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Impact of climate change on the distribution of a giant land snail from South America: predicting future trends for setting conservation priorities on native malacofauna

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Abstract Many land snails are vulnerable to climate change as a consequence of small distribution ranges and poor dispersal. South America is a diverse region in terms of land snail fauna, but studies about the impacts of climate change on molluscan biodiversity are virtually nonexistent. Bioclimatic models provide an important tool to assess how habitat suitability may change in a warming planet. In this study, we examine potential impacts of climate change on a giant land snail (*Megalobulimus sanctipauli*) from the Atlantic Forest to predict future shifts in its potential distribution, and to identify protected areas that may contain suitable habitat for setting conservation priorities. Using a maximum entropy algorithm, we modeled the species' potential distribution across South America under current climatic conditions and projected the results onto two climate change scenarios for two time frames. A 2.17 % of South America on the Atlantic Forest was predicted to be currently suitable for the species, comprising the border area among Argentina, Brazil and Paraguay. Prognosis of future distribution showed a trend to a northern retraction, but a southern expansion of current potential range. More than 150 protected areas were identified to contain climatically suitable habitat for the species, but on the less optimistic outlook only ~1545 km^2 of protected areas (0.009 % of South America) would remain suitable for the species by the end of the century. Our findings are expected to improve understanding of climate change impacts on native giant land snails and to contribute in conservation efforts on this malacofauna.

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1 Introduction

Climate change is recognized as one of the major drivers of biodiversity changes across the globe. Some of the documented effects of climate change on biodiversity during the 20th century include alterations in the distribution, phenology, and increase in extinction risk of many species (Vale et al. 2009 and references therein). A rapid and greater climate change has been predicted for the 21st century, which is expected to affect all the levels of biodiversity, from organisms to biomes (Cordellier et al. 2012; Bellard et al. 2012). Moreover, a growing body of data indicates that climate change will be one of the major drivers of species extinction in this century (Thomas et al. 2004; Foden et al. 2008).

Five trait groups associated with extinction risk due to climate change form the basis of IUCN's criteria to assess species susceptibility to climate change (Foden et al. 2008): a- habitat specialization, b- narrow environmental tolerances, c- dependence on specific environmental triggers, d- dependence on interspecific interactions, and e- poor ability to disperse to or colonize a new range. The latter trait group has been pointed out as particularly important for those species with low dispersal rates that are unlikely to migrate fast enough to more suitable environmental conditions, such as land snails (Foden et al. 2008; Kramarenko 2014). Thus, because of small distribution ranges and poor dispersal, many land snails will face elevated extinction risk as their habitats become exposed to substantial climatic changes (Foden et al. 2008; Sen et al. 2012).

South America is a diverse region in terms of land snail fauna, harboring high species diversity and endemism (Fernández 1973; Quintana 1982; Salgado and Coelho 2003; Ramírez et al. 2003; Simone 2006; Breure and Romero 2012; Gutiérrez Gregoric et al. 2013). Among the most distinctive elements of malacofauna of South America are the species of the endemic genus *Megalobulimus* Miller, 1878. This genus includes the largest land snails of the continent, many of which are tied to the rich cultural heritage of South America (Eggers et al. 2011; Jaramillo Roldán et al. 2014). *Megalobulimus* are mostly nocturnal snails that have been little-studied in the wild, including few data on their distributional ranges. Most of the species within the group occur in relatively small populations, with individuals mostly hidden in the soil or under leaf litter (Hylton Scott 1939; Bequaert 1948; Miranda et al. 2015). These giant snails are of great conservation concern because many species are endangered (Santos et al. 2013). The synergistic effect of life history traits such as long lifespan, low reproductive potential, late reproductive maturity, and limited vagility (Miranda et al. 2015 and references therein) reduce the capacity for population recovery, and any disturbance in habitat requirements and/or life cycle represents a potential threat. At present, several of these snails are listed as threatened due to habitat loss by anthropogenic activities (Agudo-Padrón 2011; Santos et al. 2013; IUCN 2014; Miranda et al. 2015). In addition, in order to focus attention on the conservation of the poorly known land snails of the Atlantic Forest, especially the almost completely unknown microsnails, some species of *Megalobulimus* have been recently proposed as umbrella and flagship species (Santos 2011).

