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IGOR SOARES DE OLIVEIRA

ANÁLISE DE MÚLTIPLAS AMEAÇAS À CONSERVAÇÃO E DIVERSIDADE DE ANFÍBIOS

ASSESSMENT OF MULTIPLE THREATS TO CONSERVATION AND DIVERSITY OF AMPHIBIANS

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Tese apresentada ao Instituto de Biologia da Universidade Estadual de Campinas como parte dos requisitos exigidos para a obtenção do título de Doutor em Ecologia.

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RESUMO

As mudanças climáticas possuem potencial para alterar o funcionamento dos ecossistemas através da extinção de espécies e das conexões entre a biota e o ambiente, alterando os padrões aos quais estamos acostumados e exigindo adaptação. As alterações climáticas terão como uma de suas consequências a elevação oceânica, que pode redesenhar as costas de todos os continentes terrestres e afetar a biota associada. Nesse contexto, sobressaem-se os anfíbios como um grupo sensível que sofre diversas pressões e apresenta declínios populacionais, se destacando como vertebrados mais ameaçados da atualidade, com diversas espécies pouco conhecidas. Sendo assim, nesse trabalho analisamos múltiplos efeitos que dificultam a conservação dos anfíbios. Avaliamos os potenciais efeitos das mudanças climáticas e da elevação oceânica sobre os anfíbios com distribuição costeira. Também desenvolvemos um índice para classificar espécies com dados insuficientes com a finalidade de oferecer uma alternativa para a busca de informações para esses taxa e mudar sua classificação atual. Por fim, analisamos a disponibilidade histórica de clima adequado para uma linhagem endêmica do fungo quitrídio em busca de padrões que pudessem explicar sua distribuição e raridade atuais. Utilizamos ferramentas como modelos de distribuição de espécies e sistema de informação geográfica em busca de respostas às nossas questões. Nossos resultados corroboram as mudanças climáticas como um fenômeno com potencial devastador e alertam para potenciais perigos da elevação oceânica. Além disso, nosso índice para espécies deficientes em dados pode auxiliar a direcionar esforços em busca de novas informações. Por fim, nossas análises com relação ao fungo quitrídio corroboram a hipótese de endemismo para a linhagem *Bd*-Brazil e também evidenciam hábitat adequado passado para o *Bd*-GPL. Além disso, verificamos baixa sobreposição de nicho climático entre essas duas linhagens, indicando possibilidade de competição. Assim, esperamos que nossos resultados tenham contribuído para o conhecimento de múltiplas ameaças à conservação dos anfíbios e sirvam para direcionar futuros estudos.

Palavras chave: Modelos de distribuição de espécies, Mudanças climáticas, Nível do mar, Anfíbios - Clasificação, *Batrachochytrium dendrobatidis*

ABSTRACT

Climate change has the potential to change ecosystem functioning through species extinction and disrupting connection between biota and environment, thus changing natural patterns and requiring adaptation. One certain consequence of climate change is the sea level rise, which is expected to redraw coastal shorelines worldwide and broadly affect coastal-associated biota. In this context, amphibians represent a sensitive group under several current pressures, exhibiting population decline, highlighted as the most current threaten vertebrates on Earth, and also, with several "data deficient" species. Thus, herein we analyzed multiple effects that hamper amphibian conservation. We evaluated potential climate change effects and sea level rise on amphibians with coastal distribution. Also, we developed an index to classify data deficient species in order to offer an alternative further research of such species to gather sufficient information to change their current status. Finally, we analyzed historical availability of suitable habitat for and endemic lineage of the chytrid fungus searching for patterns that explain its current distribution and rarity. We used tools as species distribution models and geographic information system to answer our questions. Our results corroborate climate change as a potentially devastating phenomena and we stress potential threatens derived from sea level rise. Moreover, the index we developed for data deficient species seems to work properly and may drive further effort in searching for further information for those species. Finally, our analyzes related to the chytrid fungus supported the hypothesis of endemism of *Bd*-Brazil, and also showed past environmental suitability for *Bd*-GPL. In addition, we verified low environmental niche overlap these two lineages, indicating possibility of competition. Thus, we expect our results may improve current knowledge about multiple threats to amphibian conservation, as well as, they may be used to guide further research.

Keywords: Species distribution model, Climate change, Sea level, Amphibians - Classification, *Batrachochytrium dendrobatidis*

SUMÁRIO

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Esposa, amiga e companheira...

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INTRODUÇÃO GERAL

Nas últimas décadas questões relacionadas aos hábitos humanos e à conservação de espécies tem ganhado destaque, tanto na comunidade acadêmica (e.g., Peterson et al. 2003, Berkes 2004) quanto na mídia voltada ao público geral (e.g., Gardiner 2009, Barringer 2012), passando a fazer parte da agenda de políticos e tomadores de decisão (e.g., Rio 92, Rio + 20, Conferências (anuais) das Partes (COP/MOP)). Entretanto, apesar do crescente esforço a favor da conservação biológica, declínios populacionais e extinções de espécies têm sido detectados em taxas preocupantes (e.g., Butchart et al. 2010, Wake 2012, IUCN, 2014).

Dentre os diversos fatores que podem levar à extinção de espécies, como a fragmentação de hábitat (e.g., Becker 2009), o surgimento de doenças (e.g., Cheng 2011) ou a perda de hábitat natural (e.g., Batalha et al. 2010, Luck et al. 2013), as mudanças climáticas (MC) ocupam um papel de destaque, pois seus potenciais efeitos sobre a biodiversidade são esperados por afetar diversos grupos de organismos em escala global (Thomas et al. 2004, Bellard et al. 2012). Nesse aspecto, apesar dos crescentes esforços que avançam na tentativa de antecipar os efeitos das MC sobre a biodiversidade (Thomas et al. 2004, Foden et al. 2013, Loyola et al. 2014), muitos efeitos potenciais desse fenômeno ainda permanecem pouco estudados ou compreendidos. Como exemplo, podemos citar a elevação oceânica (EO), a qual possui potencial de levar efeitos negativos a comunidades costeiras (Mendoza-González et al. 2013, Bellard et al. 2014, Courchamp et al. 2014), mas que ainda carece de maior compreensão, não somente com relação aos processos que a geram (Stefan et al. 2012), mas também sobre a magnitude de seus potenciais impactos (Bellard et al. 2014). Dessa forma, identificar, avaliar e antecipar os efeitos potenciais das

MC sobre a biodiversidade constitui um desafio importante para a conservação de espécies global.

Nesse contexto, os anfíbios constituem o grupo vertebrado atualmente mais ameaçado (Hoffmann et al. 2010), sendo muito sensíveis às MC (Foden et al. 2013) e, portanto, estando altamente sujeitos a seus efeitos negativos (Hof et al. 2011, Loyola et al. 2014). Anfíbios também representam um dos grupos vertebrados mais diversos, embora com o maior número de espécies com carência de informações (IUCN, 2014). Entretanto, os anfíbios representam um dos grupos vertebrados atualmente mais estudados (Foden et al. 2013), contando com uma grande disponibilidade de dados acessíveis, como por exemplo os disponíveis nas bases online da *International Union for Conservation of Nature* (acessível em http://www.iucnredlist.org), Specieslink (http://splink.cria.org.br/), Amphibiaweb (http://amphibiaweb.org/), *Amphibian Species of the World* (http://research.amnh.org/vz/herpetology/amphibia/) ou *Global Biodiversity Information Facility* (http://www.gbif.org/). Essas bases oferecem informações diversas sobre ocorrência, taxonomia e história natural para quase todas as espécies de anfíbios conhecidas atualmente, constituindo ferramentas de uso essencial. Assim sendo, podemos considerar o grupo dos anfíbios como um bom modelo biológico para investigações relacionadas às MC e também de interesse conservacionista, devido à sua sensibilidade, ao número de ameaças às quais estão sujeitos e à sua diversidade.

