

Climate change and lizards: changing species' geographic ranges in Patagonia

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Abstract Ectothermic organisms strongly depend on temperature, making them an excellent model to study the impact of global climatic change (GCC). Under global warming, species may be forced to move toward colder environments, such as higher latitudes, higher elevations or both. However, several studies show that responses may vary significantly in different groups of species. Therefore, it is unclear whether species' current distribution range sizes will be affected in future climatic scenarios. In addition to the specific possible effect of range size changes, the potential consequences of distributional range shifts also should be considered. Here, our aim is to assess whether GCC may affect a group of *Liolaemus* lizard species based on their current geographic distribution range size and whether the effect is uniform across all species using species distribution models (SDMs). Our results

show that range boundaries of the fourteen species switch toward higher altitude and latitude in future scenarios. Additionally, there is not a unique pattern in terms of increase or decrease in potential range for lizards in Patagonia in future scenarios. Finally, our results show that the original distribution range size is determinant for the resultant SDMs projections, suggesting that species with a high degree of endemism may be susceptible to a greater impact of GCC.

Keywords Patagonia · Lizards · *Liolaemus* · Species distribution models (SDMs) · Global climate change · Range of distribution

Introduction

During the last century, the global temperature of Earth increased about 0.7 °C, additionally since 1976, the rate of warming is two times higher (IPCC 2007). With the detection of this global climate change (GCC), several studies have documented changes in the structure and dynamics of ecosystems (e.g., Root et al. 2003; Parmesan 2007; Beaumont et al. 2011; Bellard et al. 2012). These changes may critically alter several biological features (see Penman et al. 2010 and citations there), such as the starting and duration of reproductive activity (e.g., Winkler et al. 2002; Pike et al. 2006), offspring sex ratio in reptiles with temperature sex determination (e.g., Janzen 1994; Mitchell et al. 2008), availability of resources (Visser and Both 2005), land and habitat use (Telemeco et al. 2009), survival (Chamaille-Jammes et al. 2006) and distribution (Parmesan et al. 1999; Hughes 2000). It was hypothesized that these potential alterations may lead to changes and loss of biodiversity (e.g., Thomas et al. 2004; Hoegh-Guldberg and

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Bruno 2010; Yang et al. 2011; Bellard et al. 2012; Hanna 2012). Predicting how biodiversity responds to climate change is central for the production of an effective conservation plan based on conceptual and methodological advances (Svenning et al. 2009). Given differing results from numerous studies (e.g., Walther et al. 2002; Araújo et al. 2005; Araújo and Rahbek 2006; Pearson et al. 2006), one of the greatest conceptual challenges is coming to a consensus regarding trajectories of a biota in light of climate change.

Organisms are exposed to constant climate change and respond to these changes using two possible compensatory mechanisms: (a) adaptation to new climatic conditions (either by behavioral or physiological plasticity) or (b) modifying their distribution range to areas with suitable climatic conditions. Failure to use any of these mechanisms will result in populations collapsing or extinction (Henle et al. 2008; Huey et al. 2009, 2010; Sinervo et al. 2010; Gunderson and Leal 2012).

Thus, under a global warming scenario, it is expected that species may be forced to move toward colder environments, such as higher latitudes and/or elevations (Parmesan 1996; Parmesan et al. 1999; Pounds et al. 1999; Thomas and Lennon 1999; Parmesan and Yohe 2003; Wilson et al. 2005), especially if the ability to cope with such change through behavioral and physiological plasticity is not possible or extremely difficult. In this context, it was predicted that future suitable climatic areas will be different, becoming increasingly restricted or too isolated from the current geographic distribution for the species (Hill et al. 2002; Midgley et al. 2002; Williams et al. 2003; Thomas et al. 2004; Wilson et al. 2005). Although it is obvious that widely distributed species are less prone to suffer these problems than species with narrowly restricted ranges, surprisingly, this aspect has not yet been formally tested. Thus, knowing to what the extent species will be affected depending on the current distribution range size is still unknown.

Patagonia is characterized by its harsh climate (strong winds and low winter temperatures) and inhabited by a fauna adapted to this climate. Several previous studies indicate that macroecological patterns of faunal composition of this area is mainly related to temperature (Cussac et al. 2004; Cruz et al. 2005; Fergnani et al. 2010; Bonino et al. 2011; Moreno Azocar et al. 2013; Werenkraut and Ruggiero 2013). Additionally, there is a high degree of endemism in the Patagonian fauna (Ceï 1986; Grigera and Úbeda 1997; Perotti et al. 2005), including the southernmost lizard species on the planet (Ibargüengoytía and Casalins 2007; Ibargüengoytía et al. 2010; Bonino et al. 2011). Recently, climatic variation in this region has been related to global change, for example an increase in wet periods, higher rainfall in winter periods, thermal

warming trends and glacier retreat (Thompson and Solomon 2002; Solomon et al. 2007). Although it is recognized that climatic fluctuations may affect ecosystems, communities and organisms (Parmesan et al. 2000; Meserve et al. 2003), our knowledge of environmental factors affecting the Patagonian fauna is limited.

