

Translating niche features: Modelling differential exposure of Argentine reptiles to global climate change

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Abstract Global climate change affects the distributions of ectotherms and may be the cause of several conservation problems, such as great displacement of climatic suitable spaces for species and, consequently, important reductions of the extent of liveable places, threatening the existence of many of them. Species exposure (and hence vulnerability) to global climate change is linked to features of their climatic niches (such as the relative position of the inhabited localities of each species in the climatic space), and therefore to characteristics of their geographic ranges (such as the extent of the distributions or altitudinal range inhabited by the species). In order to analyze the pattern of response of Argentine reptiles to global climate change, we ran phylogenetic generalized least squares models using species exposure to global climate change as a response variable, and (i) niche properties (breadth and position of the species in the climate space) and (ii) general features of the distribution of species (maximum latitude, altitudinal range, maximum elevation, distributional range and proximity to the most important dispersal barrier) as predictors. Our results suggest that the best way to explain climate change exposure is by combining breadth and position of climatic niche of the species or combining geographic features that are indicators of both niche characteristics. Our best model shows that in our study area, species with the narrowest distributional ranges that also inhabit the highest elevations are the most exposed to the effects of global climate change. In this sense, reptile species from Yungas, Puna and Andes ecoregions could be especially vulnerable to the effects of climate change. We believe that these types of models may represent an interesting tool for determining species and places particularly threatened by the effects of global climate change, which should be strongly considered in conservation planning.

Key words: climate change exposure, climatic niche, phylogenetic generalized least square model, species distribution.

INTRODUCTION

Species responses to global climate change are complex. Among other effects, global climate change induces changes in the distributional patterns of species. These changes are produced by displacements of areas with climatically suitable conditions as a consequence of movements of climatic niches of species (Thomas *et al.* 2004; Chen *et al.* 2011; Dawson *et al.* 2011; Dullinger *et al.* 2012). In many cases, global climate change can trigger significant losses of habitable areas (Loyola *et al.* 2012; Nori *et al.* 2014). This phenomenon has been pointed out as the cause of several extinction events (Thomas *et al.* 2004; Lenoir *et al.* 2008). Additionally, increases in conservation problems and extinction events because of global

climate change have been forecasted for the near future (Sinervo *et al.* 2010; Hof *et al.* 2011; Dullinger *et al.* 2012). For these reasons, understanding and predicting species responses to global climate change is important for developing strategies to manage and preserve biodiversity (Loyola *et al.* 2012; Faleiro *et al.* 2013).

A key step in estimating and understanding species vulnerability is to measure the exposure of the species to global climate change. Exposure refers to the extent of changes in climatic conditions to be experienced by a species within its current distribution (Dawson *et al.* 2011). Based on the study of exposure to climate change, previous authors have postulated that species response to global climate change strongly depends on the characteristics of their ‘climatic niches’, with two characteristics being meaningful. First is the position, which refers to the relative location of the suitable climate conditions for the species in relation to the

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available climate conditions in the area; if the climatic requirements of a species are highly dissimilar to the mean conditions of a region (it is a marginal species), then exposure increases (Swihart *et al.* 2003; Thuiller *et al.* 2005; Broennimann *et al.* 2006; Tingley *et al.* 2009). Second is the climatic niche breadth, which is a measure of the climatic tolerance of the species; species with narrower niche breadths are less tolerant to climatic changes, and therefore are more vulnerable to global climate change (Thuiller *et al.* 2004, 2005; Kotiaho *et al.* 2005; Broennimann *et al.* 2006; Boulangeat *et al.* 2012; Bonino *et al.* 2015).

Species exposure to global climate change is also linked to geographic features of its distribution, such as latitudinal or altitudinal position, distance to geographic dispersal barriers, or the extent of its distributional ranges (Thuiller *et al.* 2005; Broennimann *et al.* 2006; Lenoir *et al.* 2008; Bonino *et al.* 2015). In fact, these geographic characteristics are what define the features of climatic niches of species. For this reason, species with distributional ranges with specific characteristics, dependent on the geographic context, may need additional attention in light of global climate change. Additionally, phylogenetic relationships also need to be considered when studying vulnerability to climate change, as related species could show similar exposure to global climate change (Hof *et al.* 2010; Loyola *et al.* 2014). In this context, it is very important to consider that the estimated exposure of species to global climate change could be reflecting a common history between the species.