Pelas razões expostas acima, nesse trabalho utilizamos anfíbios como modelo biológico principal com o intuito de gerar informações que auxiliem na conservação do grupo. Utilizamos modelos de distribuição de espécies (MDE) e sistema de informação geográfica (SIG) na tentativa de identificar e quantificar ameaças ainda pouco compreendidas sobre a diversidade de anfíbios. Assim, essa tese encontra-se organizada em cinco capítulos.

Os três primeiros capítulos tratam da EO. Esse tema despertou nosso interesse ao verificarmos que poucos estudos levavam em conta as consequências sobre espécies terrestres que habitam exclusivamente terras baixas associadas à costa ou que vivem isoladas em pequenas ilhas. Também levamos em conta o número significativo de áreas de conservação associadas às zonas costeiras e que seriam potencialmente as primeiras áreas a sofrerem efeitos da EO. O primeiro capítulo constitui uma revisão não sistematizada sobre o fenômeno da EO e sobre a complexidade existente em se realizar previsões acuradas sobre as magnitudes do fenômeno. No texto, procuramos explicar de forma simplificada do que se trata o problema e como é complexo realizar previsões detalhadas em escala global. Nosso objetivo foi trazer o tema à pauta de discussões científicas para o desenvolvimento de maiores investigações sobre o assunto.

No segundo capítulo realizamos um levantamento global das espécies de anfíbios com distribuição costeira e utilizamos MDEs e SIG para analisar possíveis sobreposições entre distribuição potencial e o avanço do mar. Utilizamos diferentes cenários climáticos e de EO na tentativa de avaliar a magnitude dos efeitos isolados e em conjunto, e também em que região global os efeitos futuros seriam potencialmente maiores.

O terceiro capítulo surgiu como uma consequência natural do segundo, onde avaliamos novamente os efeitos potenciais das MC e EO, mas na escala da Mata Atlântica brasileira. Incorporamos espécies endêmicas do bioma não analisadas no estudo anterior devido a restrições metodológicas e de disponibilidade de dados. Novamente quantificamos os efeitos potenciais em busca de espécies sob significativa ameaça no futuro com a finalidade de fornecer informações para antecipar estratégias visando sua conservação.

O quarto capítulo foi idealizado com o objetivo de fornecer uma ferramenta para auxiliar a busca de informações sobre as espécies pouco conhecidas (DD). Ao nos depararmos com o frequente problema da presença de espécies DD em nosso conjunto de dados, gerando diversas restrições metodológicas, organizamos informações disponíveis de diversas fontes e desenhamos um índice de prioridade de pesquisa para essas espécies. Acreditamos que o cálculo pode ser aplicado para qualquer grupo biológico e que pode ser desenvolvido em estudos futuros.

Por fim, o quinto capítulo trata do estudo do fungo *Batrachochytrium dendrobatidis* (*Bd*), um fungo reconhecidamente causador de declínios em populações de anfíbios em nível global. Nesse capítulo analisamos a oferta de nicho climático para a linhagem recém-descoberta *Bd*-Brazil, à qual se distribui pela Mata Atlântica e é presumidamente endêmica do país. Avaliamos se a hipótese de endemismo é suportada pelo clima passado e também avaliamos a sobreposição de nicho climático entre as linhagens *Bd*-Brazil e *Bd*-GPL, com o objetivo de verificar possíveis padrões que expliquem a distribuição conjunta dessas linhagens e a raridade da linhagem *Bd*-Brazil.

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CAPÍTULO 1

Potential worldwide impacts of sea level rise on coastal-lowland anurans

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Abstract

Amphibians are the most severely threatened terrestrial vertebrates and we are witnessing a global decline phenomenon, which is even suggested to be on the same level as historical mass extinctions. Although, a plethora of causative stressors have been identified in the last decades, future sea level rise (SLR) and its impact on coastal terrestrial fauna remains essentially unreported. Although there is no consensus on the magnitude of the future SLR, several studies suggest that it is likely to be greater than previously reported by the Fourth Assessment Report (AR4) of Intergovernmental Panel on Climate Change (IPCC). Therefore, it is reasonable to expect severe impacts on coastal terrestrial fauna worldwide. Hence, we assembled a data set of coastal-lowland anuran species worldwide in an attempt to quantify potential habitat loss caused by flooding in three different SLR scenarios. We also assessed potential habitat suitability under climate change (CC) in order to evaluate its potential effects on species' climatic niches, by building species distribution models for three future scenarios (A2a, A1b and B2a). Our results reveal that SLR has the potential to produce negative impacts on ~86% of the selected coastal-lowland species in different magnitudes, whereas CC is expected to produce a greater impact on these taxa. Thus, species predicted to persist under the new climatic conditions may be exposed to effects associated with SLR. Breaking our results down to biogeographic realms, we identified the anurans from Australasia as the most threatened by SLR and CC, with proportionally more species potentially threatened. Based on our results, we advocate for the inclusion of SLR future impacts in conservation action plans, anticipating and preventing biodiversity loss.

Key-words: Amphibians, BIOCLIM, climate change, declining populations, species distribution models

Introduction

Global climate change (CC) is claimed to be one of the drivers of changes on biodiversity (Barnosky et al. 2011; Bellard et al. 2012). The expected increase in the amount of atmospheric CO_2 for the year 2100 is expected to affect several other climatic parameters such as temperature, moisture and precipitation rates (IPCC 2007). This is predicted to impact life on several levels of organization, i.e., from organisms to entire ecosystems (Yasuhara et al. 2008; Svenning et al. 2011; Bellard et al. 2012; Lučan et al. 2013; Sorte & White 2013). Likewise, it is plausible to assume that such changes are potential drivers of generalized biodiversity loss (Wake & Vredenburg 2008; Blaustein et al. 2010; Alford 2011; Hof et al. 2011), since CC *per se* has the potential to modify environmental conditions and push species to their physiological boundaries (Huey et al. 2010; Silva et al. 2013), leading taxa to shift their geographical ranges or simply to succumb *in locus*, when they are not able to overcome barriers (Early & Sax 2011; Wake 2012). In addition, the existing synergisms between CC and other factor are expected to interact with or boost other established hazards (e.g., Hayes et al. 2010; Hof et al. 2011; Foden et al. 2013).

Another disturbing factor that may become relevant for the future of biodiversity is the expected sea level rise (SLR) (Menon et al. 2010; Bellard et al. 2013). This phenomenon is an expected consequence of CC owing to two main reasons, namely water expansion caused by the increasing entropy of water molecules and also the progressive melting of glaciers and ice sheets, both as a result of warmer temperatures (IPCC 2007). Furthermore, although the IPCC's Fourth Assessment Report (AR4) (2007) predicts a SLR not higher than 60 cm, several studies present more pessimistic SLR scenarios (e.g., Overpeck et al. 2006; Grinsted et al. 2007; Rahmstorf 2007; Rahmstorf 2010), with SLR potentially reaching up to 6 m in the coming centuries. In fact, a precise and definitive SLR projection for the 21th century is still absent owing to the lack of knowledge on the polar ice sheet dynamics (Church et al. 2013). Nonetheless, only few studies have discussed the SLR impacts on the biodiversity (Menon et al. 2010; Wetzel et al. 2012; Bellard et al. 2013) preventing the anticipation and adoption of relevant conservation actions. Thus, assessment of the potential impacts of SLR on terrestrial fauna is imperative for the effective conservation of biodiversity.

