



Effects of climate change on distribution and areas that protect two neotropical marsupials associated with aquatic environments

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ABSTRACT

The contraction of the amount of suitable habitat due to climate change can result in a species becoming threatened with extinction. Strong evidence supports that this effect will be pronounced for several species of small mammals in the near future. We address these issues using the *ensemble* technique to generate potential distribution models for Neotropical marsupials associated with aquatic environments, *Chironectes minimus* and *Lutreolina crassicaudata*, and predict the effects of climate change on the distribution of these two species. We later evaluate the effectiveness of the Fully Protected Areas for the two species in the present and future scenarios. Based on our models, we recommend priority areas for the conservation of these species, emphasizing conservation efforts across borders between countries. Our results indicated that both species will suffer a significant restriction of their potential distributions until 2050. Our models predicted that the loss of suitable areas will be greater for *C. minimus*, with only ~33% of the original distribution area remaining. The models also indicated that the current system of Fully Protected Areas in the Neotropical region will protect *L. crassicaudata* in a small area of its current and future potential distribution, inserted in climatically stable areas (~14%). These scenarios for these species support strong impacts on the biodiversity protection in aquatic environments in the Neotropical region. We strongly recommend the priority planning and implementation of transboundary Fully Protected Areas in stable areas of distribution of these species to maintain the protection of these marsupials and the ecosystems to which they are associated.

1. Introduction

Rapid climate change has contributed to altering the geographic distribution of species (Burrows et al., 2014; Román-Palacios and Wiens, 2020; Root et al., 2003; Rosenzweig et al., 2008). Species population are naturally dynamic and tend to change their range in search of suitable climatic habitats, resulting in wider or narrower ranges (Gutiérrez et al., 2019; Singh, 2020). That effect has been documented in many species of small mammals, including rodents (Lacerda, 2013; Tocchet, 2013; Waller et al., 2017) and marsupials (Freitas-Oliveira et al., 2021; Loyola et al., 2012; Prieto-Torres and Pinilla-Buitrago, 2017). This is worrisome because the contraction of climatically suitable areas for the persistence of species is a critical factor that makes them more susceptible to threats of extinction (Siqueira et al., 2009).

Protected Areas (PAs) have a key role in the protection and management of biodiversity in climate change scenarios (Lockwood et al., 2012; Mackey et al., 2008). However, PAs are geographically fixed and often fragmented. Therefore, they provide limited support in scenarios of species distribution shifts, which has raised some questions about their maintenance and conservation efficiency (Rodrigues et al., 2004; Wiens et al., 2011). To achieve long-term conservation goals, the first step is to understand what are the conservation gaps, including the effects of climate change (Araújo and New, 2007; Hannah et al., 2007; Langhammer et al., 2007). Species distribution models (SDM) are often useful in filling these knowledge gaps (Bruner et al., 2001; Loyola et al., 2013; Pressey et al., 2007).

SDM combines occurrence records data with predictor variables to identify regions with ideal environmental conditions that allow species

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to occur (Elith and Leathwick, 2009). In part, the scarcity of occurrence data can be linked both to the lack of our understanding of dispersal capacity (Jackson and Sax, 2010) and to interactions between species (VanDerWal et al., 2009), limiting the application of the SDMs. Nevertheless, it is known that SDMs, along with a careful interpretation of their results, can be useful tools for habitat suitability analyses under scenarios of climate change (Giannini et al., 2012; Lawler et al., 2011; Parmesan et al., 1999; Warren et al., 2001), as well as providing valuable knowledge for species conservation, such as the current and future ranges of Neotropical marsupials (Freitas-Oliveira et al., 2021; Loyola et al., 2012; Prieto-Torres and Pinilla-Buitrago, 2017).

The Didelphidae marsupials *C. minimus* (Zimmerman, 1780) and *L. crassicaudata* (Desmarest, 1804) are distributed across the Neotropical region (see Brandão et al., 2015; Damasceno and Astúa, 2016; Martínez-Lanfranco et al., 2014). In contrast, they are species with specific needs for river ecosystems and wetlands (lotic and lentic). *Chironectes minimus*, the water opossum, is the only semi-aquatic marsupial in the world, adapted to live in the aquatic and terrestrial environment. This species inhabits well-preserved gallery forests, environments always close to water bodies, preferring rivers, streams, and clear water ponds (Galliez et al., 2009). In turn, *L. crassicaudata*, the big lutrine opossum, in addition to areas with herbaceous and shrub vegetation and wetlands, also inhabits areas with bodies of water and gallery forest (Marshall, 1978; Regidor et al., 1999). The natural habitats of both species are vulnerable and threatened over much of their distributions (Brandon et al., 2005; Lees and Peres, 2008; Loyola et al., 2012), including under climate change scenarios (Freitas-Oliveira et al., 2021; Loyola et al., 2012; Prieto-Torres and Pinilla-Buitrago, 2017). At the same time, the two species are possible indicator species for the conservation of lotic and lentic ecosystems because of their specific habitat needs. Conservation efforts focused on *C. minimus* and *L. crassicaudata* can also assist in the protection of other endemic or endangered species of mammals, reptiles, amphibians and birds. Migratory birds from both hemispheres use especially lentic environments, being significantly impacted by alterations and disappearance of this type of habitat (Culp et al., 2017).

Thus, in this study, we analyze and predict the potential geographic distribution of *C. minimus* and *L. crassicaudata* for the current climate scenario and model their potential future distributions based on predicted climate scenarios. From these models, we aim to answer two important questions: a) what are the possible climatic influences on the distribution dynamics of *C. minimus* and *L. crassicaudata* over time? and b) are these species being protected by protected areas that do not allow extractive activities (here called Fully Protected Areas, FPAs) for the present, and will they be in the future? We expect that in the future climatic changes scenarios, the distribution ranges of both species will suffer a critical reduction, and that, currently and in 2050, these distributions are or will be mostly outside FPAs.