As stated above, previous studies have analyzed the relationship between the exposure of species to global climate change and different individual characteristics of their climatic niches, and of their geographic distributions. As far as we know, none of these studies has combined these variable running models in order to find the best way of explaining the exposure to global climate change, while additionally considering phylogenetic relationships among species. Argentina, and specifically the northwestern portion of the country, is extremely diverse in regard to its climate and topography, harbouring an important diversity of reptile species with different ecological requirements (see Appendix S1). Therefore, the exposure to global climate change may vary widely between species and places. Understanding this 'variation' is a key step in achieving accurate conservation policies in light of climate change. However, this has not yet been explored in the country. Additionally, reptiles are especially vulnerable to the effect of global climate change, given the ecological characteristics of the group (Sinervo *et al.* 2010).

In this study, we aim to fill some of the mentioned gaps of information in order to provide valuable data for the conservation of Argentine reptiles. Specifically, we determined the exposure to global climate change

for 17 reptile species that inhabit northwestern Argentina (Appendix S1) based on bioclimatic envelope models (BEMs), calibrated with records from their entire distributional ranges. Then, we ran phylogenetic generalized least squares models (PGLS) in order to model differential exposure of species to global climate change based on (i) breadth and position of their climatic niche and (ii) different geographic variables related to niche features. In both cases, our main aim was to find a pattern to explain the exposure of these reptiles to climate change.

METHODS

Distributional data

We obtained 960 records corresponding to the known distribution of 17 reptile species present in northwestern Argentina (Appendix S1). Data were obtained from herpetological collections, relevant literature and the Global Biodiversity Information Facility (Appendix S2). We tried to represent the taxonomical and biogeographic diversity of reptiles of the study area by selecting species occurring in all of the ecoregions present in the study area (*sensu* Olson *et al.* 2001), and comprising a great phylogenetic diversity (*sensu* Pyron *et al.* 2013). We included species of more than 90% of the taxonomical families of reptiles occurring in the study area.

Climatic data

We used 20 variables for both current and future conditions: 19 bioclimatic plus elevation (available from: <http://www.worldclim.org> for present conditions; <http://ccafs-climate.org/> for future scenarios). Environmental data were downloaded at a spatial resolution of 2.5 arcminutes for continental South America. We performed a pairwise Pearson correlation between all pairs of climatic variables and then selected five that did not exhibit high collinearity (retaining those with $r < 0.75$): mean diurnal range of temperature, maximum temperature of warmest month, mean temperature of the warmest quarter, precipitation of the warmest quarter and precipitation seasonality (see <http://www.worldclim.org/bioclim>). The future scenario corresponded to the Global Circulation Model INM-CM3 for the A1B emission (considered as a 'median' scenario, forecasting changes of between 1.7°C and 4.4°C between the periods 1980–1999 and 2090–2099).

Analyses

Exposure to climate change

We ran BEMs in order to estimate the exposure of the selected species to global climate change. We projected the models for current climatic conditions to estimate climatic suitable spaces for the species, and then re-projected these

models into future conditions with the aim of estimating changes in suitable climatic spaces. Models were projected in a 1500 km buffer zone of the minimum convex hull, generated with the records of each species in order to avoid spurious projections to very remote sites of the known distribution, where although the climate is suitable, these species could never reach, for example due to their life history, or the fragmentation and anthropization of environments. Later, we estimated gain/loss of climatic suitable spaces toward the future (expressed as a percentage). This percentage was used as a measure of exposure to climate change for each species.