In the current extinction crisis amphibians are the vertebrates that are facing a severe loss of biodiversity (Wake 1991; Stuart et al. 2004; Barnosky et al. 2011), including dramatic population declines and species extinctions worldwide (Kiesecker et al. 2001; Wake & Vredenburg 2008). This alarming situation is attributed to several causes such as habitat loss, habitat split, invasive alien species, over-exploitation, infectious diseases and climate change as well (Becker et al. 2007; Wake & Vredenburg 2008; Blaustein et al. 2010). Besides assembling a complex puzzle, these factors may interact synergistically (Blaustein et al. 2010; Hayes et al. 2010; Hof et al. 2011), making amphibians into the most threatened vertebrates on Earth (Hoffman et al. 2010). However, parallel to studies on multiple effects, during the last two decades researchers employed great efforts to understand the causative aspects of the amphibian decline puzzle. As an example, after the discovery of the *Batrachochytrium dendrobatidis* in 1999 (Longcore et al. 1999), more than 600 articles have been published in regard to several aspects of chytridiomycosis. Although this gain of knowledge is a great step forward, other pieces of the amphibian crisis puzzle remain unclear. Thus, in order to uncover additional threats we must evaluate the whole scenario in a comprehensive fashion to play an effective role in conservation.

The vast majority of the amphibians cannot live in salty water, i.e., the salinity is lethal for most species in any stage of their life cycle (Wells 2007). However, many amphibian species worldwide are exclusively distributed in association to coastal-lowland zones (mainland and/or islands) with several cases of restricted distribution ranges and endemism in such regions (Vences et al. 2009). Thus, in this sense, it is expected that coastal-lowland amphibian species are likely to suffer some effects of SLR.

Hence, herein we investigate coastal-lowland amphibian species and global coastal regions most likely to suffer potential impacts associated with SLR using anurans as biological models. We used species distribution models (SDM) (Franklin 2009) in a species-specific approach to explore the potential magnitude of the immediate effects of SLR on coastal-lowland anuran species worldwide. We focused our approach on anurans because they have some particular features, as susceptibility to environmental changes (Wake 2012, Foden et al. 2013), notoriously low ability to migrate (Wells 2007; Kovar et al. 2009; Heermeyer & Lannoo 2012), and low tolerance to salinity (Wells 2007). Also, their position as endangered group (Hoffman et al. 2010) is another element that encourages studies with this group. We specifically addressed the following questions: 1) which anuran species in the world are most susceptible to suffer the impacts of SLR?; 2) is there a specific region worldwide where such effects are expected to be greater?; 3) how will SLR affect the habitat availability for the coastal-lowland anuran species?

Methods

Data sources

We assessed the comprehensive global data set comprising 5487 anuran species provided by The IUCN (International Union for Conservation of Nature and Natural

Resources) Red List of Threatened Species, version 2010.4 (IUCN 2010), to select those taxa that may be potentially affected by the future SLR. Our selection predominantly followed three criteria: i) species with distribution range associated with coastal zones or restricted to islands; ii) taxa presenting populations at sea level (especially those with altitudinal range in a band between sea level up to 100 m above sea level (asl)); iii) taxa considered as typically lowland species by specialists. However, even gathering these characteristics, species that presented missing (e.g. original polygon unavailable) or imprecise (inaccurate altitudinal range distribution) information that prevented modeling were excluded from the subsequent analyzes.

Although commonly used in several modeling approaches, herein we avoided using point location for three reasons: i) on the scale at which the analyses were performed (i.e. global), exact species records are available only for part of our data set, which could lead to a bias in results; ii) in our case, the cost of additional field surveys to assemble a comprehensive set of species record is prohibitive; iii) point location may offer additional bias, since samples are often performed in areas with easy access, increasing omission errors (Loyola et al. 2013; Ficetola et al., 2014). Instead, we transformed the IUCN shape files into rasterized digital range maps with spatial resolution of 2.5 arc-minute (approximately 5 km). The available range information in terms of polygons summarizes the area of occupancy or the extent of occurrence (Gaston & Fuller 2009; Ficetola et al., 2014). We used these maps to generate presence-only point locations by randomization within the polygons. Number of points varied from 10 up to 8348, and was generated considering the range extent of polygon for each species.

To assess potential effects of SLR, we used raster files of 1, 2 and 3 m of SLR scenarios provided by the Center for Remote Sensing of Ice Sheets (www.cresis.ku.edu).

Likewise, current climatic data used to build the distribution models were obtained from WorldClim (www.worldclim.org) (Hijmans et al. 2005), whereas future climatic scenarios were downloaded from the CIAT webpage (www.ccafs-climate.org). We used a comprehensive set of 19 bioclimatic variables (see details in www.worldclim.org/bioclim) to build distribution models for the present and also for three future scenarios (A1b, B2a and A2a) for the year 2080. We used future scenarios developed by the IPCC AR4 (IPCC 2007) and, in order to minimize the source of uncertainty, we averaged the following climatic models: MPI-ECHAM5, NCAR-CCSM3, UKMO-HADCM3, UKMO-HADGEM1, CCMA-CGCM2, CSIRO-MK2, HCCPR-HADCM3, and NIES99.

Distribution model development

We built all the distribution models based on bioclimatic variables in the statistical software R (R Development Core Team 2013) using the BIOCLIM algorithm as implemented in the dismo package (Hijmans & Elith 2013). SDMs outputs included model for present and future (2080) conditions, and were evaluated by the inspection of the area under the receiver operating characteristic curve (AUC) values. Although there are several techniques for modeling a species' potential distribution (Franklin 2009), there is a lack of consensus on the finest method to predict species' presence or absence giving the environmental variables. Therefore, to choose a reliable modeling technique is important to avoid or minimize errors inherent to the modeling (Lobo et al. 2008). Thus, we carefully selected the BIOCLIM algorithm, which may best fit the rather coarse nature of the input data. BIOCLIM is a correlative presence-only modeling tool that summarizes a species' climatic envelope to predict its potential distribution (Beaumont et al. 2005). It is largely used for modeling purposes and also has shown good performance in modeling (e.g. Tôrres et al. 2012), especially when the aim is to assess a species' potential distribution rather than its realized distribution (Jiménez-Valverde et al. 2011).

Modeling algorithms build models inferred from abiotic variables without considering biotic interactions (Franklin 2009); usually generating overpredictions (i.e. commission errors). One possibility to avoid this undesired outcome is to incorporate historical and biotic attributes to the resulting map (Soberón & Nakamura 2009). We worked under the general assumption that anurans are not able to migrate long distances, especially those species that have restricted distributional range (e.g. Becker et al., 2007; Semlitsch 2010). Thus, we applied a buffer of 100 km to the species' original polygons in order to assess potential distribution and shift under different conditions within the buffer, attempting to generate feasible outputs.

Computing the SLR potential impacts

We calculate the percentage of future range loss caused by the SLR per species and per scenario, considering both current (1950 - 2000) and future (2080) distributions. We evaluated the potential consequences of SLR including the current species' distribution because several of them presented distribution ranges restricted to islands. Since for such species migrations overseas are unlikely, we opted to analyze the potential loss of available land considering the current distribution, including the complete data set to avoid or minimize sources of unbalance. To calculate the percentage of range loss caused by flood per scenario, we overlaid the current distribution estimate in terms of IUCN shape files and the potential distributions derived from the SDM with raster files of three SLR simulations, and then we subtracted the overlap using ArcGIS 10 (ESRI 2011). The SLR scenarios were cautiously chosen to simulate optimistic, intermediate and pessimistic possibilities, in agreement with the relevant literature (e.g. Rahmstorf 2007; Grinsted et al. 2010; Rahmstorf 2010). We attempted to reduce under and overestimations concerning SLR projections, since the debate about the magnitude of the reach of the SLR remains inconclusive (Rahmstorf 2010), and the comprehension about ice sheet dynamics and its contribution to this phenomenon is still in progress (Bamber et al. 2009; Mitrovica et al. 2009; Gomez et al. 2010; Shepherd et al. 2012).

