspots” for *Leptodactylus*, with partial spatial congruence with the biodiversity “hostpots.” In addition, it showed that regions of maximum richness host species with medium range sizes. The dependence on hydrological and temperature regimes, in line with the potential geographical displacements under future climate scenarios, turns amphibians into particularly vulnerable species to climate change (Early and Sax 2011). The prediction of higher beta diversity in the future indicated an overall biotic heterogenization process, consistent with the idea that the originally diverse *Leptodactylus* assemblage would be reduced to small and isolated patches and impoverished communities. The biotic heterogenization of *Leptodactylus*, in contrast to the biotic homogenization reported for other assemblages (e.g., woody flora of the Atlantic Forest, Zwiener et al. 2017), shows a dual effect of climate change as a driver of regional biodiversity. Although protected areas tend to be less susceptible to certain disturbances like habitat loss (Oliveira Paiva et al. 2015), climate change would lead to the same processes of biotic heterogenization at the regional level compromising their long-term efficiency. This effect would be greater in the areas that house the greatest richness of species and that also have medium- to small-sized ranges. Reduction in the release of greenhouse gases along with the management and control of disturbances outside protected areas will be required for a more effective protection of the biodiversity of ecosystems and the services they provide. The results obtained for this assemblage of Neotropical anurans should be contrasted and complemented with those obtained for other regional taxa. This would allow reaching robust conclusions and recommendations for the optimization of the available resources aiming at biodiversity management and conservation.

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References

Abouheif E (1999) A method for testing the assumption of phylogenetic independence in comparative data. Evol Ecol Res 1:895–909

Alroy J (2015) Current extinction rates of reptiles and amphibians. Proc Natl Acad Sci 112:13003–13008. https://doi.org/10.1073/pnas.1508681112

Arita T, Christen AJ, Rodríguez P, Soberón J (2008) Species diversity and distribution in presence-absence matrices: mathematical relationships and biological implications. Am Nat 172:519–532. https://doi.org/10.1086/590954

Arita T, Christen AJ, Rodríguez P, Soberón J (2012) The presence–absence matrix reloaded : the use and interpretation of range–diversity plots. Glob Ecol Biogeogr 21:282–292. https://doi.org/10.1111/j.1466-8238.2011.00662.x

Barreto Nascimento L, Eterovick P, Silvano D (2004) *Leptodactylus camaquara*. The IUCN Red List of Threatened Species. Downloaded on December, 2017. https://doi.org/10.2305/IUCN.UK.2004.RLTS.T57117A11583646.en

Barve N, Barve V (2016) ENMGadgets: tools for pre and post processing in ENM workflow. R package, version 0.0.13. See https://github.com/narayanibarve/ENMGadgets

Barve N, Barve V, Jiménez-Valverde A et al (2011) The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecol Model 222:1810–1819. https://doi.org/10.1016/j.ecolmodel.2011.02.011

Bellard C, Leclerc C, Leroy B et al (2014) Vulnerability of biodiversity hotspots to global change. Glob Ecol Biogeogr 23:1376–1386. https://doi.org/10.1111/geb.12228

Bilton DT, Mcabendroth L, Bedford A, Ramsay PM (2006) How wide to cast the net? Cross-taxon congruence of species richness, community similarity and indicator taxa in ponds. Freshw Biol 51:578–590. https://doi.org/10.1111/j.1365-2427.2006.01505.x

Blomberg SP, Garland T, Ives AR (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution 57:717–745. https://doi.org/10.1111/j.0014-3820.2003.tb00285.x

Brook BW, Sodhi NS, Bradshaw CJA (2008) Synergies among extinction drivers under global change. Trends Ecol Evol 23:453–460. https://doi.org/10.1016/j.tree.2008.03.011

Cavender-Bares J, Kozak KH, Fine PVA, Kembel SW (2009) The merging of community ecology and phylogenetic biology. Ecol Lett 12:693–715. https://doi.org/10.1111/j.1461-0248.2009.01314.x

Ceballos G, Ehrlich PR (2006) Global mammal distributions, biodiversity hotspots , and conservation. Proc Natl Acad Sci U S A 103:19374–19379. https://doi.org/10.1073/pnas.0609334103