2. Material and methods

2.1. Occurrence records

We obtained occurrences for *C. minimus* and *L. crassicaudata* from published records (both peer-reviewed and gray literature), and from online databases: Global Biodiversity Information Facility (GBIF, www.gbif.org), speciesLink (www.splink.cria.org.br), iNaturalist (<https://www.inaturalist.org>) and Arctos (Collaborative Collection Management Solution, <http://arctos.database.museum/>). We also carried out consultations on scientific collections, the Mammal Collection of the Universidade Federal de Santa Catarina, the Museu Nacional – UFRJ, and the Museu de Zoologia da Universidade de São Paulo. Because of their unique habits and fur colour patterns (not found in any other co-occurring opossum species), these two species are easily identifiable visually, which also allowed us to use direct observations by experienced and trustworthy field researchers. We verified the geographical coordinates empirical sample collection points using Google Earth

software version 7.3 (<https://earth.google.com/>) and Google Maps (<https://maps.google.com.br>). To avoid a spatial autocorrelation of the sampling effort or sample bias (Araujo and Guisan, 2006; Veloz, 2009), we used a spatial data filter. We created a grid with pixels of 2.5' of arc of the equator and in Google Earth software, a buffer of 3 km using the Geographic Information System QGIS (QGIS; Team, 2022). Thus, we selected only one occurrence record within each pixel and buffer, eliminating points with low variations in the values of climatic variables.

The final dataset resulted in 72 presence records for *C. minimus* and 60 for *L. crassicaudata*, distributed across Central and South America. However, 57 and 48 (*C. minimus* and *L. crassicaudata*, respectively) had precise coordinates. After rarefaction, records with spatial autocorrelation and imprecise coordinates were removed. Thus, only 55 presence records were used in potential distribution models of *C. minimus* and 47 presence records for *L. crassicaudata* (Online Appendix, Table A.1 and A.2; Fig. B.1).

2.2. Predictor variables

In this study, we used bioclimatic variables layers at 2.5' resolution of arc (~5 km of the equator), suggested for analyses on a continental scale by Chapman et al. (2005) and Giannini et al. (2012). We used the Neotropic limit proposed by Morrone (2014) and available by (<https://sites.google.com/site/biochartis/>) for *C. minimus* and adjusted for South America for *L. crassicaudata*, removing all the island systems, leaving only the mainland, which encompasses the historical distribution limit of the two species.

We extracted 19 bioclimatic variables from the WorldClim v2.1 (www.worldclim.org) dataset generated by interpolated climatic data from the thirty years between 1970 and 2000 (Hijmans et al., 2005) to construct the present-day models and projection of future distribution models for the year 2050. We used two General Circulation Climate Models (GCMs), the first was the Model for Interdisciplinary Research on Climate version 6 (MIROC6) and the second, the Canadian Earth System Model version 5 (CanESM5) (Collins et al., 2011; Navarro-Racines et al., 2020). Both GCMs are used from the greenhouse gas emission scenarios Representative Concentration Pathways (RCP) are combined with the Shared Socioeconomic Pathways (SSP): ssp245 (updates RCP4.5 using SSP2, which configures an intermediate scenario of greenhouse gas (GHG) emissions until 2100), and ssp585 (updates RCP8.5 using SSP5, which is the worst-case scenario for greenhouse gas (GHG) emissions until 2100) (O'Neill et al., 2016; Riahi et al., 2017; Rogelj et al., 2018). All variables, present and future, were adjusted to the spatial limit of the study areas using the sf (Pebesma, 2018) and raster (Hijmans, 2021) packages in R language (R Core Team, 2021).

We selected bioclimatic variables for present-day with low multicollinearity using the Variance Inflation Factor (VIF) less than 2.0 (Dormann et al., 2013), and use the same to the future scenarios. We made this selection using the values of the entire study area, for the two species separately. Despite that, the selection returned the same variables for both species: Isothermality (BIO03, mean diurnal range / temperature annual range ($\times 100$)), Mean Temperature of Wettest Quarter (BIO08), Precipitation Seasonality (BIO15, coefficient of variation), Precipitation of Warmest Quarter (BIO18) and Precipitation of Coldest Quarter (BIO19). The values of VIF are presented in the Appendix Table A.3 for two species.

2.3. Modeling

Presence-only data are only observations of the organism and fall short in relation to the reliability of the data, as they do not allow showing, reliably, where the species was not found (Pearce and Boyce, 2006). In this study, in addition to the presence data, we also included pseudo-absence data. At the time of modeling, we selected 1000 points randomly for the entire study area of each species and these were treated

as points of absence of the species (Lobo and Tognelli, 2011). To model the potential distribution of species, we used the Ensemble of Forecasts approach (Araújo and New, 2007). We applied three algorithms with different techniques using the sdm R-package (Naïmi and Araújo, 2016): i) machine learning method that estimates species' distributions by finding the maximum entropy distribution, MaxEnt (Phillips et al., 2006); ii) artificial intelligence method, Random Forest (Breiman, 2001), which uses a combination of predictive regression tree predictors; and iii) multiple discriminant analysis (MDA) method, a classification based on multiple models (Hastie et al., 1994).