We estimated the potential loss of land for each species by calculating the differences in terms of grid cells through the different scenarios to verify which set of variables (CC or SLR) is expected to produce larger magnitude of effects. Then, we transformed the results in percentage of gain or loss of land per species in each scenario. Finally, we assessed the final results to verify and compare the magnitude of the different potential threats (SLR and CC) on the current and suggested future distribution for each species in the three future scenarios. It is important to emphasize that we considered different effects of the SLR and CC to reach our aims. Although SLR is a consequence of CC, we take into account the primary SLR effect of loss of available land where a given species could occupy. On the other hand, we compute the CC effects of changing environmental conditions, which may influence the suitability of the climatic niche for a given species. Ultimately, we compared the results through six different world biogeographic realms, namely Palearctic, Nearctic, Neotropic, Afrotropic, Indo-Malay and Australasia (Olson et al. 2001), following the anuran distribution worldwide (Stuart et al. 2008). We estimated whether the potential threats are expected to cause larger impact in distinctive regions of the world.

Results

Global threatened taxa

The final data set comprised 123 lowland anuran taxa worldwide (~ 2 % of the global anuran diversity), from which 33 % (n = 41) are distributed exclusively below 60 m asl. We excluded 55 species from analyzes owing to lack or imprecise information. We analyzed a total of 1845 models considering outputs of current and future climatic conditions and SLR scenarios. All models were considered acceptable presenting AUC values of 0.98 in average (± 0.02). Approximately 34 % (n = 42) of the species are current listed as “least concern” (LC) by the IUCN (2013), and ~ 37 % (n = 46) are assigned as “near threatened” (NT: ~ 13 %; n = 6) or at some category of threat, i.e., “vulnerable” (VU: ~ 28 %; n = 13), “endangered” (EN: ~ 48 %; n = 22), and “critically endangered” (CR: ~ 11 %; n = 5). Finally, ~ 28 % (n = 35) are current listed as “data deficient” (DD). The family Hylidae presented the highest number of species (n = 23), followed by Microhylidae (n = 21). On the other hand, the families Petropedetidae and Ceratobatrachidae had the highest proportion of species potentially at risk (~ 16 % (n = 2) and ~ 15 % (n = 13), respectively).

Besides loss of land by flooding, we detected fragmented potential suitable extents by marine water intrusions on lowland areas. Nevertheless, the overall magnitude of the suggested impacts through the three SLR scenarios were similar, i.e., the amount of loss of land for the species’ current distributions were merely slightly different, increasing proportionally as the sea level rises in the simulations (1, 2 and 3 m). In fact, for most of the species (n = 74), potential losses by SLR are expected to be less than 10 %. However, we detected loss of land in any degree by flood for ~ 86 % (n = 106) of the analyzed taxa under the present conditions. For four species (all endemic to islands), we detected a 100 % of potential loss of land by flood owing to the SLR, i.e., complete habitat unavailability (see an example in Figure 1a and b). We also detected potential habitat losses greater than 10 % and perceptible fragmented habitat suitability for at least 28 species (~ 23 %) (Figure 1c and d).

Under the perspective of the biogeographic realms, an overview on the anuran species richness revealed an unbalanced magnitude of potential impacts throughout the world (Figure 2). Whereas for the Palearctic, Nearctic, Neotropic, Afrotropic and Indo-Malay regions the predicted loss of land for their local coastal-lowland anurans is approximately 1 %, for the Australasian region ~ 8 % of its local coastal anuran richness may be displaced. Likewise, we detected potential loss of land by flood in magnitudes greater than 10 % for at least one species in the Afrotropic, Indo-Malay and Australasia regions. However, most species of these biogeographic realms are expected to have losses below 10 %. We also identified possible 100 % loss of land and fragmented suitable habitat owing to marine intrusion for certain species in the Neotropic, Afrotropic and Australasia regions. Thus, Australasia was identified as the biogeographic realm most likely to receive severe potential impacts caused by SLR.

Future habitat suitability

According to our SDM outputs, we categorized three distinctive possibilities in terms of future climatic conditions (Figure 3): increase, decrease, and complete habitat unsuitability. Although the amount of suitable habitats within a 100 km buffer is expected to increase for some species in the near future (further details in the supplementary material, Table S1), decreases may be expected for the majority of analyzed taxa, with several cases of apparent spatial shifts where taxa may be pushed completely outside of their currently distribution. However, in such cases a small portion of suitable habitat remains. Nevertheless, in a third possibility, the models suggest complete habitat unsuitability for several species through the different scenarios, i.e., numerous species are expected to be pushed out of their currently realized niches, even within a buffer of 100 km around their current distributional ranges. As observed in the SLR simulations, the magnitude of possible CC impacts is similar among the scenarios and we cannot distinguish an optimistic or pessimistic scenario (Figure 4).

The potential effects of CC on future habitat suitability by biogeographic realms also revealed a similar pattern (further details in Table S1 and S2). In the Palearctic realm, no future suitable habitats can be expected for ~ 0.5 % of the local coastal-lowland anuran richness, as well as decreasing suitable areas were identified for another ~ 0.5 %. In the Nearctic, it is expected a complete habitat unsuitability for an average of ~ 1 % of the local richness, and a decrease in suitable areas for an additional one species (~ 0.7 %). At the same time, we observed increasing suitable habitats for some species (~ 0.6 %, n = 5) in the Neotropic region, but decreased or complete unsuitability for ~ 28 % of the local coastal-lowland anuran richness. As for the present conditions, the Afrotropic, Indo-Malay and Australasia realms showed similar patterns in terms of CC potential impacts, with few cases of expected increasing suitable habitats. However, several cases of decreasing suitable habitats were detected in Afrotropic, Indo-Malay, and Australasia, as well as, complete habitat unsuitability were detected for the future in these regions. As for the present, Australasia remains as the biogeographic realm most likely to be severely affected by future CC in terms of coastal-lowland anuran richness.

Analyzing the potential SLR effects for the future species' distribution under the imminent climate conditions, we also detected distinctive magnitudes of such possible implications (Figure 4). The overlapping layers (modeled distributions and SLR scenarios) followed by the calculation of loss of land by flood suggest future losses for only twelve species (~ 9 %) of the complete data set, most of them (n = 7) with losses estimated to be below 1 %. However, we identified losses of ~ 20 % for two species (*Crinia tinnula* and *Litoria olongburensis*) in at least one SLR and CC scenario. In addition, we identified loss of land greater than 10 % for four species (*Crinia insignifera*, *Crinia tinnula*, *Litoria olongburensis* and *Uperoleia martini*) in a scenario, and also a potential total loss by flood for one exclusively insular species (*Leptodactylus fallax*), which is considered as CR by the IUCN. Specifically for this species, the potential distribution suggested by the SDM is only one suitable grid in the B2 scenario, which may be inundated in the future.

Moreover, after the intersection of the SDMs and SLR scenarios, we noticed that, for those species for which an increase or decrease in suitable habitats may be expected, most of them tend to shift their distribution range from the current condition toward inland (~ 38 % (n = 47, A2a), ~ 42 % (n = 51, A1b), ~ 46 % (n = 57, B2a); Figure 5). On the other hand, SDMs suggest that some species may be able to shift their distribution ranges and stand in the coastal region, even under the new climatic conditions (n = 6 (A2a and A1b), n = 12, (B2a)). In such cases, suitable habitats fragmented by marine water intrusion can be expected.

Discussion

As far as we are aware, this is the first global approach focused on the potential impacts of SLR on the coastal-lowland anuran species. Previously, Bellard et al. (2013) identified several living taxa (plants and terrestrial and freshwater vertebrates) in insular biodiversity hotspots that may be threatened by SLR, which included one to two anurans species in two to three meters of rising sea simulations. Our study comprises continental species as well, and we showed potential losses by SLR (*per se*) for four to five species, depending on the scenario in the same sea level simulations used by Bellard et al. (2013). However, if we include the potential effects of CC on the species' niche for future suitability, approximately 50 % of our data set is predicted to suffer severe impacts in some future scenario, independently of SLR. In other words, at this point, it is important to emphasize that our results revealed that CC has the potential to produce greater negative impacts on coastal-lowland anurans than SLR itself. Although SLR is a consequence of CC, the potential effects incurred by each one are different in several aspects. For example, whereas CC is expected to produce consequences on the species' climatic niche (Lemes & Loyola 2013; Loyola et al. 2013), SLR has the potential to submerge climatic available areas that could be occupied in the future, i.e., turning them into unavailable habitats.