In recent years, the knowledge about the possible impacts of climate change over South America has markedly increased (Vale et al. 2009). However, studies about the effects on molluscan biodiversity are virtually nonexistent and impacts on giant land snail fauna remain unexplored. In this context, species distribution models (SDMs, also known as bioclimatic models and ecological niche models) constitute important tools to predict future changes in the species geographic ranges, and are currently the most widely used approaches to examine potential impacts of climate change on biodiversity (Jeschke and Strayer 2008; Franklin et al. 2013; Vogler et al. 2013).

Here, we investigate potential impacts of climate change on a giant land snail by modeling the potential distribution of *Megalobulimus sanctipauli* (Ihering and Pilsbry, 1900) across its known distributional range in South America, under current and future climatic conditions. *M. sanctipauli* is known to inhabit the Atlantic Forest, and living specimens were recently confirmed to occur in the southernmost areas of this forest (Fig. 1; Beltramino et al. 2012; Beltramino 2013; Gutiérrez Gregoric et al. 2013). This species is being severely impacted by human activity due to habitat loss and environmental degradation (Di Bitetti et al. 2003; Bonard et al. 2012). An additional threat to this snail today is from control programs being developed in Argentina, Brazil and Paraguay against invasive species, specifically the giant African snail *Achatina fulica* Bowdich, 1822 (Fischer and Costa 2010; Gutiérrez Gregoric et al. 2013), as local populations of *M. sanctipauli* are being reduced because their individuals are often confused with those of the invasive snail.

Our main goals were to determine: a- the potential distribution of *M. sanctipauli* in South America under current climatic conditions; b- the areas that are likely to be most affected by climate change in different time slices and under different climate change scenarios; and c-

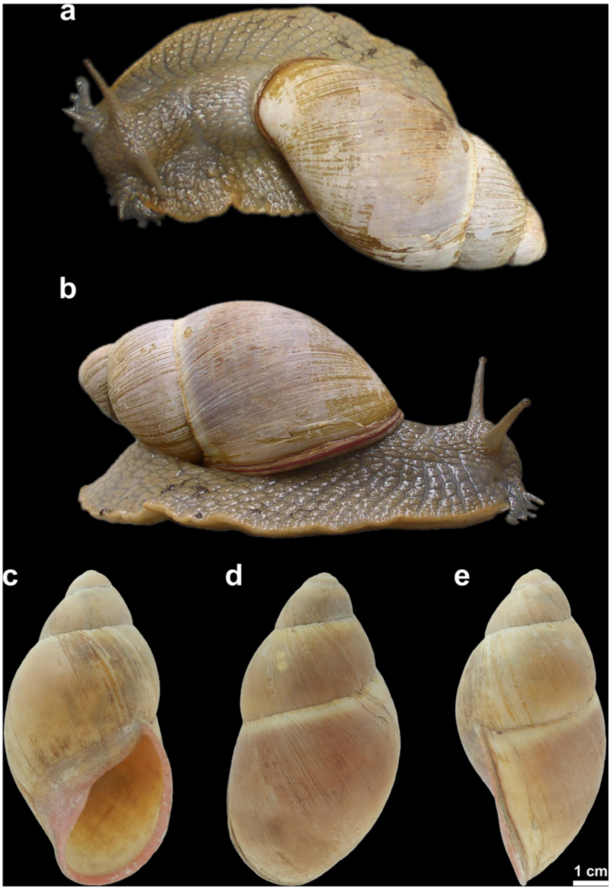

Fig. 1 Adult specimen of *Megalobulimus sanctipauli* from Puerto Iguazú city, northeastern Argentina (25°35′47″S, 54°35′26″W). **a**, **b** living specimen: **a** dorsal, and **b** lateral view. **c**-**e** shell views: **c** frontal, **d** dorsal, and **e** lateral view

protected areas that contain climatically suitable habitat at present and future for setting conservation priorities and research in this species. Our findings are expected to improve understanding of the effect of climate change on native giant land snails.