Because alternative BEMs algorithms have different levels of accuracy under different circumstances and there is no single ‘best’ method, we combined multiple algorithms into an ensemble (Araújo & New 2007). This ensemble approach identifies areas of high consensus between algorithms, producing more conservative projections than using a single algorithm. Here, we implemented three different algorithms: Genetic Algorithm for Rule-set production with the selection of the better subset (Anderson *et al.* 2003), Maxent (Phillips *et al.* 2006) and the support vector machine (Schölkopf *et al.* 2001). We selected a threshold value by assuming absence of the species in all pixels with values of suitability lower than the value at which at least 95% of the records are included in the prediction (omission errors less than 5%). In order to test all the individual projections, we assessed model performance using 20% of the records as ‘validation data’ in order to calculate the area under the curve (AUC) of the receiver operating characteristic curve.

Climatic niche position

We performed a canonical outlying mean index analysis to estimate the position of each species along the environmental gradient of South America. The result of this analysis is a description of the mean niche position on each selected gradient (niche position) for each species, which represents a measure of the distance between the mean conditions used by the species and the mean conditions of the study area for that gradient. This index is a measure of the ‘marginality’ of each species in the environmental gradient, meaning that a species is more marginal as the further its environmental requirements are from the mean conditions available in the continent (Appendix S3; Doledec *et al.* 2000 and Supplementary material of Darmon *et al.* 2012).

Climatic niche breadth

In order to estimate the climatic niche breadth of each species, we first ran a principal component analysis (PCA) using the values of the climatic variables included in the BEMs for all records of each species plus 5000 random points within a convex hull generated with the records of all species together (in order to represent available climate conditions in the study area). Then, we mapped the records of each species on the first two axes of the PCA (which explain the 97% of the variance of the ‘climatic space’) and calculated the range including 90% of the records on each axis.

The final climatic breadth was calculated as the sum of the value of each axis weighted by the percentage of the total variance that it explained (Appendix S4).

Geographic characteristics of species distributions

Using ArcGis, we extracted the following variables for each occurrence record: elevation, latitude, longitude and minimum distance to the Andes (considering the imaginary line connecting the highest peaks, which match the political watershed). From these values, we estimated the following: maximum latitude and maximum elevation reached by each species, altitudinal range covered by each species, and proximity between the Andes and each species. Additionally, we calculated species distributional ranges as the surface of the projection of the final models in current conditions (i.e. the surface (km²) of current suitable space for each species). It is important to note that the altitudinal range and distributional range covered by the species may be considered as indirect indicators of niche breadth because these variables are a measure of the ‘range of tolerance’ of the species. On the other hand, maximum altitude and latitude reached by the species and distance to the Andes are indicators of the position of the species in the climatic space (niche position).

Patterns of exposure to global climate change

Given that species share a common evolutionary history (so they are related under a hierarchic basis), we studied the relationship between exposure to global climate change and (i) the position and breadth in the environmental gradient and (ii) species geographic distribution variables using PGLS. These models include the species phylogenetic relationships, estimating Pagel’s phylogenetic signal (λ) from the residual errors simultaneously with the regression parameters, thus controlling the regression for phylogenetic collinearity. The PGLS procedure is preferred, as it has been shown to outperform equivalent either to phylogenetic or to non phylogenetic procedures depending on the λ value obtained (Revell 2010). Phylogenetic relationships between the studied species were reconstructed from Pyron *et al.* (2013) (Appendix S5). We applied Pagel’s branch length transformation method to run PGLS by using the branch transformation tool of Mesquite (Maddison & Maddison 2011). These analyses were performed using the packages ‘caper’ (Orme 2013) and ‘ape’ (Paradis *et al.* 2004) in R 3.1.1 (R Core Team 2014).

In order to determine the exposure of species based on characteristics of their climatic niches, we generated three possible PGLS models using niche breadth and position as predictors. Then, to study the relationship between exposure of the species and geographic features of their ranges, we ran 31 possible models including 5 measured geographic variables. We used the Akaike information criterion (AIC) to select the model with the best fit among the candidate models (Angilletta 2006). We used Akaike weights as a measure of the strength of evidence for each model, indicating the probability that a given model was the best among a series of candidate models (Burnham & Anderson 2002).