By analyzing different scenarios we showed that these two phenomena have the potential to affect more than 100 anuran species worldwide. Some taxa in our data set are already classified as threatened, but several others are considered LC or NT. If the SLR is taken into account in future evaluations, it is likely that some of these non-threatened species may have their threat status changed. Besides the plethora of current pressures (Blaustein et al. 2010; Becker et al. 2007; Wake 2012) SLR may represent an additional threat by the potential flooding of habitats and/or fragmentation of future suitable areas (Menon et al. 2010; Wetzel et al. 2012; Bellard et al. 2013). Besides this, some threats may not be so definite as SLR will be. For example, the chytridiomycosis may be lethal to some individuals, but not to others (Pilliod et al. 2010), therefore, population declines due to fungal infection is not certain. On the other hand, amphibians may not tolerate flooding by salt water.

In the global biogeography context, the anuran species richness in Tropical regions is high (Frost 2013, especially in the Neotropics (Stuart et al. 2008). Consequently, this region could be expected to be the most severely affected in terms of potential losses in biodiversity as a result of SLR. However, although Australasia is not the richest biogeographic realm concerning the anuran biodiversity, our results indicate it to be the region with proportionally most anuran taxa potentially at risk by SLR in terms of magnitude of impacts. Australasia is characterized by the presence of numerous islands and fjords (Olson et al. 2001), which may be more susceptible to marine water intrusions (Michener et al. 1997). Additionally, including the potential effects of CC, comparably higher impacts along coastal lines in some continents may be expected (e.g. Loyola et al. 2013) and also in associated islands (Bellard et al. 2013), since distribution range shifts by dispersion or migration may be hindered for freshwater vertebrates in such cases (e.g. Furlan et al. 2013). Furthermore, the sea level is rising more rapidly in the West Pacific (Nicholls & Cazenave 2010), which may represent an immediate threat for the coastal associated terrestrial fauna in this region. Indeed, Wetzel et al. (2012) identified several endemic mammals potentially threatened by SLR in Indo-Malasyan islands, whereas Bellard et al. (2013) stressed that several species (plants and other vertebrates) from the Caribbean islands may suffer the most severe impacts from the SLR, and Menon et al. (2010) revealed Southeast Asia as the most potentially region impacted by flood with SLR. Therefore, it seems that several ecoregions in the world may be threatened by SLR in the next century. This is a bleak panorama that reinforces how complex it is to anticipate the SLR effects and, at the same time, highlights that SLR cannot be ignored.

Moreover, there are also the potential local effects of SLR, which are difficult to predict precisely. Potential marine water intrusions into coastal fresh water bodies (Menon et al. 2010; Nicholls & Cazenave 2010), even sporadically, have the potential to increase salinity, creating an unsuitable habitat and jeopardizing larval development (e.g. Rios-López 2008), in the case of amphibians. Another possibility is the introduction of unusual potential marine predators (fishes and invertebrates) to fresh water bodies (Blaustein et al. 2010), which could reduce anuran populations. Ultimately, extreme events as hurricanes and flood tides are expected to become more frequent and intense with CC (Michener et al. 1997; IPCC 2007), potentially increasing the incidence of marine water intrusions and consequently boosting the issues mentioned above.

Concurrently, our results clearly corroborates that CC is one of the most certain future stressors that will lead to loss of biodiversity worldwide (Hof et al. 2011; Loyola et al. 2013; Foden et al. 2013). Although there are several uncertainties inherent to SDMs (Diniz-Filho et al. 2012), there are biological traits that support the observed patterns for our SDMs. For instance, one cause for predicted unsuitability or range contraction may be related to the reproductive mode of the species. Species with more specialized reproductive modes have narrow habitat requirements for reproduction and could be more susceptible to environmental changes (Loyola et al. 2013). In this frame, our data set is composed of several stream dwelling species with aquatic eggs (e.g. Hylodidae, Cycloramphidae) and taxa with direct development (e.g. Eleutherodactylidae). Thus, range decrease and habitat unsuitability as a consequence of deforestation by warming temperatures can be expected for such taxa (Loyola et al. 2013). Moreover, at a finer scale, anurans that exhibit low thermal tolerance may experience physiological constrains under elevated temperatures in their microhabitats (Duarte et al. 2012). Although tadpoles of some species have a higher tolerance for warm temperatures, adults may experience different effects of climate change (e.g. higher air temperatures or dehydration) (Duarte et al. 2012), which also support our

SDM predictions. Besides, CC is expected to require adjustments in some biological traits (e.g. reproduction, calling phenology), consequently altering breeding seasons and promoting niche overlap among species (Geyer et al. 2011; Todd et al. 2011; Walpole et al. 2012), which ultimately may lead to modifications on the community level (e.g. Walpole et al. 2012), or even local extinctions of sensitive species (Geyer et al. 2011; Loyola et al. 2013).

Simultaneously, in regard to those species for which habitat suitability is expected to increase, CC could be misinterpreted as beneficial for such species. In fact, it seems that CC has the potential to favor species that are able to tolerate warmer and variable conditions, relatively increasing their performance to stand in a new climatic state (Blois et al. 2013). Such species probably represent taxa that are able to tolerate higher temperatures (e.g. Duarte et al. 2012). Consequently, these taxa will potentially have their distribution ranges enhanced in the future. Conversely, it is important to remember that SDMs possess several caveats and limitations, and they only suggest habitat suitability based on bioclimatic variables (Franklin, 2009). Thus, for a complete statement on the species' realized future distributions, we need to take into account processes at several levels, such as the interactions among species (e.g. Todd et al. 2011; Blois et al. 2013), habitat fragmentation (e.g. Becker et al. 2007), dissemination of emergent diseases (e.g. Hof et al. 2011), and capacity of migration (e.g. Heermeyer & Lannoo 2012), especially upslope migration, i.e., toward to cooler conditions (e.g. Loyola et al. 2013). All of these conditions may affect the future persistence of species in the current and suggested distributional locations.

The SLR issue is far from being completely elucidated and further studies are welcomed. We recommend the development of additional modeling approaches at finer scales, regional and more accurate SLR projections (Nicholls & Cazenave 2010; Willis & Church 2012), local monitoring programs (Verdade et al. 2012), and the inclusion of biological traits (e.g. physiological limits) in the models to better understand the magnitude and anticipate the impacts of SLR on biodiversity. Rise in sea level worldwide is an assured result caused by global warming (Nicholls & Cazenave 2010) and will play an important role in the amphibian decline puzzle. Thus, since SLR was largely ignored in previous conservation plans for amphibians (e.g. Gascon et al. 2005; Verdade et al. 2012), we strongly suggest its inclusion in future actions.

Conclusions

We answered our questions by identifying which anuran species in which global regions may be potentially threatened by SLR, and we depicted possible effects (flood or habitat fragmentation) in a comprehensive manner. Moreover, we reinforced CC as a major threat for the coastal-lowland anuran biodiversity worldwide and exposed SLR as a potential threat that cannot be ignored. Nevertheless, our approach emphasized the importance to search for unreported threats related to future environmental changes and provided a new starting point for additional investigations. Although we used anurans as biological models to explore potential SLR effects, it is likely that several other taxa, particularly those terrestrial, with small distribution ranges, low capacity of dispersal or migration, and low tolerance to salinity, may suffer from the SLR effects in a similar way that we presented. Yet, our goals in this study were to evaluate which species (and not many) could be endangered by SLR. Finally, we strongly recommend the inclusion of SLR effects on subsequent Amphibian Conservation Action Plans (e.g., Gascon et al. 2005; Verdade et al 2012).