2 Materials and methods

2.1 Study area and species records

Historical distribution of *Megalobulimus sanctipauli* involves Argentina, Brazil and Paraguay (Beltramino 2013). As the potential distribution of the species may not necessarily be limited to the mentioned countries, we chose to evaluate its distributional range across all South American countries (17,825,184 km^2): Argentina, Bolivia, Brazil, Chile, Colombia, Ecuador, French Guiana, Guyana, Paraguay, Peru, Suriname, Uruguay and Venezuela. *M. sanctipauli* comprises three nominal subspecies: *M. sanctipauli sanctipauli* (Ihering and Pilsbry, 1900), *M. sanctipauli pygmaeus* (Bequaert, 1948) and *M. sanctipauli eyerdami* (Bequaert, 1948). This study was based on presence data (n=20) for *M. s. sanctipauli* that were obtained from the scientific literature (Fernández 1978; Beltramino et al. 2012; Beltramino 2013 and references therein). For those localities where the coordinates were not provided by the source, a georeferenced position was derived secondarily by using the point-radius method described in Wieczorek et al. (2004). In relation to the other subspecies, only a single presence record is currently available for each of them from the original descriptions (Bequaert 1948; Beltramino et al. 2012). Given the magnitude of uncertainty due to the extent of the locality, these records could not be used here as presence data (i.e., the type locality for *M. s. pygmaeus* is Brazil, without a definitive locality; the specimen examined for delineating *M. s. eyerdami* is referred to as coming from “*Argentina, near Tartagal, Prov. Salta, close to the Bolivian border*”).

2.2 Environmental data

Environmental variables for current climatic conditions were obtained from WorldClim v.1.4 (http://www.worldclim.org), at a spatial resolution of 30 arc seconds (~1 km^2). Nineteen bioclimatic variables and a topographic variable (altitude) were used as predictors (Table 1). These data were derived from weather station data spanning 1950–2000 (Hijmans et al. 2005). To estimate the influence of climate change on the potential future distribution, the same bioclimatic predictors for the time intervals 2040–2069 and 2070–2099 (hereafter referred to as 2050 and 2080, respectively) were downloaded from the Climate Change, Agriculture, and Food Security website (CCAFS; http://www.ccafs-climate.org), at a resolution of 30 arc seconds. The Intergovernmental Panel on Climate Change (IPCC) has defined various political and economic scenarios that are regularly used to make predictions about climate change (IPCC 2007). In this study, the A2 and B1 scenarios were evaluated using the Hadley Centre Coupled Model, v.3 (HadCM3), which has been reported to provide good results for South America (Marengo 2006; Souza et al. 2011). We included only one global climate model by the arguments provided in Cordellier et al. (2012). The A2 scenario can be considered as pessimistic (it describes a very heterogeneous world with continuously increasing population, and regionally oriented economic growth), whereas B1 is more optimistic (it supposes a convergent world with the same global population, that peaks in mid-century and declines thereafter, with rapid changes in economic structures toward a service and information

Table 1 Bioclimatic variables used in model development. Temperatures are expressed in °C *10, precipitations in mm, and elevation in m above sea level

Variable	Description
alt	Altitude
bio1	Annual mean temperature
bio2	Mean diurnal range (monthly mean, T° max-T° min)
bio3	Isothermality (bio2/bio7) × 100
bio4	Temperature seasonality (standard deviation × 100)
bio5	Maximum temperature of warmest month
bio6	Minimum temperature of coldest month
bio7	Temperature annual range (bio5-bio6)
bio8	Mean temperature of wettest quarter
bio9	Mean temperature of driest quarter
bio10	Mean temperature of the warmest quarter
bio11	Mean temperature of coldest quarter
bio12	Annual precipitation
bio13	Precipitation of wettest month
bio14	Precipitation of driest month
bio15	Precipitation seasonality (coefficient of variation)
bio16	Precipitation of wettest quarter
bio17	Precipitation of driest quarter
bio18	Precipitation of the warmest quarter
bio19	Precipitation of the coldest quarter

economy, with reductions in material intensity and the introduction of clean and resource-efficient technologies) (IPCC 2007; Xu et al. 2013). All environmental layers were clipped to the extent of the study area.