RESULTS

The BEMs showed values of AUC ranging from 0.83 to 0.98 ($\bar{X} = 0.93$; $SD = 0.04$) (Appendix S6). Climatically suitable surfaces at present conditions varied in area from 660 km² for *Phymaturus antofagastensis* to 2 065 756 km² for *Bothrops diporus*. For the future scenarios, the surfaces varied between 370 km² (*P. antofagastensis*) to 1 897 496 km² (*B. diporus*) (Fig. 1, Appendix S7). In summary, exposure to climate change varied from an increase of 35% of climatically suitable space for *Phimophis vittatus* for future scenario, to a loss of almost 45% of the original surface of climatically suitable space for *P. antofagastensis* (Table 1, Fig. 1). Niche position of the species varied between -2.1281 and -0.0029 ; with *P. antofagastensis* being the most marginal species and *Liolaemus cuyanus* the species with closest requirements to the mean conditions of the study area (Table 1, Appendix S3). *Ameivula abalosi* was the species with the smallest niche breadth (0.81) and *Stenocercus roseiventris* with the biggest one (3.91) (Table 1, Appendix S4). Values of geographic variables for all the species are shown in Table 1.

Patterns of exposure to global climate change (PGLS)

For the models generated with niche properties as variables, the best model (the lowest AICc and the highest Wi values) included both niche position and breadth as predictor variables (Fig. 2, Table 2, Appendix S8). The best models are those run with geographic variables as predictors, combining maximum elevation with distributional range and maximum latitude ($\text{exp} \sim \text{mlat} + \text{rdist} + \text{alt}$; $Wi = 0.23$, $r2\text{adj} = 0.75$). The model with the maximum elevation reached by the species was the second best model ($Wi = 0.20$, $r2\text{adj} = 0.66$). Finally, the model $\text{exp} \sim \text{rdist} + \text{alt}$ also showed good performance ($Wi = 0.14$, $r2\text{adj} = 0.68$; see Table 3, Fig. 2, Appendix S8).

DISCUSSION

Our results support the hypothesis that position and breadth of climatic niches are good indicators of a species exposure to global climate change (Swihart *et al.* 2003; Thuiller *et al.* 2004, 2005; Broennimann *et al.* 2006). Another 'self-evident' general conclusion is that although position in the climatic space alone explains the exposure of a species to climate change, the combination of both features (position and breadth) is the best model explaining this phenomenon (Table 2, Appendix S8). Moreover, we show that the pattern of exposure to global climate change can

be well explained by the combination of specific features of distributions of the species (related to breadth and position of its niches). Based on the models, we are able to estimate those species and places for which strong exposures are expected. In this sense, this transferable 'geographic model' may be useful for incorporating differential exposures to global climate change of species in conservation policies.

We used BEMs as a tool for estimating the exposure of species to global climate change (by comparing projections on the current and future climatic conditions). More realistic models (incorporating for example land use and other anthropogenic variables such as economical cost) have been used in conservation planning (e.g. Kremen *et al.* 2008; Nori *et al.* 2013; Faleiro *et al.* 2013). Another approach for predicting the impact of global climate change are the mechanistic models, which require specific life history and ecological data of organisms, such as activity patterns, reproductive potential, metabolic rates, prey abundance and development rate (Kearney & Porter 2009; Buckley *et al.* 2011; Ceia-Hasse *et al.* 2014). Still, the information needed to apply those models for many species remains scarce. In previous studies, BEMs have been shown to be useful tools to analyze similar patterns based on climate and species distributional data (e.g. Thuiller *et al.* 2005; Araújo *et al.* 2006; Broennimann *et al.* 2006).

Previous studies pointed out different geographic variables as good indicators of the exposure of species to global climate change (e.g. Swihart *et al.* 2003, Broennimann *et al.* 2006, Araújo *et al.* 2006, Lenoir *et al.* 2008). However, it is important to note that the relative importance of a given geographic variable is location specific. For example, latitudinal position of the species, distance to sea coast or altitudinal ranges have been reported in some studies as important variables for understanding global climate change exposure and vulnerability (e.g. Thuiller *et al.* 2005; Broennimann *et al.* 2006). However, in the present study, these variables on their own did not explain the exposure of global climate change. The most important variable explaining climate change exposure in this study was the maximum elevation reached by a species, a variable that has also been highlighted in previous studies (e.g. Lenoir *et al.* 2008). The characteristics of our study area (with a wide altitudinal gradient, steep slopes, far from coastlines, as well as with a high diversity of reptiles in high regions; see Appendix S1) make elevation the most associated variable to the position of the species in the climatic gradient (and hence with their exposure to global climate change).