Christensen JH, Hewitson B, Busuioc A, et al (2007) Regional climate projections. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller L(eds) Climate Change, 2007: The physical science basis. Contribution of Working group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge: University Press, pp 847–940

de Sá RO, Grant T, Camargo A et al (2014) Systematics of the neotropical genus Leptodactylus Fitzinger, 1826 (Anura: Leptodactylidae): phylogeny, the relevance of non-molecular evidence, and species accounts. South Am J Herpetol 9:1–100. https://doi.org/10.2994/SAJH-D-13-00022.1

Duan R-Y, Kong X-Q, Huang M-Y et al (2016) The potential effects of climate change on amphibian distribution, range fragmentation and turnover in China. PeerJ 4:e2185. https://doi.org/10.7717/peerj.2185

Duellman WE, Trueb L (1994) Biology of amphibians. The John Hopkins Press, Baltimore, MD

Early R, Sax DF (2011) Analysis of climate paths reveals potential limitations on species range shifts. Ecol Lett 14:1125–1133. https://doi.org/10.1111/j.1461-0248.2011.01681.x

Eeley HAC, Foley RA (1999) Species richness, species range size and ecological specialisation among African primates: geographical patterns and conservation implications. Biodivers Conserv 8:1033–1056. https://doi.org/10.1023/A:1008831320469

Elith J, Graham CH, Anderson RP et al (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x

Farji Brener AG, Ruggiero A (1994) Leaf-cutting ants (Atta and Acromyrmex) inhabiting Argentina: patterns in species richness and geographical range sizes. J Biogeogr 21:391–399. https://doi.org/10.2307/2845757

Feder ME, Burggren WW (1992) Environmental physiology of the amphibians. University of Chicago Press, Chicago, IL

Fitzinger LJFJ (1826) Neue Classification der Reptilien nach ihren Natürlichen Verwandtschaften nebst einer Verwandtschafts-Tafel und einem Verzeichnisse der Reptilien-Sammlung des K. K. Zoologisch Museum's zu Wien. Wien: J. G. Heubner

Fouquet A, Gilles A, Vences M et al (2007) Underestimation of species richness in neotropical frogs revealed by mtDNA analyses. PLoS One 2:e1109. https://doi.org/10.1371/journal.pone.0001109

Fouquet A, Blotto BL, Maronna MM et al (2013) Unexpected phylogenetic positions of the genera *Rupirana* and *Crossodactylodes* reveal insights into the biogeography and reproductive evolution of leptodactylid frogs. Mol Phylogenet Evol 67:445–457. https://doi.org/10.1016/j.ympev.2013.02.009

Freckleton RP, Harvey PH, Pagel M (2002) Phylogenetic analysis and comparative data. Am Nat 160:712–726. https://doi.org/10.1086/343873

Frost DR (2018) Amphibian species of the world: an online reference. Electronic Database accessible at http://research.amnh.org/herpetology/amphibia/index.html. American Museum of Natural History, New York, USA. Version 6.0 (October, 2018)

Garcia RA, Cabeza M, Rahbek C, Araújo MB (2014) Multiple dimensions of climate change and their implications for biodiversity. Science 344:1247579. https://doi.org/10.1126/science.1247579

Giaretta AA (2010). *Leptodactylus jolyi*. The IUCN Red List of Threatened Species. Downloaded on December, 2017. https://doi.org/10.2305/IUCN.UK.2010-2.RLTS.T57134A11589035.en

Graves GR, Rahbek C (2005) Source pool geometry and the assembly of continental avifaunas. Proc Natl Acad Sci 102:7871–7876. https://doi.org/10.1073/pnas.0500424102

Harris I, Jones PD, Osborn TJ, Lister DH (2014) Updated high-resolution grids of monthly climatic observations—the CRU TS3.10 Dataset. Int J Climatol 34:623–642. https://doi.org/10.1002/joc.3711

Hengl T, de Jesus JM, MacMillan RA et al (2014) SoilGrids1km—global soil information based on automated mapping. PLoS One 9:e105992. https://doi.org/10.1371/journal.pone.0105992

Heyer WR (1969) The adaptive ecology of the species groups of the frog genus *Leptodactylus* (Amphibia, Leptodactylidae). Evolution 23:421–428

Heyer WR (1975) A preliminary analysis of the intergeneric relationships of the frog family Leptodactylidae. Smithson Contrib Zool 199:1–55. https://doi.org/10.5479/si.00810282.199

Hijmans RJ (2015) Raster: geographic data analysis and modeling. R package, version 2.5–2. Available at https://CRAN.R-project.org/package=raster