2.3 Distribution modeling

Low density populations and individuals buried in the soil, even after they die, confirm the inherent difficulties involved in validating absence for *Megalobulimus* (Hylton Scott 1939; Bequaert 1948). For this reason, the potential distribution of *M. sanctipauli* was estimated by using the MaxEnt algorithm (MaxEnt v.3.3.3 k; Phillips et al. 2006; Phillips and Dudík 2008). We chose MaxEnt as it requires presence-only data, and because several SDMs have been successfully generated by using this algorithm with very few presence records (e.g., Pearson et al. 2007; Kumar and Stohlgren 2009; Thorn et al. 2009). MaxEnt models the species' ecological niche (a set of ecological conditions habitable by a species) by examining the relationship between the locations of known species presence and the environmental characteristics of that area and then extrapolating from this the areas where similar conditions occur in the study area (Paredes-García et al. 2011; Vogler et al. 2013). 75 % of presence records were randomly selected and used in the model training while the remaining 25 % were used in the model testing. The potential distribution was computed as *logistic* under current climatic conditions first, and then projected onto future climate scenarios. This output returns a continuous map with an estimated probability of presence between 0 (no probability of the species presence) and 1 (high probability of presence), which permits fine distinctions between the suitability of different areas modeled (Giovanelli et al. 2008). All other parameters were used by default. The resulting model was evaluated using the Area Under the Curve (AUC) of the Receiver Operating Characteristic curve (ROC curves analyses; Fielding and Bell 1997). The AUC is a threshold independent index commonly used to assess prediction maps (Graham et al. 2011), which can take values between 0.5 (no predictability) and 1 (perfect prediction). According to Loo et al. (2007), values above 0.8 indicate a strong prediction. In order to compare and combine current and future potential distributions, binary maps (suitable/unsuitable habitat) were derived using the *10 percentile training presence logistic* threshold, which considers the probability at which 10 % of the most extreme training presence records are omitted (Morueta-Holme et al. 2010; Escalante et al. 2013). This strategy allowed us to identify those distribution areas strongly affected by climate change, as well those stable areas and new suitable areas for the species in the future. The extent of suitable areas (current and future) was quantified and analyzed with ArcGIS v.9.3 (ESRI 2008).

2.4 Protected areas analysis

In order to determine the potential extent of protected areas that are bioclimatically suitable for *M. sanctipauli*, the future distribution maps for the different scenarios and time slices were overlapped onto the current network of South American protected areas. The network was downloaded, considering all available categories, from the World Database of Protected Areas (UNEP-WCMC 2012; http://protectedplanet.net). Calculations were performed using ArcGIS v.9.3 (ESRI 2008).

3 Results

The potential distribution area for *M. sanctipauli* under current climatic conditions is shown in Fig. 2. The model had very good performance, with AUC values of 0.992 for training data and 0.966 for test data, with a standard deviation of 0.018. The 10 percentile training presence

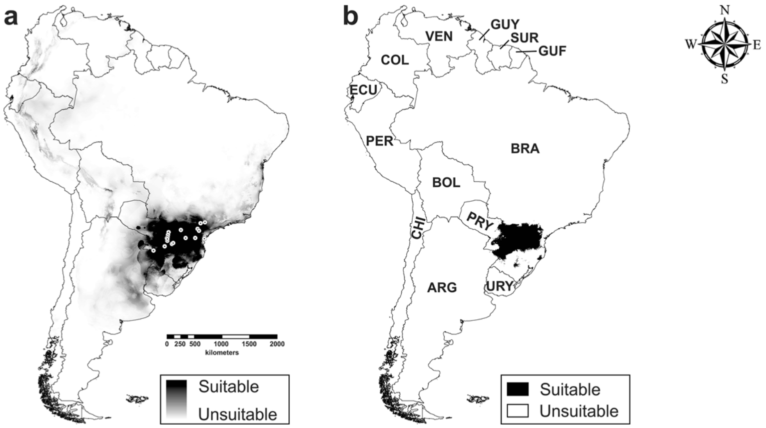

Fig. 2 Present potential distribution of *Megalobulimus sanctipauli* in South America. **a** logistic format, **b** thresholded format (*10 percentile training presence*). Darker areas indicate high suitability areas. Point indicate occurrence records used in study. ARG: Argentina; BOL: Bolivia; BRA: Brazil; CHI: Chile; COL: Colombia; ECU: Ecuador; GUF: French Guiana; GUY: Guyana; PRY: Paraguay; PER: Peru; SUR: Suriname; URY: Uruguay; VEN: Venezuela

logistic threshold used for binomial conversion was 0.360. At this threshold, the area predicted as suitable for the species was about 2.17 % of the extent of South America (~386,543 km^2; Fig. 3).