Models carried out with niche properties, as well as those including geographic variables, confirm the same hypothesis: the most accurate way to explain species exposure to global climate change (obviously,

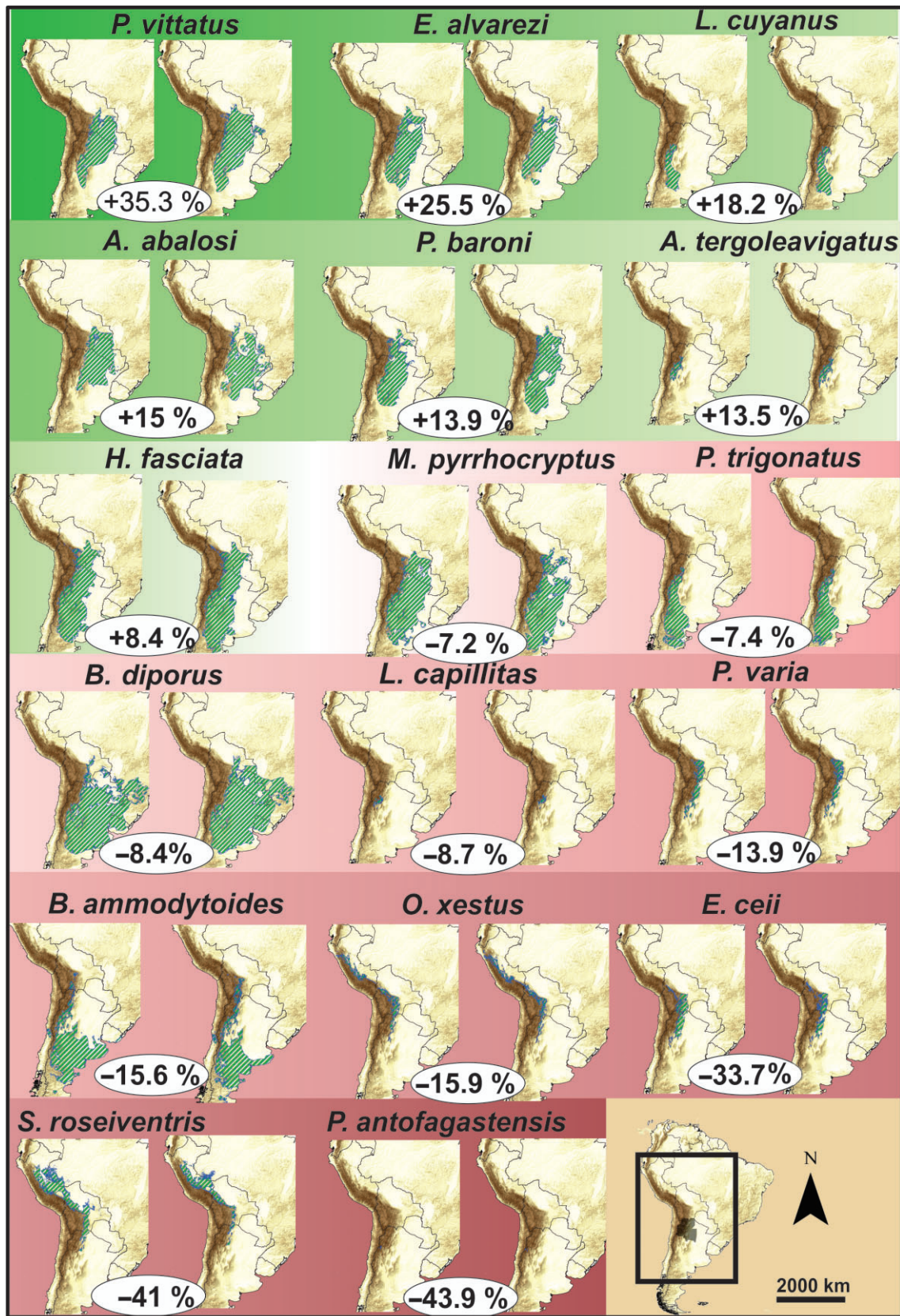


Fig. 1. Final projections in which we assume suitable climatic conditions for each of the species at current conditions (left) and future conditions (right).