Patagonia is a vast region in the southern cone of South America. It has a complex geological history subjected to a variety of events, such as the uplifting Andes, volcanic extrusions, marine transgressions and climatic oscillations with periods of glacial advances and retractions (Rabassa et al. 2005; Rabassa 2008). Climatically, this region is defined as temperate or cold-temperate (Paruelo et al. 1998). Mean annual temperature ranges from 12 °C in the northeast to 3 °C in the southern region (Rusticucci and Barrucand 2004); thus, Patagonia is a climatically challenging ecosystem for ectotherms.

Here, we propose to study the potential effects of GCC on fourteen species of Patagonian *Liolaemus* lizards. This species-rich genus has more than 240 described species (Abdala and Quinteros 2014) and occupies a wide variety of environments, from the Atlantic to the Pacific and from sea level to elevations above 5,000 masl (Hellmich 1951; Ceï 1986, 1993; Etheridge and Espinoza 2000; Abdala 2007). *Liolaemus* is one of the most conspicuous groups of small vertebrates of Patagonia and is considered an important genus for conservation (Corbalán et al. 2011). Lizards, as ectotherms, are particularly susceptible to climate changes because their physiology is strongly linked to ambient temperature (e.g., Huey and Stevenson 1979; Huey 1982; Deutsch et al. 2008; Kingsolver 2009). We studied the potential responses (trajectories) in relation to GCC using SDMs on fourteen *Liolaemus* species from Patagonia representing nearly 20 % of the Patagonian *Liolaemus* species (Abdala et al. 2012). We also considered distribution range size as a factor to elucidate whether species with restricted geographic range sizes are more vulnerable to GCC than species with broad or extended geographic range sizes. In addition, our tests incorporate phylogenetic information on these species.

We selected species corresponding to three different *Liolaemus* clades in the region. We chose these species because: (a) there are three groups of at least four species corresponding to closely related species within each of the studied clades and (b) the set of species show variable geographic ranges (within and among the three clades). Finally, we consider the direction and magnitude of responses, evaluating and comparing vulnerability of these species. Additionally, we discuss some ecological and biogeographical aspects that could be related to the patterns of distribution and the projected shifts.

Materials and methods

The geographic area of this study is located on continental Patagonia of Argentina corresponding to the provinces of Neuquén, Río Negro, Chubut and Santa Cruz. The geographic boundaries of this region are the Atlantic Ocean to the East, the Magellan strait to the South, large rivers (Neuquén and Colorado) to the North and the Andes to the West.

Here, we study fourteen species corresponding to three different *Liolaemus* clades; (1) *L. elongatus*, *L. coeruleus*, *L. petrophilus* and *L. kriegi* (*L. chiliensis* group); (2) *L. kingii*, *L. baguali*, *L. escarchadosi*, *L. hatcheri*, *L. lineomaculatus* and *L. sarmientoi* (from the *L. lineomaculatus* section) and (3) *L. fitzingerii*, *L. xanthoviridis*, *L. boulengeri* and *L. rothi* within the *L. boulengeri* series (sensu Lobo et al. 2010).

We obtained data on species geographic distribution (species occurrence data) from detailed bibliographic surveys (Morando et al. 2003; Avila et al. 2006; Breitman et al. 2011), museum specimens in herpetological collections and georeferenced capture sites during our field trips. The herpetological collections visited were as follows: Herpetological collection of the Museo de Ciencias Naturales de la Universidad Nacional de Salta (MCN); Instituto de Herpetología de la Fundación Miguel Lillo (FML), Tucumán; Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA-CONICET), Mendoza; Instituto de Biología Animal-Facultad de Ciencias Agrarias (IBA-UNCuyo), Mendoza; Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN), Buenos Aires; Museo de Ciencias Naturales de La Plata (MLP), La Plata; Museo de Historia Natural de San Rafael (MHNSR), Mendoza and Universidad Nacional de San Luis (herpetological collections of Dr. J.M. Cei), San Luis.

Data were filtered by removing any unreliable locality or uncertain species determination. We obtained a total of 537 species-presence localities under study as follows: 139 for *L. elongatus*, 12 for *L. coeruleus*, 86 for *L. petrophilus*, 54 for *L. kriegi*, 37 for *L. kingii*, 9 for *L. baguali*, 27 for *L. escarchadosi*, 11 for *L. hatcheri*, 28 for *L. lineomaculatus*, 21 for *L. sarmientoi*, 61 for *L. fitzingerii*, 23 for *L. xanthoviridis*, 15 for *L. boulengeri* and 14 for *L. rothi*. Some species have a restricted geographic range; for this reason, we only have a small number of localities recorded for them.