To assess the efficiency of each model, we used the True Skill Statistic (TSS) test (Allouche et al., 2006; Shabani et al., 2018). TSS is an intuitive method of measuring the performance of SDMs in which forecasts are expressed as presence-absence maps. This test provides a score between -1 and $+1$, with values >0.6 considered good, $0.2 - 0.6$ regular to moderate and <0.2 low (Landis and Koch, 1977; Shabani et al., 2018). We also present Area Under the Curve (AUC), Correlation and Deviance values for each model in Appendix Table A.4 for two species. To calculate the TSS, we randomly partitioned the presence and pseudo-absence data 30 times using the 'sub-sampling' method. We used a dataset for training the algorithm with 70% of data and testing with 30% for the species. With the models fitted, we created predictive maps using current and future data (GCMs: CanESM2 and HaGEM2; Scenarios: SSP245, future mild, and SSP585, future worst-case). Finally, we create ensembles using "weighted average" by TSS values; for the future, we averaged the values for each GCMs. As the last step, we estimated the potential geographical limits of presence and absence of species from a threshold that maximizes the sum of sensitivity and specificity (Max SSS) (Liu et al., 2013), using the mean of TSS values for each replica. This method resulted in the construction of binary maps (presence = 1, and absence = 0), where cells with values above the decision threshold are considered climatically suitable areas for species distribution, and those below the threshold are inadequate.

2.4. Calculation of areas

We calculated the final models for the present-day and future scenarios with QGIS (QGIS; Team, 2022) in square kilometers, except in regions in which the presence of some type of effective barrier - geographic or climatic - constricting the distribution of the species. We calculated the total suitable area of the potential distribution of a species for the present-day, future scenarios and also maintained areas over time, which we call here "stable areas". Finally, we calculated the climatically suitable areas placed in FPAs. We considered the following categories: Ia (Strict Nature Reserve), Ib (Wilderness Area), II (National Park), and III (Natural monument or feature) (IUCN, 2001). The Protected Areas data were obtained through the protectedPlanet (Juffe-Bignoli et al., 2014).

3. Results

3.1. Potential distribution models

The three algorithms, MaxEnt, Random Forest and MDA presented almost successful performance in the present-day models, with reasonable TSS values to *C. minimus* (average and standard deviation: 0.41 ± 0.13) and good TSS values to *L. crassicaudata* (average and standard deviation: 0.67 ± 0.09). The MaxEnt algorithm has higher TSS values and MDA the lowest values for both species (Appendix Online, Table A.4). The predicted environment suitable for the distribution of *C. minimus* and *L. crassicaudata* varied in the three scenarios (Online Appendix, Fig. B.2 and B.3).

3.2. Gain/loss of area and stable areas

We calculated the total potential distribution area for the present-

day model for *C. minimus* to be $4,808,833 \text{ km}^2$ and for the future model $1,943,746 \text{ km}^2$ (future mild) and $1,592,043 \text{ km}^2$ (future worst-case), with high loss of climatically suitable area (~ 60 to $\sim 67\%$, respectively), mainly in the northwestern limit of Brazil. We observed that only $\sim 40\%$ of the present-day area can be considered stable over time for the future mild, and $\sim 22\%$ for the future worst-case. The hot-spots of distribution in the present-day scenario were concentrated in the south and center of the Neotropical region and further to the north in the transition zone of South America, mainly in Brazil and Colombia. In Central America, the potential distribution of *C. minimus* extended from southern Panama to northern Mexico. We observe a larger continuous area of potential distribution in southeastern and southern Brazil, Colombia, Ecuador, and Peru in South America, and Panama, Costa Rica, Honduras, Guatemala, and Belize in Central America (Fig. 1).

The potential distribution consensus model of *L. crassicaudata* predicted an area of $2,608,254 \text{ km}^2$ using the present-day model and for the future model $1,654,902 \text{ km}^2$ (future mild) and $1,685,863 \text{ km}^2$ (future worst-case). The area climatically suitable for species' presence would decline by $\sim 35\%$ by 2050. The range of potential distribution in both climatic scenarios was limited to a mostly continuous area in the South American meridional region. In the current scenario, these areas are included, principally, in Brazil, Paraguay, Uruguay, and Argentina. When comparing projections between the present-day scenario and the future, we observed a reduction of suitable areas in all countries (Fig. 2).

3.3. Conservation gaps

The current system of FPAs in South and Central America covers $\sim 6.7\%$ ($320,349 \text{ km}^2$) of the present-day potential distribution of *C. minimus*. In the future scenario, the species would be protected at $\sim 11.9\%$ (future mild) and $\sim 13.2\%$ (future worst-case). Ecuador and Bolivia, which held a large patch of stable area, did not have overlap with FPAs in either the present-day or future scenarios. Although Nicaragua and El Salvador have adequate areas, there is a deficiency of protected areas in these countries. In the west and northeast regions of Brazil, we noticed isolated patches not covered by FPAs. Finally, there are large stable areas intersected by international borders between northeastern Argentina with Brazil, southeastern Peru with Bolivia, northeastern Brazil with Venezuela and Guyana, eastern Honduras with Nicaragua, and western Colombia with Ecuador (Table 1 and Fig. 3).

Corroborating our expectations, in the present-day scenario, only $\sim 6.97\%$ of climatically suitable areas for the potential distribution of *L. crassicaudata* are contained within the limits of FPAs, mostly clustered in southern and southeastern Brazil, Colombia, and Venezuela. The low number of protected areas is maintained into the future, ~ 9.1 (future mild) and $\sim 6.95\%$ (future worst-case). Although Uruguay and Argentina have been countries with a large portion of stable areas, they present only $\sim 0.14\%$ and $\sim 4.50\%$ of protection for the species in the present-day. Bolivia, in the present-day scenario, does not present FPAs, and by 2050, Uruguay (future mild) will no longer host this species within FPAs. We also observed spots without similar FPAs between international borders in Brazil and Uruguay, Bolivia and Peru, Colombia, Ecuador and Venezuela, and Argentina and Chile (Table 2 and Fig. 4).