Under current conditions, the highest suitability values were found to be restricted to the Atlantic Rainforest, involving central-eastern Paraguay, north-eastern Argentina and southern Brazil (Fig. 2b). Projections of future distribution showed marked differences in habitat suitability among the different scenarios and times slices (Fig. 4). Under the low-emission B1 scenario, the suitable area for *M. sanctipauli* in South America was estimated to be about 2.59 % (~461,881 km^2) by 2050, and 2.51 % (~447,049 km^2) by 2080 (Fig. 3). When compared with the currently suitable area, this was translated into a relative increase of 19.35 % (~75,338 km^2) and 15.67 % (~60,506 km^2) for 2050 and 2080, respectively. In this predicted future distribution, the area gain was at expense of a northern retraction, but a southern expansion of the area indicated as suitable at present (Fig. 4a, b). The future projection with the high-emission A2 scenario was more extreme than the B1 scenario. Under the A2 scenario, the suitable area for the species in South America was estimated to be about 1.31 % (~233,622 km^2) by 2050, and 0.59 % (~104,525 km^2) by 2080 (Fig. 3); which represented a relative decrease in present potential range of 39.63 % (~152,921 km^2) and 72.81 % (~282,018 km^2) for 2050 and 2080, respectively. Under this scenario, a retraction in the north and an expansion towards the south of the present potential distribution were predicted by 2050 (Fig. 4c). By 2080, most of the suitable area of the present potential distribution was projected to be lost, with an extreme northern retraction and the gain of a new disjunct area toward the south (Fig. 4d).

A total of 172 protected areas located in Argentina (*n=47*), Brazil (*n=107*), and Paraguay (*n=18*) were found to contain climatically suitable habitat for the species at present and future; although the suitability differed among scenarios and periods analyzed (Electronic Supplementary Table). The amount of suitable habitat in protected areas under both scenarios for 2050 and 2080 is shown in Fig. 5. The simultaneous analysis under both scenarios and periods showed that from protected areas listed in the Electronic Supplementary Table, only four in Argentina and 20 in Brazil, accounting for ~1545 km^2 (0.009 % of South America), would remain suitable for the species by the end of the century (Table 2, Fig. 5).

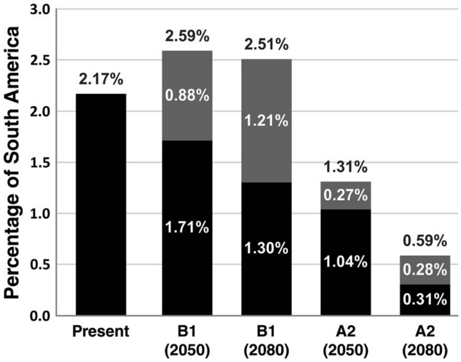

Fig. 3 Percentage of areas of South America suitable for *Megalobulimus sanctipauli*. Under future climate scenarios, black bars indicate areas suitable at present and future (stable), whereas grey bars indicate new suitable areas at future (expansion)