Table 1. Values of all the variables for each species

| Species | Exp | Breadth | Position | Mlat | Alt | Ralt | Rdist | And |
|-----------------------------------|--------|---------|----------|--------|------|------|--------|--------|
| <i>Bothrops ammodytoides</i> | -15.64 | 8.14 | -1.22 | -43.05 | 3744 | 3735 | 107.51 | 66.89 |
| <i>Bothrops diporus</i> | -8.41 | 7.01 | -1.15 | -38.7 | 1516 | 1488 | 206.58 | 138.56 |
| <i>Ameivula abalosi</i> | 14.97 | 5.34 | -1.37 | -29.54 | 806 | 775 | 99.21 | 304.99 |
| <i>Aurivela tergoaevigatus</i> | 13.55 | 6.12 | -1.3 | -29.84 | 2533 | 1795 | 7.69 | 71.01 |
| <i>Epicrates alvarezi</i> | 25.51 | 5.3 | -1.3 | -32 | 1261 | 1184 | 76.73 | 256.26 |
| <i>Erythrolophus ceii</i> | -33.67 | 7.19 | -0.75 | -28.26 | 3822 | 3560 | 22.41 | 130.41 |
| <i>Homonota fasciata</i> | 8.36 | 8.11 | -1.23 | -39.77 | 1957 | 1833 | 136.45 | 72.34 |
| <i>Liolaemus capillitas</i> | -8.7 | 6.29 | -0.91 | -28.81 | 3473 | 1588 | 1.86 | 101.07 |
| <i>Liolaemus cuyanus</i> | 18.17 | 4.78 | -1.53 | -38.12 | 1774 | 1460 | 23.08 | 87.39 |
| <i>Micrurus pyrrhocryptus</i> | -7.23 | 7.28 | -1.23 | -39.1 | 2550 | 2522 | 149.14 | 100.15 |
| <i>Opipеuter xestus</i> | -15.86 | 6.38 | -0.21 | -23.78 | 2927 | 2568 | 17.89 | 70.45 |
| <i>Philodryas baroni</i> | 13.87 | 5.55 | -1.19 | -31.98 | 1681 | 1609 | 96.79 | 192.89 |
| <i>Philodryas varia</i> | -13.85 | 6.62 | -0.77 | -28.14 | 3082 | 2355 | 15.65 | 191.9 |
| <i>Phimophis vittatus</i> | 35.3 | 4.96 | -1.38 | -33.11 | 1217 | 1132 | 90.49 | 211.51 |
| <i>Phymaturus antofagastensis</i> | -43.9 | 3.87 | -0.13 | -27.38 | 4697 | 704 | 0.07 | 15.78 |
| <i>Pseudotomodon trigonatus</i> | -7.36 | 8.31 | -1.38 | -43.99 | 2374 | 2284 | 59.53 | 51.78 |
| <i>Stenocercus roseiventris</i> | -41 | 5.59 | -0.24 | -25.18 | 2859 | 2713 | 55.99 | 171.36 |

And, distance to the Andes (km); Alt, maximum altitude (m); Breadth, niche breadth; Exp, exposure to global climate change; Mlat, maximum latitude (m); Position, niche position; Ralt, altitudinal range (m); Rdist, distributional ranges (100 km²).