4. Discussion

We demonstrated that the climatically suitable areas for distribution of *C. minimus* and *L. crassicaudata* will be reduced by 2050, *C. minimus* will suffer the greatest loss of climatic space ($\sim 67\%$). As we expected, the current FPA system proved to be insufficient for the protection of *C. minimus* and *L. crassicaudata*. Less than $\sim 14\%$ of the climatically suitable areas for the species are within FPAs and, although *L. crassicaudata* has a larger climatic stable area, more than $\sim 94\%$ of this region is legally unprotected. Our results corroborate with prior studies on the influence of climate change on species dependent on lotic and lentic ecosystems (Bogoni and Tagliari, 2021; Freitas-Oliveira et al., 2021;

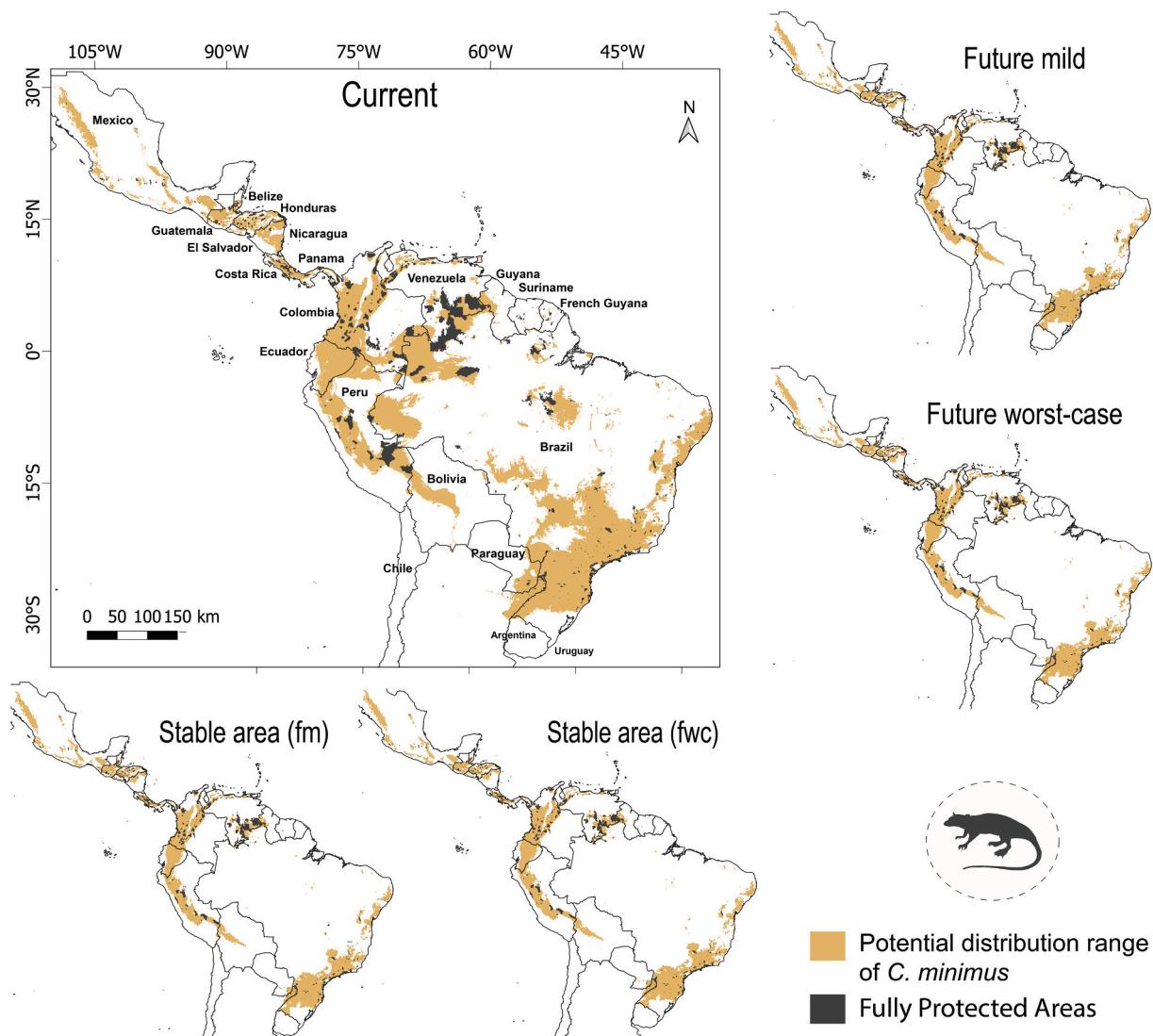


Fig. 1. Consensus map of potential distribution in the present, future scenario (future mild and worst-case) and stable areas of *C. minimus*.

Prieto-Torres and Pinilla-Buitrago, 2017).

4.1. Climatic limitations

Chironectes minimus has a potential distribution in areas with high variation in the seasonality of temperature and precipitation (southern and eastern South America), with average annual precipitation <100 mm (northern South America) and precipitation in the driest month ≥60 mm (Central America, southern and Amazonian region of South America). In contrast, areas that may be unsuitable for the maintenance of populations of this species, have an annual average temperature <18 °C, drier winters, and low annual precipitation (Chaco domain and the Chilean Andes).