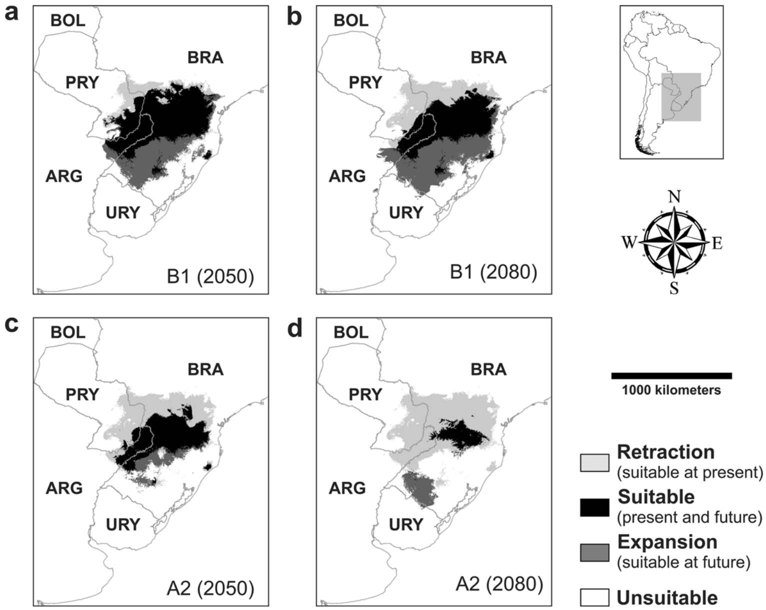

Fig. 4 Comparison among results of projections at present and future. Each map shows potential suitable areas for *Megalobulimus sanctipauli* under a future scenario for a time slice. **a** B1, 2050; **b** B1, 2080; **c** A2, 2050; and **d** A2, 2080. All maps are classified in: retraction (suitable areas at present but not at future), expansion (suitable areas at future but not at present), suitable areas at present and future, and unsuitable areas

4 Discussion

Land snails belong to the second most diverse animal phylum in terms of number of described species, and the estimated number of terrestrial gastropods comprises about 24,000 valid species (Lydeard et al. 2004). However, mollusks have the highest number of documented extinctions of any major taxonomic group (Lydeard et al. 2004). In particular, land snails are at disproportionately high extinction risk. Of the 310 mollusk species listed as extinct in the 2014 IUCN Red List of Threatened Species, 204 (~66 %) are land gastropod species (IUCN 2014). Furthermore, the number of known extinctions is certainly underestimated (Régnier et al. 2009).

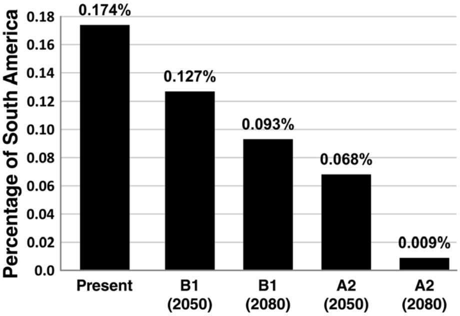

Fig. 5 Percentage of protected areas of South America suitable for *Megalobulimus sanctipauli*. Under future climate scenarios, only stable areas (suitable at present and future) are shown

Table 2 Protected areas predicted to be suitable at present that will remain climatically suitable in the future for *Megalobulimus sanctipauli* under both scenarios and time slices examined

Name	IUCN management category	Type of protected area	Designation type
Argentina			
Cruce Caballero	II	Provincial Park	National
General Belgrano	VI	Forest Reserve	National
Piñalito	II	Provincial Park	National
San Antonio	Ia	Strict Nature Reserve	National
Brazil			
Araucárias	II	State Park	National
Boa Vista - PR	Not Reported	Indigenous Area	National
Buriti	IV	State Area of Outstanding Ecological Interest	National
Caçador	VI	National Forest	National
Campos de Palmas	III	Wildlife Refuge	National
Mangueirinha	Not Reported	Indigenous Reserve	National
Mata Preta	Ia	Ecological Station	National
Palmas	II	State Park	National
Palmas	Not Reported	Indigenous Area	National
Palmital	Not Reported	Indigenous Area	National
Pinhão	VI	State Forest Reserve	National
Rio Areia	Not Reported	Indigenous Area	National
Rio das Cobras	Not Reported	Indigenous Area	National
Rio dos Pardos	Not Reported	Indigenous Area	National
Rio dos Touros	Ia	State Ecological Station	National
Santana	VI	State Forest	National
Serra da Esperança	V	State Environmental Protection Area	National
Toldo Imbu	Not Reported	Indigenous Area	National
Três Barras	VI	National Forest	National
Xapecó (Pinhalzinho-Canhadao)	Not Reported	Indigenous Area	National

In general terms, the conservation status of most land snails of the Neotropical Region remains unknown (Ramírez et al. 2003; Gutiérrez Gregoric et al. 2013). Despite this uncertainty, what is certain is that the group of giant land snails belonging to *Megalobulimus* is highly imperiled (Santos et al. 2013 and references therein). Six species are on the IUCN Red List: one extinct, two critically endangered, and three endangered (IUCN 2014). Furthermore, several species not listed that were formerly widespread are now fast declining in nature, as the result of anthropogenic pressures (Agudo-Padrón 2011). In this context, our study shows that climate change may pose an additional serious threat to giant land snails, where impacts on distributional ranges should be expected following the progressive warming predicted for the Neotropical region (IPCC 2007).