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Table and figure caption page

Figure 1 SLR has the potential to submerge current distributional areas for coastal-lowland anurans as we observed for (a and b) *Mertensophryne howelli*, an endemic insular lowland species from Zanzibar with a potential flood of 100 % of its distributional range; and (c and d) *Arenophryne rotunda*, an endemic species from Western Australia for which SLR may fragment suitable habitats. Current distributional range is represented by black lines.

Figure 2 Proportion of species potentially threatened by future sea level rise (SLR) (light grey bar), climate change (CC) (dark grey bar), and the corresponding local richness (LR) (black bar) within the sampling universe (numbers after bars indicate number of species) per world biogeographic realm (adapted from Olson et al. 2001): Palearctic (yellow), Nearctic (light blue), Neotropic (green), Afrotropic (dark yellow), Indo-Malay (light green), and Australasia (pink).

Figure 3 Three patterns of SDM outputs observed for three emission scenarios (A2a, A1b, and B2a). Future habitat suitability is expected to increase for few species (**a** to **d**: *Batrachyla nibaldoi*, an endemic South American species), but for several other taxa a decrease in habitat suitability (**e** to **h**: *Batrachylodes mediodiscus* from the Solomon Islands) or total unsuitability (**i** to **l**: *Craugastor yucatanensis* from Mexico, in the Caribbean Sea) is predicted for the year 2080. Current distribution is represented by black lines.

Figure 4 Comparative magnitude of the potential effects from CC and SLR in terms of loss of suitable grids (a) and potential losses for persistent species under CC in terms of loss of suitable grids by flood in different SLR scenarios (b).

Figure 5 An example of predicted habitat suitability toward inland for *Rhinella pygmaea*, an endemic toad from the Brazilian Atlantic forest lowlands. Its current distribution is showed in (a), and the potential suggested future suitable areas for three emission scenarios are presented as follows: (b) A2a, (c) A1b, and (d) B2a.

Figures

Figure 1

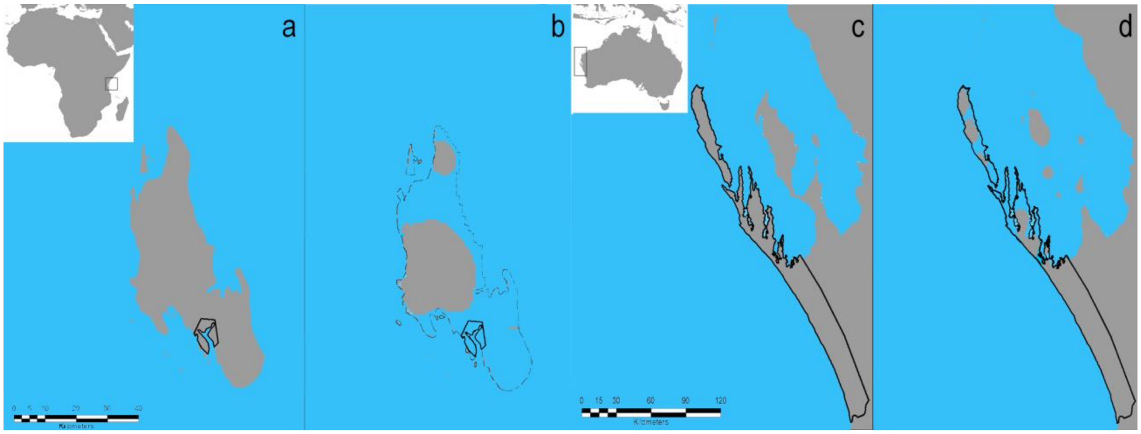
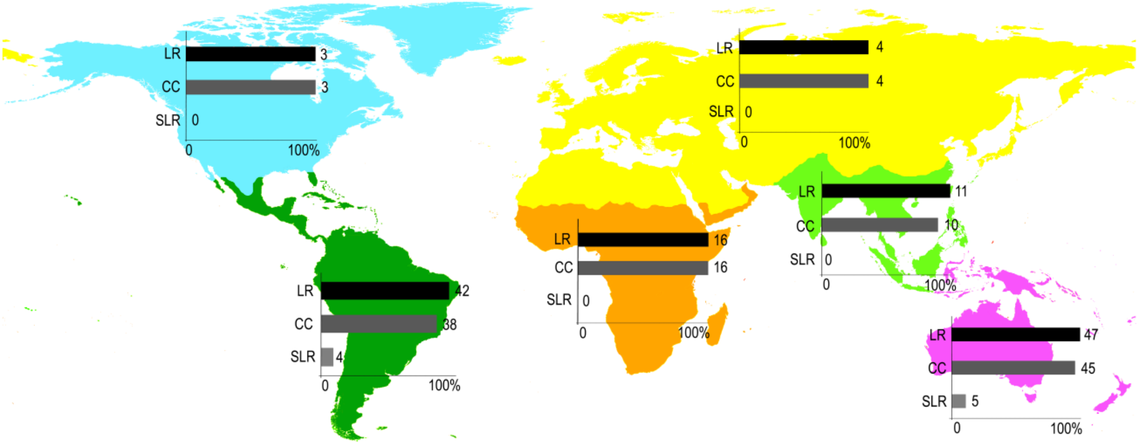


Figure 2



LR 3
CC 3
SLR 0
0
100%
LR 4
CC 4
SLR 0
0
100%
LR 11
CC 10
SLR 0
0
100%
LR 16
CC 16
SLR 0
0
100%
LR 42
CC 38
SLR 4
0
100%
LR 47
CC 45
SLR 5
0
100%