These limitations may be related to marsupial physiology in general. Marsupials have low metabolic rates and low body temperatures (Dawson and Wolfers, 1978; Thompson, 1988), which could be at first interpreted as a limiting factor for their distribution. Large opossums, however, do occur in cold habitats, such as *Didelphis virginiana* in Southern Canada (Gardner, 2005), and even small opossums occur in Patagonia (Formoso et al., 2011). The effect of temperature in limiting these two species, could, however, be related to their use of water bodies, which could lead to a greater loss of body heat to the aquatic environment, as demonstrated among other semi-aquatic mammals

(Dawson and Fanning, 1981). Above all, we assume that in addition to climatic influence, other factors not considered, such as dispersion barriers, ecological and biotic interactions, effects on minor scaling the conditions of lotic and lentic environments, may limit the distribution of these species. This will be discussed further below. A significant part of *L. crassicaudata* distribution, specifically, the subspecies *L. c. crassicaudata*, appears to be present in regions with drier winters, low annual precipitation, and where there is a wide seasonal variation in temperature (southern South America) (see climate types in Beck et al., 2018). The low number of occurrence records in our study for the subspecies *L. c. turneri* (Guenther, 1879), distributed in northern South America, prevented inferences from climatic suitability.

Indeed, seasonally precipitation variable seem to have a notable influence on the distribution of *C. minimus* and *L. crassicaudata*, as they are associated with forested, water bodies and areas with herbaceous and shrub vegetation environments. In annually drier areas such as in the Northeast of Brazil and dry areas and with a low proportion of forest cover in Peru, Chile and southern Argentina, there is a single record of the presence of *C. minimus* and none for *L. crassicaudata*.

4.2. Effects of climate change and protection gaps

In our results, the total area of the potential distribution of *C. minimus*

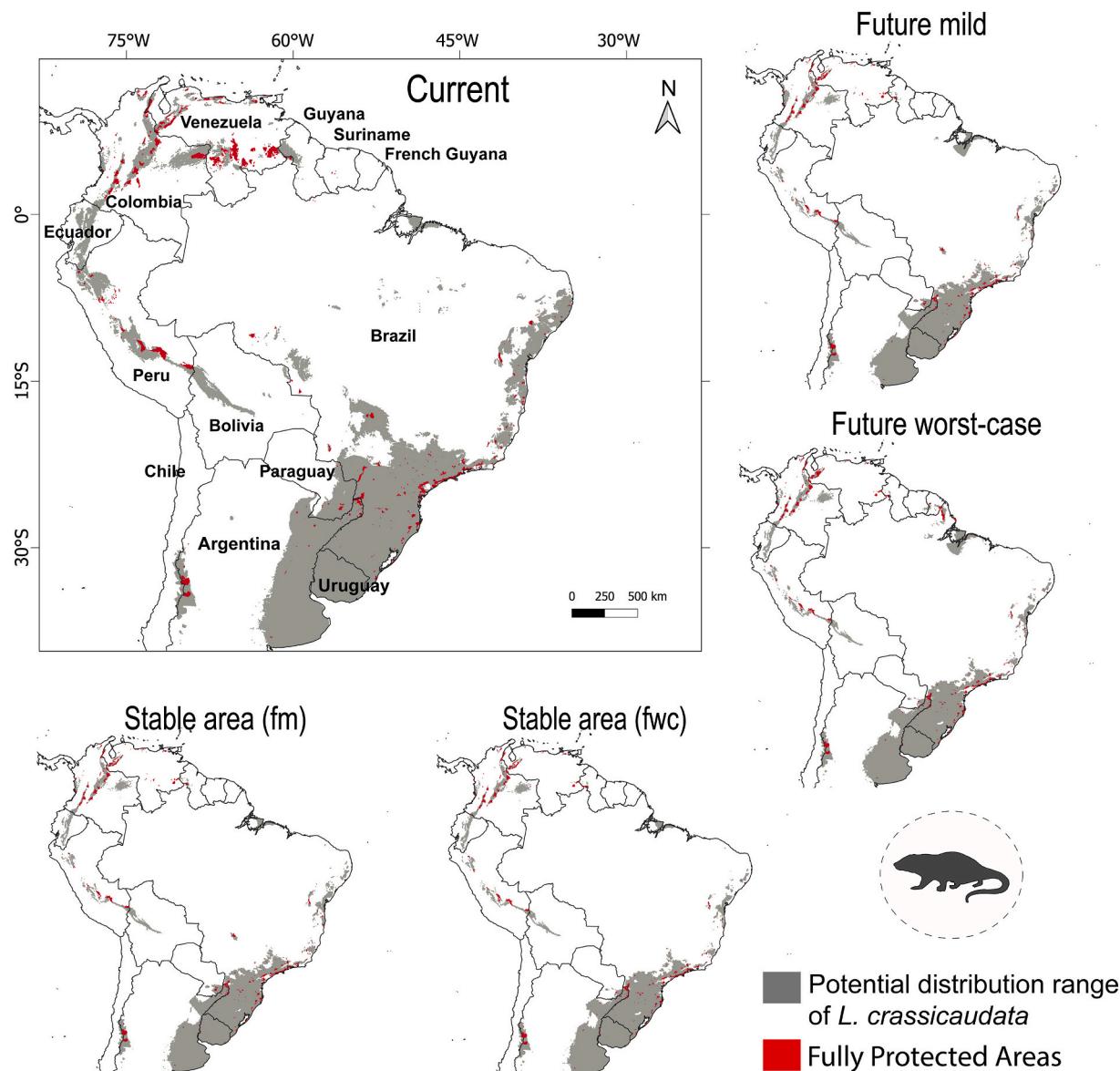


Fig. 2. Consensus map of potential distribution in the present, future scenario (future mild and worst-case) and stable areas of *L. crassicaudata*.

in the present and for the future was ~67%, smaller than those measured in previous studies (Freitas-Oliveira et al., 2021; Prieto-Torres and Pinilla-Buitrago, 2017). This was probably due to the conservative decision threshold used in the present study, which selects only areas with greater environmental suitability for the target species. This method of conservative decision threshold allows greater focus on decision-making for the conservation of *C. minimus*.