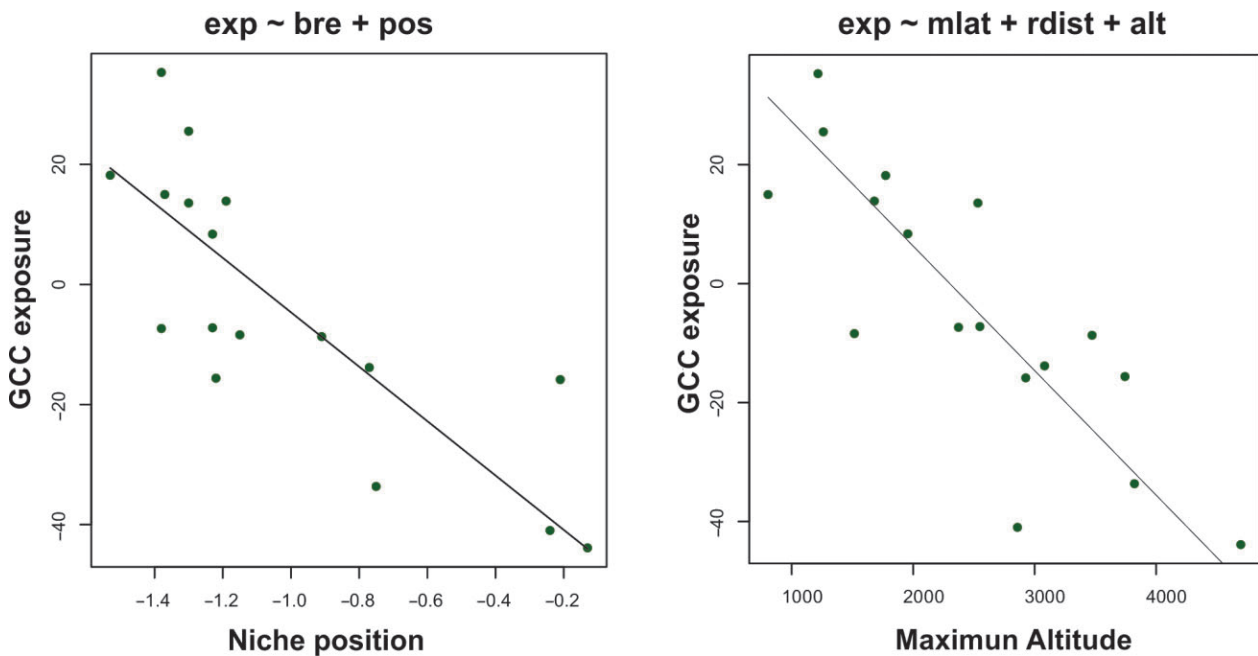


Fig. 2. Partial scatter plots of the best phylogenetic generalized least square models, carried out with (i) niche properties and (ii) geographic variables. The plot for each model shows the response variable with the best adjustment. alt, maximum altitude (m); bre, niche Breadth; exp, exposure to global climate change; GCC, global climate change; mlat, maximum latitude (m); pos, niche position; rdist, distributional ranges (100 km²).

considering the variables examined in this study) is through the combination of niche position and niche breadth, or indirect measurements of each. Both variables (niche position and breadth) have been pinpointed as important in previous studies (e.g. Swihart *et al.* 2003; Thuiller *et al.* 2005; Broennimann *et al.* 2006; Tingley *et al.* 2009). In regard to the models with geographic variables, the best one included three

variables (two of them with a significant effect): the maximum elevation reached by the species, the amplitude of the distributional range of the species and the maximum latitude (without significant effect). As stated in the methods section, maximum elevation can be seen as an indicator of the position of species in the climatic space, whereas amplitude of distributional range may be a good indicator of the niche breadth

Table 2. Phylogenetic generalized least squares models performed with climatic niche breadth and position as predictors

| Model | r2adj | AICc | δ_i | Wi |
|-----------------|--------------|----------------|--------------|--------------|
| exp ~ bre + pos | 0.732 | 136.714 | 0.000 | 0.872 |
| exp ~ bre | -0.043 | 158.007 | 21.293 | 0.000 |
| exp ~ pos | 0.627 | 140.553 | 3.839 | 0.128 |

AICc, Akaike information criterion for small sample size; Wi, Akaike weight; bre, niche Breadth; exp, exposure to global climate change; pos, niche position. Bold letter indicate the best possible model.