We used 20 environmental variables (19 bioclimatic variables and elevation) obtained from the global meteorological database Worldclim (<http://www.worldclim.org/>), at a 1 km × 1 km resolution. All layers were clipped to the study area. Despite this, the use of a large set of predictor variables involves a risk of overfitting when working with more than one species; it is assumed that potential errors

are constant in all of them (Munguía et al. 2008). Furthermore, Elith and Leathwick (2009) argue that using MaxEnt (Phillips et al. 2006) results are more stable using a greater number of variables. Thus, we did not remove any variable a priori.

According to the Intergovernmental Panel on Climate Change, Special Report on Emission Scenarios (IPCC SRES 2000), several future climatic scenarios depending on demographic, socioeconomic and technological developments might be expected. We consider two different scenarios of CO₂ emissions (A1B and B2A) for 2080 in order to represent different possible situations. These data were generated by the widely used Atmosphere–Ocean Global Circulation Model (AOGCM), Hadley Centre for Climate Prediction and Research's General Circulation Model (HadCM3) from scenarios developed by IPCC's Fourth Assessment Report (IPCC 2007). AOGCMs have different equilibrium climate sensitivity values ranging from 2.1 to 4.4 °C. Equilibrium climate sensitivity is the annual mean surface air temperature change experienced by the climate system after it has attained a new equilibrium in response to a doubling of CO₂ concentration and is within the range of all AOGCMs available from IPCC (2007).

Current and future distributions were modeled using MaxEnt version 3.3.3e (Phillips et al. 2006). MaxEnt proceeds only with presence records, and therefore, absence data are not required. In addition, MaxEnt runs with a small number of presence data points (Hernandez et al. 2006; Phillips et al. 2006); this is particularly relevant when working with rare species and low record numbers (Elith et al. 2006).

To evaluate performance of each model, we used the area under the curve (AUC) of the receiver operating characteristics (ROC) curve. AUC shows the proportion of correctly and incorrectly classified predictions in a range of probability thresholds (Pearce and Ferrier 2000). This value is interpreted as the probability that a random point positive (presence) or negative (absence) is correctly classified by the model (Phillips et al. 2006), meaning that AUC values are positively related to the predictive ability of the model (Manel et al. 2001). AUC values range between 0 and 1; we considered an AUC value of 0.75 as the critical threshold for accepting a model as valid (Elith 2002; Elith et al. 2006).

Finally, the projections obtained with MaxEnt were reclassified to convert the continuous output in a map of presence–absence (0–1). The general criterium for reclassifying was to use the highest cutoff threshold (presence–absence) without generating omissions of known localities for the species in the final map; in this way, we avoid overestimation of areas without omitting known localities in the projections.

From MaxEnt projections, we obtained (a) the total predicted area (km²) per species (the total potential distribution area after making the reclassification of MaxEnt outputs); (b) northern and southern latitudinal limits (the extreme latitudes of the projected distribution); and (c) altitudinal limits (the higher and lower altitude of the projected distribution). Then, departing from these parameters, we calculated for each species and under each of the scenarios: (1) stable area: the portion of the original geographic area remaining with suitable climatic conditions, corresponding to the overlap area between future and present maps of potential distributions; (2) the new potential area: the expansion of area (km²) with suitable climatic conditions under the new conditions (obtained by subtracting the stable range to the future potential area); and (3) the proportion of original area lost: the portion of the original geographic area that in the future will lose suitable climatic conditions (obtained by subtracting the future potential range at the original potential range). To assess magnitude of response from climate change, we used two approaches, correlations between the parameters mentioned above and amplitude of distribution range of the different species, and ANOVAs between these parameters categorizing species in small or wide amplitude of distribution range.

Because species share a phylogenetic history, data for the focal species are not independent (Martins 1996). For this reason, we used phylogenetically informed statistics (Felsenstein 1985; Martins 1996); in this case, we calculated independent contrasts (Felsenstein 1985; Harvey and Pagel 1991; Garland et al. 1993) for correlations. We compared whether species with smaller distribution ranges (less than 80,000 km²) showed differences from species with broad distribution ranges (more than 100,000 km²) using a phylogenetically based ANOVA. For this purpose, we used the module *phyl.anova* from the *Phytools* package (Revell 2012) developed in R (R Development Core Team 2011). The criterion to divide species in two categories was arbitrary and only used to define two groups (smaller than 80,000 km² and broader than 100,000 km² to avoid overlapping). Additionally, original proportion data were transformed with the arcsin square root of the value (those set of data where proportions were higher than one we divided the complete set by 10). These analyses were based on a phylogenetic tree inferred from mitochondrial DNA sequences spanning the region ND1 to COI (Fig. 1). These data were sequenced and aligned using the molecular protocols and alignment structures described in Schulte et al. (2000). The aligned DNA sequences dataset for species included in the sample is available in TreeBASE (<http://purl.org/phylo/treebase/phyloids/study/TB2:S13386>). The phylogenetic tree was estimated from a mixed model, a priori partitioned analysis using maximum likelihood (ML)

for the fourteen *Liolaemus* species. We used the PDAP 1.15 module (Midford et al. 2003) in Mesquite 2.74 (Maddison and Maddison 2010) to run correlations between independent contrasts forced to the origin (Garland et al. 1992).