Figure 3

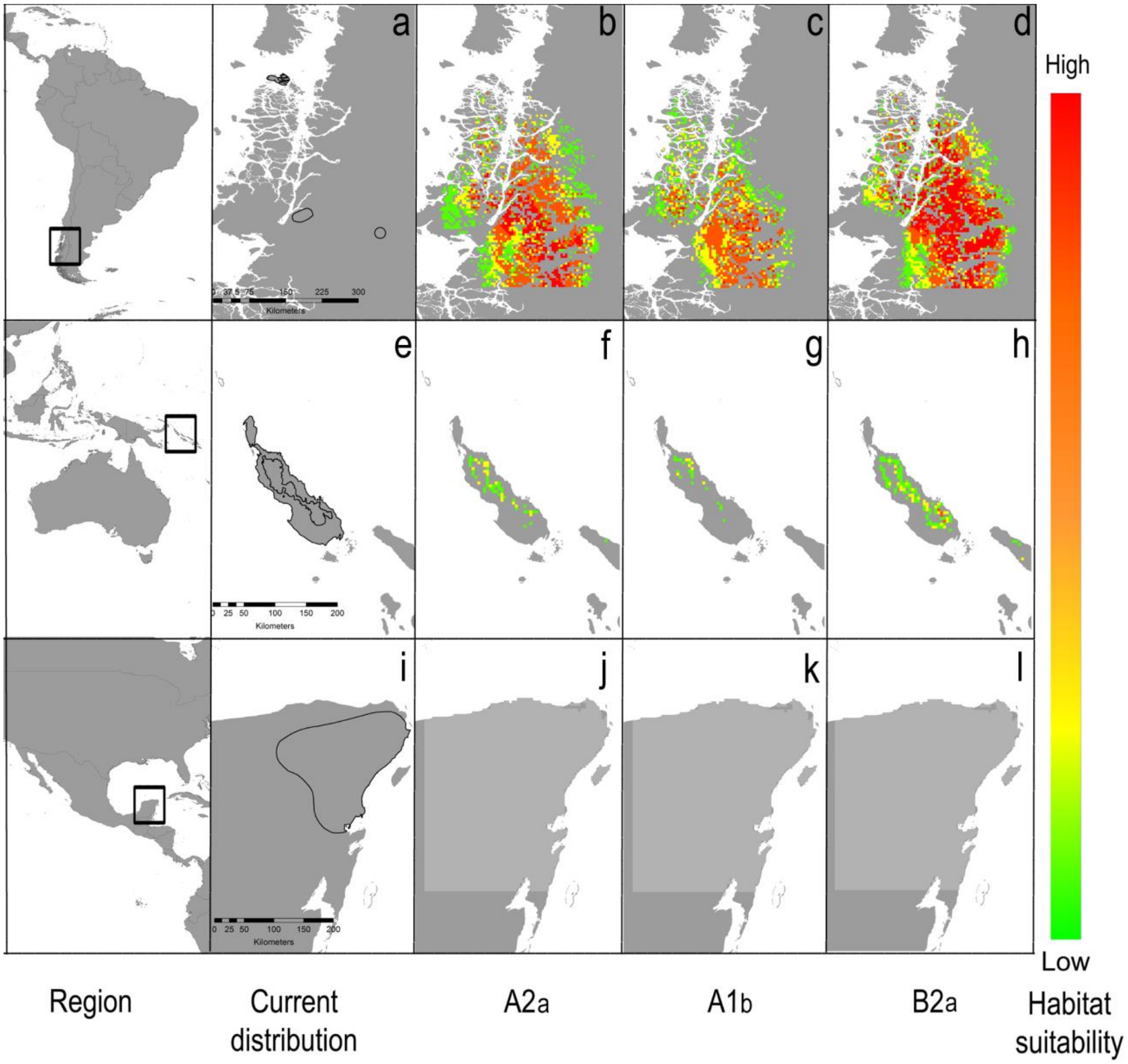

a
b
c
d
High
0 37.5 75 150 225 300
Kilometers
e
f
g
h
0 25 50 100 150 200
Kilometers
i
j
k
l
0 25 50 100 150 200
Kilometers
Low
Region
Current distribution
A2a
A1b
B2a
Habitat suitability

Figure 4

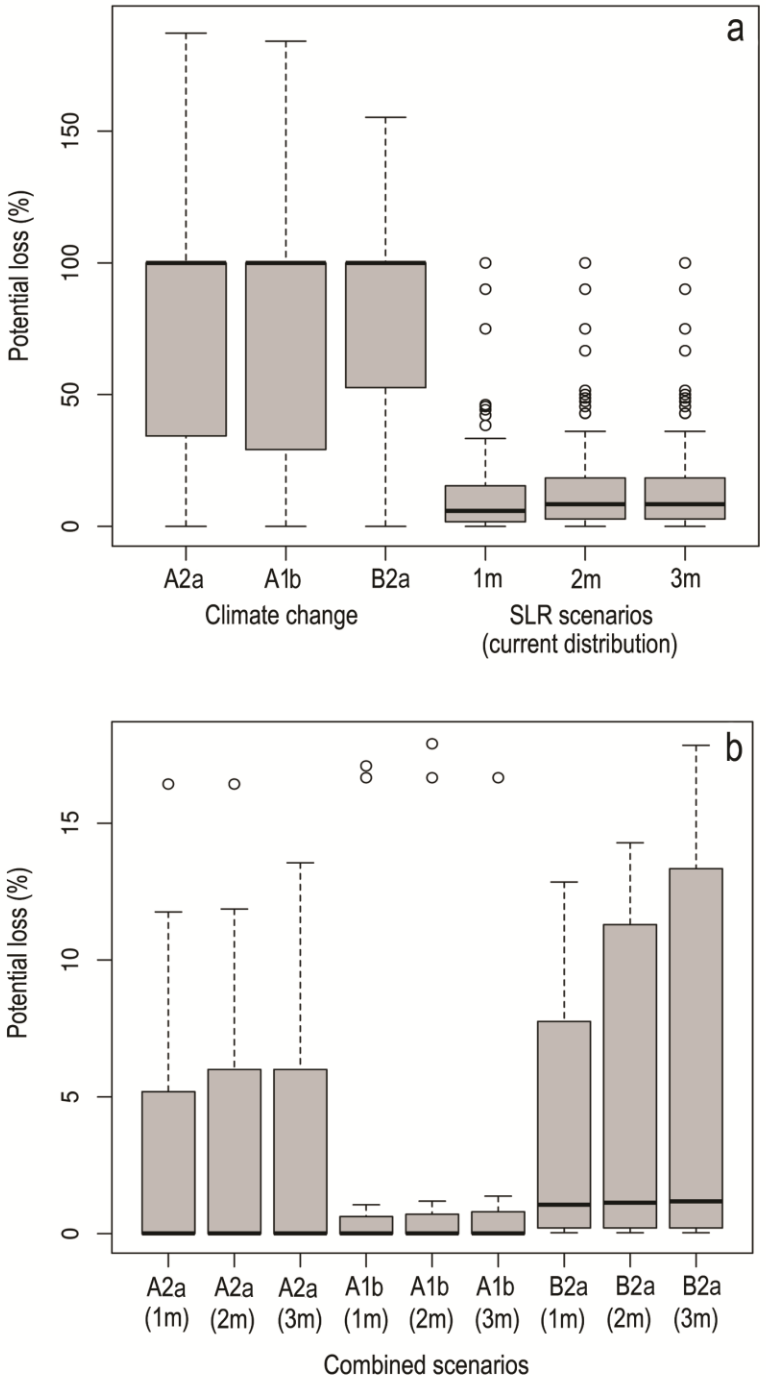
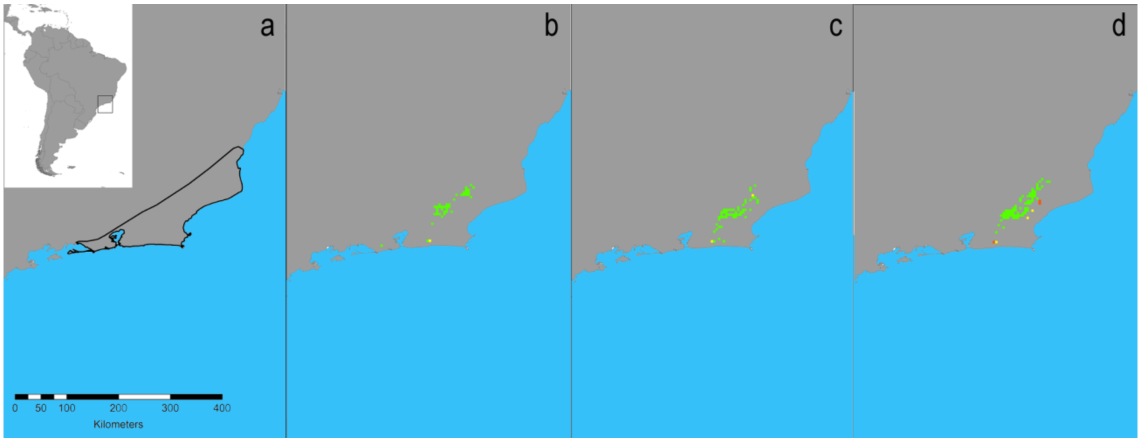

a
Potential loss (%)
0
50
100
150
A2a
A1b
B2a
1m
2m
3m
Climate change
SLR scenarios
(current distribution)
b
Potential loss (%)
0
5
10
15
A2a (1m)
A2a (2m)
A2a (3m)
A1b (1m)
A1b (2m)
A1b (3m)
B2a (1m)
B2a (2m)
B2a (3m)
Combined scenarios

Figure 5



Supplementary material

Table S1. Potential suitable area extent estimated by Species Distribution Modelling for the year 2080 for three different climatic scenarios and estimated magnitude of loss of habitat suitability for three sea level rise scenarios. All presented values are calculated approximations based on the 2.5 arc-minutes grid cells. Taxonomy follows International Union for Conservation of Nature (IUCN) Red List of Threatened Species, version 2010.4 (IUCN 2010).