When comparing the climatically suitable areas of *C. minimus* from our present-day distributional model and its known distribution (Prieto-Torres and Pinilla-Buitrago, 2017), we observed a significant expansion of the potential area of distribution, especially in the Amazon region and northeast Brazil. However, models based on abiotic factors are expected to overestimate the potential distribution of the species, mainly where biological interactions are a determining factor (Braz et al., 2020). It has already been postulated that some antagonistic interactions, such as the presence of aquatic predators, such as *Paleosuchus* (Voss and Emmons, 1996) and mustelids, can strongly influence the absence of this marsupial (Graipel, unpublished data). The use of environmental and biotic variables and their correlations with the occurrence points of the species can contribute so that the potential distribution areas coincide with the

area of occurrence of *C. minimus*. The loss of forest cover, for example, in the future scenario will also influence the loss of suitable bands for the persistence of *C. minimus* (see Freitas-Oliveira et al., 2021; Prieto-Torres and Pinilla-Buitrago, 2017).

The predicted distribution in the present-day model for *L. crassicaudata* overlapped more closely with the current effective distribution (Flores and Martin, 2016). This situation may have been enhanced by the low sample number considered valid in this study and, consequently, the low attribution of importance to climatic variables in the north of the continent. In climate change scenarios, the species tends to maintain its distribution, there is no great loss of climatically suitable areas. In general, lack of knowledge about the taxonomy of any given species, known as the Linnean gap (Lomolino et al., 2004; Whittaker et al., 2005), constitutes a problem for conservation strategies. This may apply to *Lutreolina* in northern South America, since subspecies *L. c. turneri* may be validated as a full species (Martinez-Lanfranco et al., 2014).

Loyola et al. (2012) evaluated the loss of adequate climatic conditions for marsupials in Brazil and showed that they may lose a large climatically suitable area within between now and the year 2050. As well as Bogoni and Tagliari (2021) revealed, in their work, that the

Table 1

Calculation of area for potential distribution of *C. minimus*, in km² and its percentage (%), in the present, future and the stable areas (future mild and worst-case), within Fully Protected Areas (FPAs). Presenting the total FPAs for each country, their representativeness in different climatic scenarios (*), as well as in the total area of potential distribution (**) for comparison purposes.

Countries	Present		Future				Stable area			
			km ²		%		km ²		%	
	km ²	%	SSP2-4.5	SSP2-8.5	SSP2-4.5	SSP2-8.5	SSP2-4.5	SSP2-8.5	SSP2-4.5	SSP2-8.5
Argentina	4,242	1,3	1,604	1,444	0,7	0,7	1,604	1,679	0,8	0,8
Belize	3,690	1,2	2,540	2,183	1,1	1,0	2,540	2,540	1,2	1,2
Brazil	108,317	33,8	41,209	40,574	17,9	19,3	38,141	37,627	18,0	17,7
Colombia	40,627	12,7	32,321	33,265	14,0	15,8	32,047	30,171	15,1	14,2
Costa Rica	12,251	3,8	11,014	10,838	4,8	5,1	11,014	10,838	5,2	5,1
Guatemala	9,045	2,8	20,974	5,488	9,1	2,6	7,535	5,531	3,6	2,6
French Guyana	1,703	0,5	—	—	—	—	—	—	—	—
Honduras	5,750	1,8	4,421	4,306	1,9	2,0	1,521	3,741	0,7	1,8
Mexico	2,214	0,7	1,089	1,003	0,5	0,5	1,089	1,003	0,5	0,5
Nicaragua	1,394	0,4	855	633	0,4	0,3	842	633	0,4	0,3
Panama	1,780	0,6	1,159	1,010	0,5	0,5	991	8,369	0,5	3,9
Peru	25,461	7,9	13,036	12,010	5,6	5,7	13,036	12,010	6,2	5,7
Paraguay	901	0,3	226	220	0,1	0,1	224	220	0,1	0,1
El Salvador	574	0,2	567	547	0,2	0,3	567	547	0,3	0,3
Suriname	1,272	0,4	1,200	—	0,5	—	1,272	—	0,6	—
Venezuela	101,128	31,6	98,547	97,171	42,7	46,1	99,341	97,171	46,9	45,8
*Total	320,349	100	230,762	210,692	100	100	211,764	212,080	100	100
**Total	4,808,833	6,7	1,943,746	1,592,043	11,9	13,2	1,930,000	1,051,538	11,0	20,2