Results

We found AUC values greater than 0.95 for all species (Table 1), indicating high reliability of the models.

The projected distributions for the fourteen species studied here are summarized in Table 2 (and supplementary material), where we show projections under current climatic conditions and both future emission scenarios, A1B (A1) and B2A (B2) corresponding to 2080.

The magnitude of change in distribution range was highly variable between the species studied here (see Table 3). Results obtained varied from species with a range of stable distribution near 100 % (e.g., 97.9 % *Liolaemus elongatus* for B2 scenario, *L. fitzingerii* 94.4 % for A1 scenario) to species with stable range equal to zero (e.g., *L. baguali*, 0 % for both A1 and B2 scenarios). In general, the variation of stable projected areas in relation to the original area modeled shows a positive and significant relationship between both scenarios (scenario A1 $r^2 = 0.835$, slope = 0.863, $p < 0.001$; scenario B2 $r^2 = 0.918$, slope = 0.921, $p < 0.001$, Table 4). With respect to the lost area, the observed variation ranged between 2.1 % (e.g., *L. elongatus* 2.1 % for B2 scenario, *L. fitzingerii* 5.6 % for A1 scenario) and 100 % (i.e., *L. baguali*, 100 % for both A1 and B2 scenarios, *L. coeruleus* 90 % for B2 scenario); however, this variation was not significant with respect to the original modeled area. The new area modeled was highly variable too, for some species exceeded 100 % (e.g., *L. xanthoviridis* 241.5 %, *L. boulengeri* 139.8 %, both for A1 scenario), and others had values near zero (e.g., *L. coeruleus* 0 and 1 % in A2 and B2 scenarios, respectively, *L. escarchadosi* 0 % in both A1 and B2 scenarios, *L. sarmientoi* 0.2 % in both A1 and B2 scenarios). In the case of the new areas, the relationship observed considering the original modeled area initial point was negative and significant (the larger the original area modeled, the smaller the new area, Table 4). These partial expansions (new areas) and retractions (lost areas) are linked to movements in latitudinal range, northern latitudinal limit and higher altitudinal limit (Table 5), southern latitudinal limit and lower altitudinal limit modeled for future scenarios showed no relationship with the original limits (Table 5).

In the context of these range distribution shifts, the percentage of known localities falling outside the projected

Fig. 1 Phylogenetic tree of *Liolaemus* used in this study inferred from mitochondrial DNA sequences spanning the region ND1 to COI