Table 3. Best 15 phylogenetic generalized least squares models (based on Wi) of those performed using the 5 geographic variables

| Model | r2adj | AICc | δ_i | Wi |
|---------------------------------|--------------|----------------|--------------|--------------|
| exp ~ mlat + rdist + alt | 0.735 | 138.766 | 0.000 | 0.230 |
| exp ~ alt | 0.659 | 139.027 | 0.261 | 0.202 |
| exp ~ rdist + alt | 0.682 | 139.663 | 0.897 | 0.147 |
| exp ~ alt + and | 0.649 | 141.295 | 2.529 | 0.065 |
| exp ~ ralt + alt | 0.647 | 141.409 | 2.644 | 0.061 |
| exp ~ mlat + alt | 0.644 | 141.559 | 2.793 | 0.057 |
| exp ~ and + rdist + alt | 0.685 | 141.678 | 2.912 | 0.054 |
| exp ~ mlat + ralt + rdist + alt | 0.724 | 142.237 | 3.471 | 0.041 |
| exp ~ mlat + and + rdist + alt | 0.713 | 142.887 | 4.121 | 0.029 |
| exp ~ ralt + rdist + alt | 0.660 | 143.012 | 4.246 | 0.028 |
| exp ~ ralt + rdist + alt | 0.660 | 143.012 | 4.246 | 0.028 |
| exp ~ mlat + ralt + alt | 0.641 | 143.947 | 5.181 | 0.017 |
| exp ~ ralt + and + alt | 0.636 | 144.158 | 5.392 | 0.016 |
| exp ~ mlat + alt + and | 0.624 | 144.731 | 5.965 | 0.012 |
| exp ~ and + ralt + rdist + alt | 0.661 | 145.701 | 6.935 | 0.007 |

AICc, Akaike information criterion for small sample size; Wi, Akaike weight; and, distance to the Andes (km); alt, maximum altitude (m); exp, exposure to global climate change; mlat, maximum latitude (m); ralt, altitudinal range (m); rdist, distributional ranges (100 km²). Bold letter indicate the best possible model.

(and therefore, the climatic tolerance of the species). In summary, our best model shows that species with the narrowest distributional ranges and inhabiting the highest elevations are the most exposed to the effects of global climate change in our study area. It is important to note that all of the geographical models that explain global climate change exposure included the maximum elevation reached by the species as a predictor variable, the most important variable for explaining global climate change exposure.

Our results have important implications for the conservation of the reptiles of Argentina. In this context, range-restricted species, reaching high elevations, should be strongly considered in conservation planning. Sadly, most of the species of the most diverse lineage of reptiles in the study area (Liolaemidae) are expected to be highly exposed to global climate change, given that they inhabit high regions and are micro-endemic in most of the cases (Abdala *et al.* 2012). The great exposure to the effects of global climate change of this diverse clade of reptiles in the study area seems to suggest an important phylogenetic pattern in the exposure to global climate change for these ectotherms (Hof *et al.* 2010; Loyola *et al.* 2014).

The Puna biogeographic region (see Appendix S1) has a great diversity of micro-endemic reptiles reaching high elevations. Presently, this ecoregion is not suitable for intensive anthropogenic uses such as agriculture. For this reason, the degree of human modification and fragmentation in the ecoregion is low, and the species may be able to occupy new climatically suitable spaces in the near future. Nevertheless, these areas (together with most of the Andes in the study area) have a considerable potential for mining. It is essential that mining activities be developed together with adequate conservation policies to ensure the current and potential new habitats of endemic reptiles. Another region harbouring high elevation reptile species is the Yungas. Although in most of this ecoregion common human activities are mostly compatible with reptile conservation (e.g. wood extraction), the transitional zones between Yungas and Chaco are particularly worrisome, where the agricultural frontier is expanding quite rapidly, implying an important constrain for reptile conservation (Nori *et al.* 2013). All these findings should be considered as a part of an integrative conservation plan in order to achieve accurate decisions and policies.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Study area.

Appendix S2. Data records.

Appendix S3. Niche position.

Appendix S4. Niche breadth.

Appendix S5. Phylogenetic relationship between studied species.

Appendix S6. BEMs evaluation.

Appendix S7. Details of Figure 1 of the main text.

Appendix S8. Phylogenetic Generalized Least Square Models.