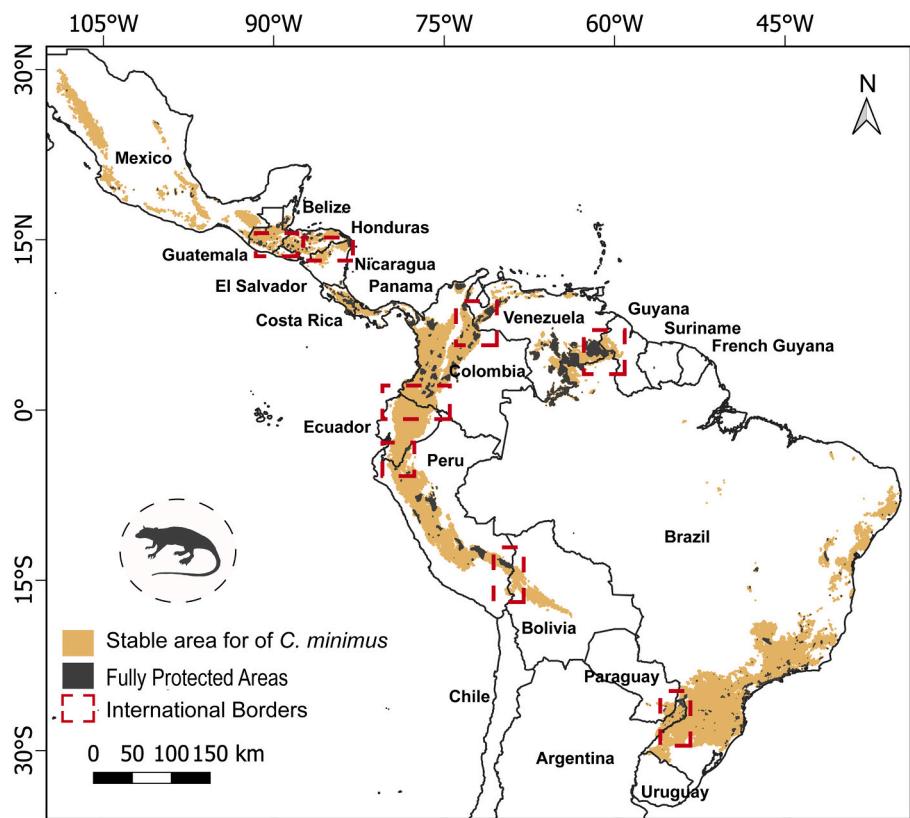


Fig. 3. Map showing the Fully Protection Areas (FPAs), overlapping the potential distribution range of *C. minimus* in the stable areas. The rectangles correspond to the priority areas for transboundary conservation and isolated or low representations of FPAs.

distribution of piscivorous mammals, including the species *C. minimus* and *L. crassicaudata*, under climate change may represent less than 6.5% in the entire Atlantic Forest, with a 30% reduction. Our analyses support that a large part of the areas presently inhabited by *C. minimus* and *L. crassicaudata*, and climatically inadequate in the future, coincide with critical regions vulnerable to climate change and loss of vegetation cover, such as Mesoamerica, the Amazon Basin and Central South

America (Hurtt et al., 2020; Pacifici et al., 2015), including developing countries, where biodiversity loss is predicted to be severe (Sayre et al., 2020). Although *L. crassicaudata* does not lose a large suitable climatic area of its geographical range, a critical portion of its distribution will be located outside FPAs, especially in Uruguay and Paraguay. This is due to the low legal protection of lentic aquatic environments, such as wetlands in the South American meridional region. Previous research with

Table 2

Calculation of area for potential distribution of *L. crassicaudata*, in km² and its percentage (%), in the present, future and the stable areas (future mild and worst-case) within Fully Protected Areas (FPAs). Presenting the total FPAs for each country, their representativeness in different climatic scenarios (*), as well as in the total area of potential distribution (**) for comparison purposes.

Country	Present		Future				Stable area			
			km ²		%		km ²		%	
	km ²	%	SSP2-4.5	SSP2-8.5	SSP2-4.5	SSP2-8.5	SSP2-4.5	SSP2-8.5	SSP2-4.5	SSP2-8.5
Argentina	8,200	4,51	8198	7,153	5,45	6,11	5,890	4,210	4,03	2,87
Brazil	58,881	32,41	27,705	23,218	18,41	19,83	27,705	23,218	18,96	15,83
Chile	30	0,02	30	30	0,02	0,03	30	30	0,02	0,02
Colombia	31,700	17,45	25,951	23,805	17,24	20,33	25,951	23,236	17,76	15,84
French Guyana	—	—	—	936	—	0,80	—	—	—	—
Peru	42,845	23,58	50,354	55,637	33,45	47,51	48,448	42,845	33,15	29,21
Paraguay	5,635	3,10	4,975	5,289	3,31	4,52	4,975	52,891	3,40	36,06
Uruguay	258	0,14	—	258	—	0,22	—	258	—	0,18
Venezuela	34,152	18,80	33,303	788	22,13	0,67	33,156	—	22,69	—
*Total	181,701	100	150,516	117,114	100	100	146,155	146,688	100	100
**Total	2,608,254	6,97	1,654,902	1,685,863	9,10	6,95	1,553,865	1,532,037	9,41	9,57