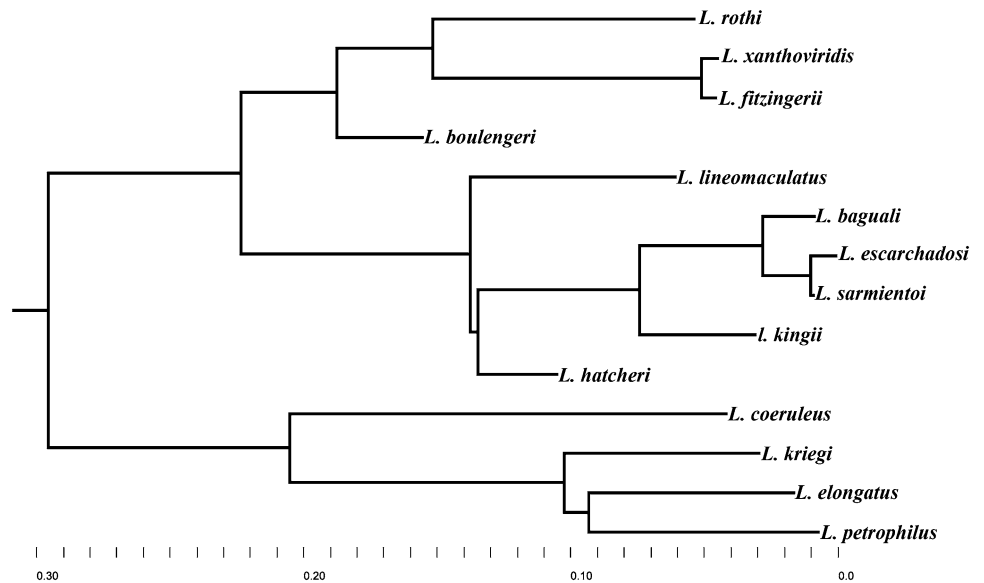


Table 1 Models validation

Species	AUC-model \pm DS	AUC-test \pm DS
<i>Liolaemus elongatus</i>	0.986 \pm <0.001	0.979 \pm 0.004
<i>L. coeruleus</i>	0.998 \pm <0.001	0.998 \pm 0.001
<i>L. petrophilus</i>	0.976 \pm 0.002	0.965 \pm 0.011
<i>L. kriegi</i>	0.992 \pm 0.001	0.980 \pm 0.012
<i>L. kingii</i>	0.988 \pm 0.002	0.973 \pm 0.017
<i>L. baguali</i>	0.992 \pm <0.001	0.993 \pm 0.003
<i>L. escarchadosi</i>	0.985 \pm 0.001	0.978 \pm 0.004
<i>L. hatcheri</i>	0.990 \pm 0.002	0.984 \pm 0.005
<i>L. lineomaculatus</i>	0.977 \pm 0.003	0.949 \pm 0.010
<i>L. sarmientoi</i>	0.985 \pm 0.003	0.979 \pm 0.007
<i>L. fitzingerii</i>	0.982 \pm 0.002	0.968 \pm 0.027
<i>L. xanthoviridis</i>	0.997 \pm 0.001	0.994 \pm 0.005
<i>L. boulengeri</i>	0.997 \pm <0.001	0.996 \pm 0.002
<i>L. rothi</i>	0.977 \pm 0.011	0.969 \pm 0.014

Values of AUC/ROC for training and testing each of the algorithms for each species

future areas varied considerably between species with small or broad geographic ranges (Table 6). In some cases, none of the original localities fell outside the projected areas for the future (e.g., *L. fitzingerii* 0 % of omitted localities for both A1 and B2 scenarios), while for other species, all original localities (e.g., *L. baguali* and *L. hatcheri*) fell out of the projected areas (Table 3).

The phylogenetically based ANOVA between species grouped in small and broad geographic ranges shows differences in the projected proportion of stable area (broadly distributed species show a larger percentage stable; Table 6) and the proportion of lost area (restrictedly

distributed species lost a higher percentage of the original area), but not when compared the proportion of new areas projected (Table 6), in the three cases under both 2080 scenarios. Additionally, the percentage of localities out of modeled range showed that for species with restricted distributions, more localities fall out of the new modeled range (Table 6).

Finally, in general, there is not a great difference between the scenarios modeled (see Tables 4, 5); only higher altitudinal limit, latitudinal range and the new modeled areas showed differences between both scenarios.

Discussion

Predicting distributional changes of organisms is a key question in the face of constant climate change, and great effort has been devoted to understanding these changes in recent years. Our results show that species responses to changes in environmental climatic conditions are complex and factors contributing to the evolution of home ranges are difficult to understand given their complexity (Tucker et al. 2014). In our dataset, we did not observe a unique pattern for *Liolaemus* lizards in Patagonia, despite the reliability of our AUC values (Thuiller et al. 2003) and controlling for phylogeny.

Previous general studies documented movement in boundaries of different species toward higher altitude and latitude (e.g., Hickling et al. 2006; Thomas et al. 2006; Harsch et al. 2009; Thomas 2010), and in some cases, these movements may be determined by topography, continental limits or mountain biogeography as well as the species pool

Table 2 Potential distribution area, latitudinal and altitudinal limits for *Liolaemus* species studied