Hijmans RJ, Cameron SE, Parra JL et al (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978. https://doi.org/10.1002/joc.1276

Houlahan JE, Fidlay CS, Schmidt BR et al (2000) Quantitative evidence for global amphibian population declines. Nature 404:752–755. https://doi.org/10.1038/35008052

IUCN SSC Amphibian Specialist Group (2010) *Leptodactylus cupreus*. The IUCN Red List of Threatened Species. Downloaded on December, 2017. https://doi.org/10.2305/IUCN.UK.2010-4.RLTS.T158473A5200398.en

Kareiva P, Marvier M (2003) Conserving biodiversity coldspots: recent calls to direct conservation funding to the world's biodiversity hotspots may be bad investment advice. Am Sci 91:344–351

Kerr JT, Packer L (1997) Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. Nature 385:252–254. https://doi.org/10.1038/385252a0

Kou X, Li Q, Liu S (2011) Quantifying species' range shifts in relation to climate change: a case study of Abies spp. in China. PLoS One 6:e23115. https://doi.org/10.1371/journal.pone.0023115

Lemes P, Melo AS, Loyola RD (2014) Climate change threatens protected areas of the Atlantic Forest. Biodivers Conserv 23:357–368. https://doi.org/10.1007/s10531-013-0605-2

McIntosh RP (1967) An index of diversity and the relation of certain concepts to diversity. Ecology 48:392–404. https://doi.org/10.2307/1932674

Medina RG, Ponssa ML, Aráoz E (2016) Environmental, land cover and land use constraints on the distributional patterns of anurans: *Leptodacylus* species (Anura, Leptodactylidae) from Dry Chaco. PeerJ 4:e2605. https://doi.org/10.7717/peerj.2605

Mittermeier RA, Myers N, Thomsen JB et al (1998) Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. Conserv Biol 12:516–520. https://doi.org/10.1046/j.1523-1739.1998.012003516.x

Mouquet N, Devictor V, Meynard CN et al (2012) Ecophylogenetics: advances and perspectives. Biol Rev 87: 769–785. https://doi.org/10.1111/j.1469-185X.2012.00224.x

Myers N (1988) Threatened biotas: "hotspots" in tropical forests. Environmentalist 8:187–208. https://doi.org/10.1007/BF02240252

Myers N, Mittermeier RA, Mittermeier CG et al (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858. https://doi.org/10.1038/35002501

Ochoa-Ochoa LM, Rodríguez P, Mora F et al (2012) Climate change and amphibian diversity patterns in Mexico. Biol Conserv 150:94–102. https://doi.org/10.1016/j.biocon.2012.03.010

Olden JD, Poff NL (2003) Toward a mechanistic understanding and prediction of biotic homogenization. Am Nat 162:442–460. https://doi.org/10.1086/378212

Oliveira Paiva RJ, Brites RS, Machado RB (2015) The role of protected areas in the avoidance of anthropogenic conversion in a high pressure region: a matching method analysis in the core region of the brazilian cerrado. PLoS One 10:1–24. https://doi.org/10.1371/journal.pone.0132582

Olson DM, Dinerstein E, Wikramanayake ED et al (2001) Terrestrial Ecoregions of the world: a new map of life on earth. Bioscience 51:933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Pavoine S, Ollier S, Pontier D, Chessel D (2008) Testing for phylogenetic signal in phenotypic traits: new matrices of phylogenetic proximities. Theor Popul Biol 73:79–91. https://doi.org/10.1016/j.tpb.2007.10.001

Peterson AT (2003) Projected climate change effects on Rocky Mountain and Great Plains birds: generalities of biodiversity consequences. Glob Chang Biol 9:647–655. https://doi.org/10.1046/j.1365-2486.2003.00616.x

Peterson AT, Ortega-Huerta MA, Bartley J et al (2002) Future projections for Mexican faunas under global climate change scenarios. Nature 416:626–629. https://doi.org/10.1038/416626a

Peterson AT, Papes M, Soberón J (2008) Rethinking receiver operating characteristic analysis applications in ecological niche modeling. Ecol Model 213:63–72. https://doi.org/10.1016/j.ecolmodel.2007.11.008

Peterson AT, Soberón J, Anderson RP et al (2011) Ecological niches and geographic distributions. Princeton University Press, Princeton

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Purvis A (2008) Phylogenetic approaches to the study of extinction. Annu Rev Ecol Evol Syst 39:301–319. https://doi.org/10.1146/annurev-ecolsys-063008-102010