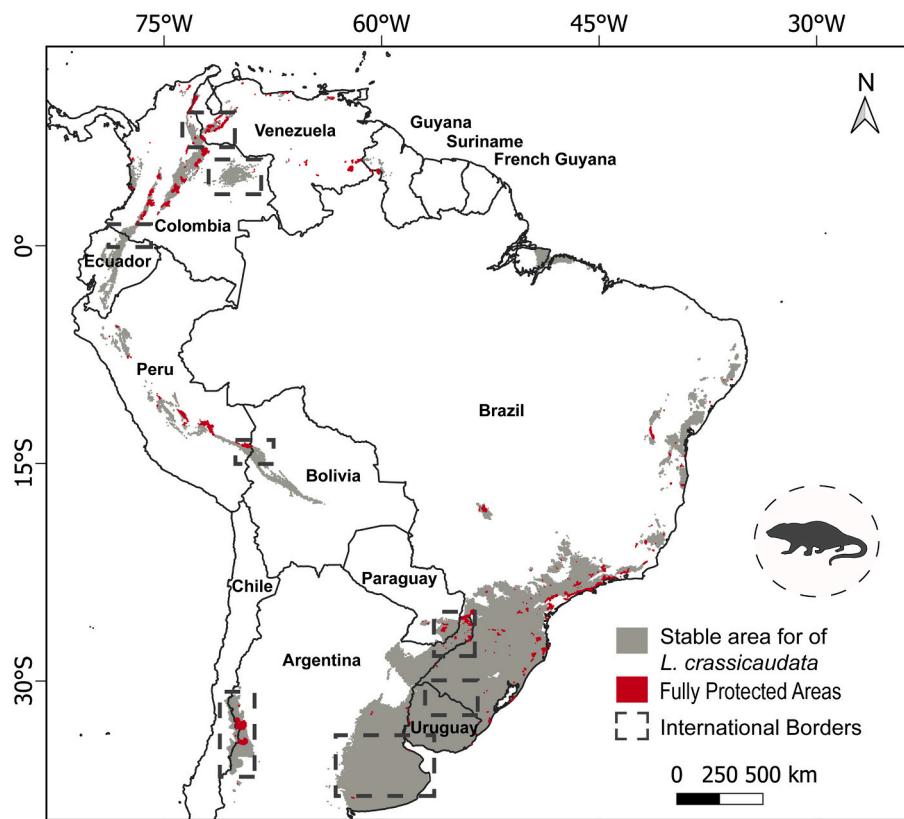


Fig. 4. Map showing the Fully Protection Areas (FPAs), overlapping the potential distribution range of *L. crassicaudata* in the stable areas. The rectangles correspond to the priority areas for transboundary conservation and isolated or low representations of FPAs.

reptiles, birds, and mammals showed results similar to ours, suggesting the reduction of distribution areas in the protected areas in the future (Corbalán et al., 2011; Lemes and Loyola, 2013; Marini et al., 2009; Ramirez-Villegas et al., 2014; Zimbres et al., 2012). However, we emphasize that these environments have unique characteristics and are essential for the conservation of species associated with them (De Meester et al., 2005).

The current FPAs system appears insufficient to protect *C. minimus* in our future model. We detected conservation gaps located mainly in Bolivia, Nicaragua, Suriname, Belize, French Guiana, Guatemala, and Ecuador. This is a critical scenario for species that are restricted to a low number of climatically stable areas and fragmented, mostly, like the ones presented here. The survival of *C. minimus* in isolated patches may

be untenable or even cause the species to move to other regions (De Castro and Fernandez, 2004; Fahrig, 2003). As a result, ecological interactions can break down, potentially resulting in the loss of additional species that depend on these interactions (Wiens et al., 2011).

Considering bioclimatic variables that outline the potential distribution of *C. minimus* and *L. crassicaudata*, the Atlantic, Amazonian, and Cerrado forests are the most suitable environments for the presence of these species. However, there is an accelerated conversion of these forests from anthropogenic pressures (Gonçalves-Souza et al., 2020; Hu et al., 2017). Previous studies (Freitas-Oliveira et al., 2021; Prieto-Torres and Pinilla-Buitrago, 2017) showed that deforestation can reduce ~40% and ~48% of the natural habitat of *C. minimus* in the future. Wetlands and gallery forests are disappearing, and there is increased river silting

and water pollution (Brandon et al., 2005; Lees and Peres, 2008). These environments act as primary habitats and dispersal corridors for many species of mammals and migratory birds (Bennett et al., 2014; Develey et al., 2008; Lees and Peres, 2008).

Therefore, climate change and the loss of forests are a challenge for the current systems of PAs, especially in the tropics (Chape et al., 2005). Our models suggest that some FPAs will become completely uninhabitable to both species. Most of all, small FPAs associated with severely fragmented environments may not ensure viable populations of *C. minimus* and *L. crassicaudata* in the long-term, even with adequate climatic conditions (Mackey et al., 2008; Peres et al., 2011), because populations in aquatic environments would be subject to extreme fluctuations such as prolonged droughts. Such FPAs that overlap stable areas should be strategically redesigned their limits and connectivity through the implementation of ecological corridors, for example, in Brazil (for *C. minimus*) and Uruguay and Argentina (for *L. crassicaudata*).

Recent studies demonstrated the importance of connectivity in protected areas that cross international borders (transboundary protected areas), being considered the most important regions for conservation efforts in the Americas (Dudley et al., 2014; Thornton et al., 2020). The Mesoamerican Biological Corridor (Escaffre et al., 2012) and the trans-boundary project implemented in the threatened region of the Gran Chaco (https://www.wwf.org.py/que_hacemos/proyectos/pacha/) are two good examples of this type of conservation policy. These efforts can favor countries where financial resources are scarce to conserve biodiversity. In addition, such initiatives facilitate the free movement of species, providing relief from unsuitable changes in portions of their distributions (Wegmann et al., 2014).

Such benefits may be felt not only by the species studied here but by the communities dependent on the same habitat. In this study, we observed the potential isolation of stable areas in the distribution of the two species in the future in areas along international borders and not protected by FPAs, which suggests an opportunity for transboundary conservation (López-Hoffman et al., 2010; Mittermeier et al., 2005). The grouping of FPAs between international borders, for *C. minimus*, can happen beyond the geopolitical limits of northeast Argentina with Brazil, southeast Peru with Bolivia, northwest Brazil with Venezuela and Guyana, eastern Honduras with Nicaragua and western Colombia with Ecuador. Similarly, for *L. crassicaudata* between Brazil and Uruguay, Bolivia and Peru, Colombia, Ecuador and Venezuela, and Argentina and Chile (Fig. 3 and Fig. 4).

5. Conclusion

Our potential distribution models of *C. minimus* and *L. crassicaudata* showed that aquatic environments, which are indispensable for the persistence of these species, presently receive low legal protection, especially in international borders. This situation may worsen, since we predict that the current system of FPAs will not shelter many of these areas for the species in this study over time, mainly for *L. crassicaudata*. Climate change can be a great factor in the potential regional extinction of *C. minimus* (in Brazil and Colombia) and *L. crassicaudata* (Brazil). Our models predicted that climatically suitable areas for *C. minimus* would be drastically reduced. As a mitigation measure, we recommend promoting connectivity between remnants of climatically suitable areas, between international FPAs through cross-border conservation actions.

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On behalf of all authors, the corresponding author states that there is no conflict of interest.

Declaration of Competing Interest

None.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoinf.2022.101570>.

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