Species	Scenario	PR (km ²)	NLL	SLL	LR	LAL (masl)	HAL (masl)
<i>L. elongatus</i>	Current	163,398	36.1° S	47.2° S	11.1°	210	3,229
	A1	170,400	36.1° S	47.4° S	11.3°	190	3,254
	B2	201,501	36.1° S	47.6° S	11.5°	192	3,238
<i>L. coeruleus</i>	Current	44,348	36.1° S	40.6° S	4.5°	441	4,658
	A1	6,826	38.2° S	39.7° S	3.4°	724	4,658
	B2	4,888	36.2° S	39.2° S	3.1°	793	4,658
<i>L. petrophilus</i>	Current	359,631	36.6° S	49.5° S	12.9°	7	2,300
	A1	168,160	36.6° S	48.7° S	12.1°	300	2,390
	B2	223,820	36.4° S	49.4° S	13°	181	2,267
<i>L. kriegi</i>	Current	145,380	36.1° S	46.8° S	10.7°	205	2,598
	A1	79,868	36.1° S	47° S	10.9°	748	3,225
	B2	123,147	36.1° S	47.3° S	11.2°	481	3,084
<i>L. kingii</i>	Current	108,842	42.2° S	51.2° S	9.0	0	1,331
	A1	178,346	45.5° S	52.2° S	6.8	0	1,724
	B2	132,249	45.0° S	52.0° S	7.0	0	1,206
<i>L. baguali</i>	Current	5,310	48.6° S	50.5° S	3.4°	188	1,200
	A1	141	47.1° S	47.3° S	0.2°	0	110
	B2	16	47.1° S	47.2° S	0.1°	0	32
<i>L. escarchadosi</i>	Current	67,546	46.2° S	52.3° S	6.1°	0	1,031
	A1	0	–	–	–	–	–
	B2	3,527	50.1° S	51.3° S	1.2°	138	660
<i>L. hatcheri</i>	Current	49,943	46.6° S	50.8° S	4.2°	0	2,764
	A1	240	47.1° S	47.3° S	0.2°	0	110
	B2	2,506	47.1° S	49.4° S	2.3°	0	985
<i>L. lineomaculatus</i>	Current	245,222	39.2° S	52.3° S	13.1°	0	1,616
	A1	81,443	41.1° S	52° S	10.9°	38	1,654
	B2	172,304	40.2° S	52.1° S	11.9°	0	1,634
<i>L. sarmientoi</i>	Current	97,055	47.6° S	52.3° S	4.7°	0	1,018
	A1	23,346	49.6° S	52° S	2.4°	39	878
	B2	46,824	48.3° S	52.3° S	4°	0	858
<i>L. fitzingerii</i>	Current	216,312	42° S	50.6° S	8.6°	0	1,256
	A1	254,951	42° S	51.2° S	9.2°	0	1,453
	B2	265,007	42.1° S	51.4° S	9.3°	0	1,231
<i>L. xanthoviridis</i>	Current	55,782	41.6° S	46° S	4.4°	0	622
	A1	159,940	42.7° S	51.8° S	9.1°	0	1,033
	B2	121,434	42° S	51.5° S	9.5°	0	1,061
<i>L. rothi</i>	Current	164,956	36.1° S	45.2° S	9.1°	368	4,658
	A1	109,161	36.1° S	44.2° S	8.1°	511	4,658
	B2	154,581	36.1° S	45.1° S	9°	367	4,658
<i>L. boulengeri</i>	Current	34,357	38.8° S	45.4° S	6.6°	126	1,546
	A1	54,788	41.2° S	51.6° S	10.4°	108	1,707
	B2	64,587	38.9° S	52° S	13.1°	76	1,792

Projections for current conditions and year 2080 considering different CO₂ emission scenarios for future (A1 and B2) according at Intergovernmental Panel on Climate Change, Special Report on Emission Scenarios (IPCC SRES), to which we refer to as A1 and B2, respectively PR potential range, NLL N latitudinal limit, SLL S latitudinal limit, LR latitudinal range, LAL lower altitudinal limit, HAL higher altitudinal limit

(Menéndez et al. 2014). Our results show that, for example, *Liolaemus coeruleus*, *L. kriegi* and *L. petrophilus* models, project a shift toward higher elevation for their lower

altitudinal limits, but not their upper limits, simply because of a topographic constraint. These displacements of inferior altitudinal limits to higher altitudes when upper limits

Table 3 Potential shift in distribution range of species studied

Species	Scenario (2080)	Stable area (%)	Lost area (%)	New area (%)	Localities omitted (%)
<i>L. elongatus</i>	A1	86.6	13.4	17.6	1.4
	B2	97.9	2.1	25.4	0.7
<i>L. coeruleus</i>	A1	15.4	84.6	0	26.7
	B2	10.0	90.0	1.0	86.7
<i>L. petrophilus</i>	A1	41.3	58.7	5.5	24.4
	B2	54.2	45.8	8.1	15.1
<i>L. kriegi</i>	A1	45.5	54.5	9.5	9.4
	B2	69.8	30.2	14.9	5.7
<i>L. kingii</i>	A1	63.1	36.9	100.8	23.7
	B2	76.0	24.0	45.5	5.3
<i>L. baguali</i>	A1	0	100.0	2.7	100
	B2	0	100.0	0.3	100
<i>L. escarchadosi</i>	A1	0	100.0	0	100
	B2	5.2	84.8	0	88.9
<i>L. hatcheri</i>	A1	0.5	99.5	0	100
	B2	4.0	96.0	1.1	100
<i>L. lineomaculatus</i>	A1	30.0	70.0	3.2	55.6
	B2	66.1	33.9	4.1	18.5
<i>L. sarmientoi</i>	A1	23.9	76.1	0.2	81.0
	B2	48.0	52.0	0.2	38.1
<i>L. fitzingerii</i>	A1	94.4	5.6	23.4	0
	B2	92.7	7.3	29.8	0
<i>L. xanthoviridis</i>	A1	45.2	54.8	241.5	91.3
	B2	54.9	45.1	162.8	34.8
<i>L. rothi</i>	A1	56.4	43.6	9.7	35.7
	B2	79.6	20.4	14.1	0
<i>L. boulengeri</i>	A1	19.6	80.4	139.8	73.3
	B2	57.3	42.7	130.7	0