For the species studied here, our results suggest a future southern displacement of its distributional range in response to climate change, in agreement with the expected trend of distributional shifts to higher latitudes (Foden et al. 2008; Johnson et al. 2010). In spite of this, although the estimated change pattern in suitable areas for *M. sanctipauli* differed depending on the scenario and period examined, the north of the current potential distribution will likely have the most damaging consequences due to habitat loss by warming; thus, such loss could be expected to result in increased extinctions of local populations. In contrast, new contiguous and discontigous areas are predicted to increase suitability toward the south of the potential distribution, which might be colonized by the species. However, even though migration or dispersal rates are unknown for the species of *Megalobulimus*, colonization of new favorable areas seems fairly improbable as it necessarily would require high dispersal abilities. This is in contrast with low dispersal of most land snails where the overall general rate of active migration has been estimated to be in the order of 2.60 m per month (Barker 2001; Foden et al. 2008; Kramarenko 2014; Miranda et al. 2015). On this basis, it can be expected that future distribution of *M. sanctipauli* will probably be restricted only to those stable areas indicated as suitable at present and future, which in the less optimistic scenario would represent 0.31 % of continental South America by 2080 (Fig. 3).

In addition to above mentioned impacts, it is important to note that the predicted potential distribution for *M. sanctipauli* refines the previous understanding about the distribution of this species, which was indicated to occur in southern Brazil, eastern Paraguay and northeastern Argentina (Parodiz 1957; Fernández 1973; Simone 2006; Beltramino et al. 2012; Beltramino 2013). Our results draw attention to the idea that this giant land snail seems to be restricted exclusively to the southernmost regions of the Atlantic Forest, and mainly to the ecoregions of the Araucaria and the Upper Paraná Atlantic Forests (Di Bitetti et al. 2003; Paviolo et al. 2008). This refined distribution analysis becomes particularly important when taking into account that the Atlantic Forest, one of the world's biodiversity hotpots, faces an increasing number of threats (Di Bitetti et al. 2003). This was one of the largest forests of the Americas, extending into tropical and subtropical regions (Ribeiro et al. 2009). However, it is currently one of the most threatened forests, in which less than 7 % of the original vegetation cover remains, essentially as the result of deforestation especially associated with the expansion of agriculture and other land uses (Di Bitetti et al. 2003; Paviolo et al. 2008; Ribeiro et al. 2009). In this context, the synergistic impact of the ongoing habitat destruction with climate change is likely to result in a serious decrease of the suitable habitat for the giant land snail studied here, as well for most of the malacofauna sharing the same habitat.

Beyond these considerations, southernmost ecoregions of the Atlantic Forest still contain some of the largest intact fragments of forest, especially in Argentina and Paraguay, many of which are represented in existing protected areas (Di Bitetti et al. 2003; Paviolo et al. 2008). In order to mitigate impacts, those protected areas indicated in our results as suitable at present that will remain climatically suitable in the future (Table 2) should deserve particular attention for setting conservation priorities. In this sense, the highlighted protected areas need to be surveyed first to confirm the real occurrence of *M. sanctipauli*, as they may actually be devoid of populations due to several interlinked factors not considered in this study which could influence the species' distribution (e.g., barriers, invasive species, interactions, predators, smaller-scale habitat properties; Barker 2001).

In addition, and in the same way as for other species, it is important to bear in mind that our prognosis is not free of methodological uncertainty due to data sources and modeling method used, and results could be different using other climate and niche models; although we consider that future trends will be similar in light of the currently available resources. Nonetheless, this study has established a baseline for assessing the impacts of climate change in native giant land snails. We consider that application of bioclimatic models for the prognosis of future events of non-model organisms as those belonging to the giant land snail fauna, in which also umbrella and flagship species are being proposed, is a promising initiative to address conservation efforts that may enable governmental authorities to develop climate-integrated conservation plans aimed to preserve threatened malacofauna diversity.

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