Pyron AR, Wiens JJ (2011) A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. Mol Phylogenet Evol 61:543–583. https://doi.org/10.1016/j.ympev.2011.06.012

QGIS Development Team (2017) QGIS geographic information system. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

Ridley M (2004) Evolution 3rd edition. Blackwell Publishing, Malden

Routledge RD (1977) On Whittaker's components of diversity. Ecology 58:1120–1127. https://doi.org/10.2307/1936932

Schalk CM, Montaña CG, Springer L (2015) Morphological diversity and community organization of desert anurans. J Arid Environ 122:132–140. https://doi.org/10.1016/J.JARIDENV.2015.06.019

Semper-Pascual A, Macchi L, Sabatini FM et al (2018) Mapping extinction debt highlights conservation opportunities for birds and mammals in the South American Chaco. J Appl Ecol 55:1218–1229. https://doi.org/10.1111/1365-2664.13074

Silvano D, Pimenta B (2004) *Leptodactylus viridis*. The IUCN Red List of Threatened Species. Downloaded on December, 2017. https://doi.org/10.2305/IUCN.UK.2004.RLTS.T57174A11579567.en

Singh BP, Cowie AL, Chan KY (2011) Soil health and climate change. Springer Science & Business Media, Springer, Heidelberg, Dordrecht, London, New York

Smith TB, Kark S, Schneider CJ et al (2001) Biodiversity hotspots and beyond: the need for preserving environmental transitions. Trends Ecol Evol 16:431. https://doi.org/10.1016/S0169-5347(01)02201-7

Soberón J, Ceballos G (2011) Species richness and range size of the terrestrial mammals of the world: biological signal within mathematical constraints. PLoS One 6:e19359. https://doi.org/10.1371/journal.pone.0019359

Soberón J, Peterson AT (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. Biodivers Informatics 2:1–10. https://doi.org/10.1093/wber/lhm022

Stuart SN, Chanson JS, Cox NA et al (2004) Status and trends of amphibian declines and extinctions worldwide. Science 306:1783–1786. https://doi.org/10.1126/science.1103538

Thomas CD, Thomas CD, Cameron A et al (2004) Extinction risk from climate change. Nature 427:145–148. https://doi.org/10.1038/nature02121

Thuiller W, Lavergne S, Roquet C et al (2011) Consequences of climate change on the tree of life in Europe. Nature 470:531–534. https://doi.org/10.1038/nature09705

Vasconcelos TS, do Nascimento BTM, Prado VHM (2018) Expected impacts of climate change threaten the anuran diversity in the Brazilian hotspots. Ecol Evol 17:7894–7906. https://doi.org/10.1002/ece3.4357

Vilela B, Villalobos F (2017) letsR: tools for data handling and analysis in macroecology. R package version 3.0. See https://cran.r-project.org/web/packages/letsR/index.html

Villalobos F, Lira-Noriega A, Soberón J, Arita HT (2013) Range—diversity plots for conservation assessments: using richness and rarity in priority setting. Biol Conserv 158:313–320. https://doi.org/10.1016/j.biocon.2012.10.002

Walther GR (2010) Community and ecosystem responses to recent climate change. Philos Trans R Soc Lond Ser B Biol Sci 365:2019–2024. https://doi.org/10.1098/rstb.2010.0021

Whittaker RH (1960) Vegetation of the Siskiyou Mountains, Oregon and California. Ecol Monogr 30:279–338. https://doi.org/10.2307/1943563

Whittaker RH (1972) Evolution and measurement of species diversity. Taxon 21:213–251. https://doi.org/10.2307/1218190

Whittaker RH (1975) Communities and ecosystems, 2nd edn. Macmillan, New York

Wieczorek J, Guo Q, Hijmans R (2004) The point-radius method for georeferencing locality descriptions and calculating associated uncertainty. Int J Geogr Inf Sci 18:745–767. https://doi.org/10.1080/13658810412331280211

WWF (panda.org) (2017). http://wwf.panda.org/about_our_earth/ecoregions/swamazon_moist_forests.cfm

Zwiener VP, Lira-Noriega A, Grady CJ et al (2017) Climate change as a driver of biotic homogenization of woody plants in the Atlantic Forest. Glob Ecol Biogeogr 27:298–309. https://doi.org/10.1111/geb.12695

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