Table 4 Response sensitivity of variables (stable area, lost area and new area) according to the original range amplitude

	r^2	Slope	p
Stable A	0.835	0.863	<0.001
Lost A	0.112	0.136	0.241
New A	0.439	-0.319	0.009
Stable B	0.918	0.921	<0.001
Lost B	0.089	0.083	0.298
New B	0.25	-0.093	0.068

Summary of correlation coefficients (r^2) passed through the origin, slope and p values between stable from independent contrasts of original data transformed to arcsin (square root value + 10), lost and new area and original modeled area for both scenarios for 2080 (A1 and B2). Significant relations are in bold

remained unchanged may be related to the loss of potential suitable area. These three species with similar trends also are closely related species (all belong to the *L. chiliensis*

Table 5 Response sensitivity according to the original latitudinal, altitudinal limits and latitudinal range

	r^2	Slope	p
NLL versus NLL A1	0.57	0.696	0.002
SLL versus Sll A1	0.031	0.145	0.565
LatR versus LatR A1	0.398	0.524	0.021
Lalt versus Lalt A1	0.252	0.692	0.081
Halt versus Halt A1	0.314	0.582	0.046
NLL versus NLL B2	0.324	0.546	0.033
SLL versus Sll B2	0.086	0.242	0.306
LatR versus LatR B2	0.123	0.334	0.217
Lalt versus Lalt B2	0.251	0.693	0.067
Halt versus Halt B2	0.461	0.617	0.007

Response sensitivity (based on independent contrasts of transformed original variables) according to the original latitudinal limits (LL; *N* northern, *S* southern), altitudinal limits (alt; *L* lower, *H* higher) and latitudinal range (LatR) for each scenario modeled for 2080 (A1 and B2). r^2 , slope and p , significant relations are in bold

Table 6 Response sensitivity between species with small (RDR%) and large geographic ranges (BDR%), distribution changes expressed in percentages

	F	p	BDR%	RDR%
Stable A	14.969	0.001	55.15	13.45
Lost A	8.626	0.002	44.85	86.55
New A	0.195	0.633	21.2375	64
Loc A	12.858	0.002	28.9	81.88333
Stable B	17.021	0.001	73.0375	21.9
Lost B	13.034	0.001	26.9625	76.43333
New B	0.117	0.757	17.7625	49.31667
Loc B	9.115	0.002	10.425	68.4

Phylogenetically based ANOVAs between species with small and large geographic ranges of the percentage [data transformed to arcsin (square root of value + 10)] of stable, lost, new areas and percentage of localities out of modeled range (Loc), corresponding to both scenarios (A1 and B2) modeled for 2080. F and p values are in bold when differences were significant

group) which emphasizes the importance of careful consideration of the species pool (Menéndez et al. 2014). Regarding continental limits, our projections clearly show that continental barriers act as a limit to a southward shift for *L. lineomaculatus* and *L. sarmientoi* that belong to the most austral clade of the world; these southward shifts of north latitudinal limits when southern limits remain unchanged are related to loss of area. These observations in particular highlight that not only the topographic altitudinal limits, but also continental limits (interface of continent and sea) should be considered when the vulnerability of species facing climate change is evaluated. In our case, the southern continental boundary is a factor unavoidable for

species of austral distribution and may be a determinant of these species' distributions in the future.

A recent global study suggests that 19.1 % of the world's terrestrial reptiles are threatened (Böhm et al. 2013). However, to date, there is no consensus on the impact of GCC as a major threat for reptiles. For example, some projections suggest that local extinctions may reach 39 % and at a global scale 20 % species loss by 2080 (Sinervo et al. 2010). On the other hand, Huey and Tewksbury (2009) argue that the impact will depend on the latitudinal occurrence, negatively affecting tropical environments more markedly. However, Araújo et al. (2006) mentioned that terrestrial vertebrate ectotherms seem to be more sensitive to climatic cooling than warming, showing under the latter scenarios an increase in potential range for a large number of species. Our study shows that four species (*L. fitzingerii*, *L. xanthoviridis*, *L. boulengeri* and *L. elongatus*) may increase their area with suitable climatic conditions, whereas most (*L. coeruleus*, *L. petrophilus*, *L. kriegi*, *L. escarchadosi*, *L. hatcheri*, *L. lineomaculatus*, *L. sarmiento* and *L. baguali*) may experience a decrease in these areas and may be seriously affected.

Lizards show limited dispersal ability (e.g., Spiller et al. 1998; Losos and Spiller 1999) and due the rate at which climate changes are projected, it is unlikely that species may move to new locations with equivalent characteristics to their original location. However, it should be noted that these scenarios are projected or considered in absence of possible compensatory mechanisms besides distribution range shifts. For example, body size may be related to the ability of escaping the potential effects of GCC, and it is known that for mammals body size and flexible activity periods is important for predictions of climate change consequences (McCain and King 2014). Additionally, other responses to climate change involve changes in body size, such as recently observed in amphibians (Caruso et al. 2014). Moreover, body size, physiology and behavioral plasticity of habitat use are among the critical aspects for considering if a species is threatened or not by GCC (Simmons 2014; Sunday et al. 2014). Thus, to predict extinction more accurately, we need an empirical validation associated with macroclimatic factors along with biophysical models (Kearney et al. 2009; Sinervo et al. 2010). Incorporating information on ecophysiological reaction norms can help us test the accuracy (or inaccuracy) of the SDMs method. In this context, mechanistic models can be useful, but the information available for many species remains scarce to apply those models. Furthermore, increases of extreme temperatures should not be considered as the only proximal cause of extinction *per se* as there may be other aspects linked to GCC (e.g., water and prey availability, Cahill et al. 2013). Additionally, we should consider the ability of species to tolerate stress associated with abiotic factors.

Most climate projections suggest that changes in the next century will be greater in speed and magnitude than over the last 10,000 years (Houghton et al. 2001; IPCC 2007). Those species without the ability to effectively disperse to new, remote areas or that tolerate or adapt to the new climatic conditions may be seriously threatened by the loss of potential range. However, we have to keep in mind that during the last glaciations, many *Liolaemus* lizard species apparently coexisted with climate change (e.g., Avila et al. 2006; Breitman et al. 2011); nonetheless, the possibility of large geographic scale dispersal events in very short time periods remains controversial (Araújo et al. 2006 and references therein). Thus, other aspects, such as plasticity, tolerance or adaptation to new conditions, may have played a role in the persistence of these lizards in Patagonia.

The particular case of future projection of *Liolaemus xanthoviridis* shows an important southward expansion (Figure 3 in supplementary material) to a clearly disjunct area relative to its original one. Additionally, the speed of climatic changes, presence of barriers and the potential dispersal ability for a 100 mm SVL lizard make it unlikely this species will occupy this distribution (Davis et al. 1998; Thuiller 2004; Araújo and Guisan 2006; Thuiller et al. 2008; Engler and Guisan 2009). Another interesting aspect is that the projections for *L. xanthoviridis* are closely allied to those observed for its sister species, *L. fitzingerii*, and highlights the importance of considering phylogenetic relatedness in climatic predictive studies. This case may be the result of niche conservatism (Wiens and Graham 2005) as observed previously by Buckley et al. (2010) for the *Sceloporus undulatus* species complex of North America.

Our results show, at least for this sample of Patagonian lizard species, that the original distribution range size is important for the resultant projections of species distribution models. These results add evidence to the idea that species with a high degree of endemism may be subject to a greater impact under the GCC, consistent with suggestions of other authors (e.g., Hulme 2005; Araújo et al. 2006). However, our results are in conflict with those of Overgaard et al. (2014) who found that tropical *Drosophila* species with narrower ranges in Australia will have similar proportional reduction in distributional range under future warming compared to widespread *Drosophila* species. Another aspect that may influence range size is climate wherein the case of ectothermic animals shows a clear relationship, such as hylid frogs (Chejanovski and Wiens 2014).

Future distribution projections for *Liolaemus* lizards in Patagonia do not follow a unique pattern, most likely the result of a number of complex interactions and factors, such as the rate at which climate change occurs, geographic scale, presence of geographic barriers, species dispersal

ability, physiological tolerance and phylogeny. Furthermore, when considering the impact of GCC on ectotherms, we should expect that animals are not “prisoners” of climate change, and there are alternatives, for example, behavioral adjustments (thermoregulation) to offset the impact or even sometimes take advantage of it (Bogert 1949; Kingsolver and Watt 1983; Huey et al. 2003; Huey and Tewksbury 2009). In addition, changes in phenology may be a direct response to climate change diminishing the effects of climatic variation and consequently avoiding population collapse (Kearney et al. 2009; Rugiero et al. 2013). We must keep in mind that some of these species (or their direct ancestors) have occupied this region for more than 10,000 years, with estimated clade ages of the groups studied here ranging from 18 to 5 million years old (see Schulte et al. 2000; Fontanella et al. 2012; Schulte 2013) and survived several climatic changes over the last ice age (e.g., Avila et al. 2006). Additionally, evidence suggests that during the late Pleistocene climatic changes occurred at a rate similar to the present or even faster, with relatively few recorded extinctions along the continents for that period (Hof et al. 2011). This suggests that many species existing today (or their ancestors) may have survived rapid climate change events in the past and we must reconsider the potential impact of projected climate change for the next century. Behavioral plasticity or adaptation to resist such changes may have played an important role in the past, and clearly many questions regarding impact of climate change on species in the future still remain unresolved.

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