Taxa	Potential suitable area (km^2)	Potential suitable área (km^2)			Loss by SLR (km^2)								
	Scenario	Scenario			Scenario								
					A1b			B2a			A2a		
	Current	A1b	B2a	A2a	1 m	2 m	3 m	1 m	2 m	3 m	1 m	2 m	3 m
Afrixalus sylvaticus	9,150	2,100	7,450	2,425	0	0	0	0	0	0	0	0	0
Alsodes australis	9,775	13,1975	174,450	114,350	250	300	300	450	525	525	225	275	275
Alsodes kaweshkari	150	2,100	1,225	125	0	0	0	0	0	0	0	0	0
Amietophrynus pantherinus	2,275	1,175	1,850	875	0	0	0	0	0	0	0	0	0
Aplastodiscus eugenioi	4,400	17,025	16,850	15,175	0	0	0	25	25	25	0	0	0
Aplastodiscus leucopygius	146,500	307,975	330,050	185,925	50	50	50	100	100	100	25	25	25
Arenophryne rotunda	4,700	0	0	0	0	0	0	0	0	0	0	0	0
Arthroleptella lightfooti	450	0	0	0	0	0	0	0	0	0	0	0	0
Atelopus flavescens	550	0	0	0	0	0	0	0	0	0	0	0	0
Austrochaperina adelphe	130,075	0	25	0	0	0	0	0	0	0	0	0	0
Austrochaperina gracilipes	93,175	325	775	300	0	0	0	0	0	0	0	0	0

Austrochaperina parkeri	175	6,275	3,500	4,525	0	0	0	0	0	0	0	0	0
Babina holsti	875	0	0	0	0	0	0	0	0	0	0	0	0
Babina okinavana	2,975	2,650	2,400	825	0	0	0	0	0	0	0	0	0
Babina subaspera	1,025	0	0	0	0	0	0	0	0	0	0	0	0
Barbourula busuangensis	3,100	950	1,175	700	0	0	0	0	0	0	0	0	0
Barygenys exsul	4,250	1,925	3,125	1,475	0	0	0	0	0	0	0	0	0
Batrachyla nibaldoi	1,950	37,375	56,050	52,600	50	50	50	75	75	75	100	100	125
Batrachylodes mediodiscus	7,825	625	3,000	1,475	0	0	0	0	0	0	0	0	0
Batrachylodes trossulus	3,575	2,400	3,950	2,750	0	0	0	0	0	0	0	0	0
Batrachylodes vertebralis	30,175	50,225	14,500	7,500	0	0	0	0	0	0	0	0	0
Batrachylodes wolfi	13,250	1,375	5,900	2,875	0	0	0	0	0	0	0	0	0
Boophis xerophilus	200	300	1,125	450	0	0	0	0	0	0	0	0	0
Breviceps macrops	11,450	0	7,175	6,825	0	0	0	100	100	100	0	0	0
Calluella brooksii	6,950	8,975	32,800	23,900	0	0	0	0	0	0	0	0	0
Calluella smithi	6,475	48,725	122,250	80,700	0	0	0	0	0	0	0	0	0
Callulops doriae	86,450	110,125	129,375	124650	0	0	0	0	0	0	0	0	0
Callulops kopsteini	625	0	0	0	0	0	0	0	0	0	0	0	0
Cardioglossa aureoli	250	0	0	0	0	0	0	0	0	0	0	0	0
Ceratobatrachus guentheri	34,475	5,325	14,025	7,450	0	0	0	0	0	0	0	0	0

Ceratophrys stolzmanni	3,925	325	425	0	0	0	0	0	0	0	0	0	0
Chiasmocleis alagoanus	300	0	0	0	0	0	0	0	0	0	0	0	0
Chiasmocleis capixaba	20,600	4,200	275	0	0	0	0	0	0	0	0	0	0
Chiasmocleis carvalhoi	21,700	23,475	33,700	27,325	0	0	0	0	0	0	0	0	0
Cophixalus verrucosus	32,725	38,800	34,725	29,150	0	0	0	0	0	0	0	0	0
Copiula oxyrhina	14,600	25	12,550	9,400	0	0	0	0	0	0	0	0	0
Craugastor yucatanensis	30,025	0	0	0	0	0	0	0	0	0	0	0	0
Crinia insignifera	8,125	100	3,800	1,475	0	0	0	250	325	400	150	175	200
Crinia nimbus	6,700	2,500	4,725	1,650	0	0	0	0	0	0	0	0	0
Crinia remota	651,525	150,500	192,475	58,050	1,575	1,775	2,050	1,375	1,650	1,825	0	0	0
Crinia tinnula	39,300	18,425	21,200	3,650	3,150	3,300	3,700	2,725	2,975	3,425	600	600	725
Cycloramphus juimirim	275	0	0	0	0	0	0	0	0	0	0	0	0
Dendropsophus gaucheri	11,150	0	100	25	0	0	0	0	0	0	0	0	0
Discodeles bufoniformis	30,150	1,400	7,650	3,350	0	0	0	0	0	0	0	0	0
Discodeles guppyi	75,225	14,525	32,525	21,500	0	0	0	0	0	0	0	0	0
Discodeles opisthodon	14,350	2,625	7,850	3,450	0	0	0	0	0	0	0	0	0
Discodeles vogti	2,175	0	0	0	0	0	0	0	0	0	0	0	0
Duttaphrynus valhallae	125	0	0	0	0	0	0	0	0	0	0	0	0
Elachistocleis surinamensis	250,825	41,150	128,625	89,175	0	0	0	0	0	0	0	0	0

Eleutherodactylus cavernicola	75	0	0	0	0	0	0	0	0	0	0	0	0
Eleutherodactylus cochranae	5,075	3,125	4,150	1,025	0	0	0	0	0	0	0	0	0
Eleutherodactylus guanahacabibes	1,050	0	0	0	0	0	0	0	0	0	0	0	0
Eleutherodactylus lentus	300	0	0	0	0	0	0	0	0	0	0	0	0
Eleutherodactylus pinarensis	2,525	25	50	25	0	0	0	0	0	0	0	0	0
Eleutherodactylus rogersi	775	0	0	0	0	0	0	0	0	0	0	0	0
Eleutherodactylus thomasi	3,275	0	0	0	0	0	0	0	0	0	0	0	0
Fejervarya andamanensis	125	0	0	0	0	0	0	0	0	0	0	0	0
Fejervarya nicobariensis	475	0	0	0	0	0	0	0	0	0	0	0	0
Genyophryne thomsoni	33,600	50,450	43,750	41,900	0	0	0	0	0	0	0	0	0
Hemisus perreti	58,150	7,650	42,825	12,275	0	0	0	0	0	0	0	0	0
Hylarana debussyi	200	0	0	0	0	0	0	0	0	0	0	0	0
Hylarana melanomenta	150	0	0	0	0	0	0	0	0	0	0	0	0
Hylodes fredi	225	0	25	0	0	0	0	0	0	0	0	0	0
Hylomantis aspera	9,550	125	675	125	0	0	0	0	0	0	0	0	0
Hyophryne histrio	550	0	0	0	0	0	0	0	0	0	0	0	0
Hyperolius mariae	88,900	163,750	235,000	166,450	0	0	0	0	0	0	0	0	0
Hyperolius puncticulatus	975	0	0	0	0	0	0	0	0	0	0	0	0
Incilius aucoinae	5,775	4,425	4,350	3,650	0	0	0	0	0	0	0	0	0

Ingerana charlesdarwini	75	0	0	0	0	0	0	0	0	0	0	0	0
Ingerophrynus kumquat	2,450	0	0	0	0	0	0	0	0	0	0	0	0
Kalophrynus bunguranus	1,525	0	0	0	0	0	0	0	0	0	0	0	0
Leptobrachella natunae	1,525	0	0	0	0	0	0	0	0	0	0	0	0
Leptodactylus fallax	250	0	25	0	0	0	0	25	25	25	0	0	0
Leptodactylus marambaiae	100	0	0	0	0	0	0	0	0	0	0	0	0
Leptodactylus thomei	7,450	0	25	0	0	0	0	0	0	0	0	0	0
Lithobates okaloosae	950	0	0	0	0	0	0	0	0	0	0	0	0
Lithobates sevosus	28,875	0	0	0	0	0	0	0	0	0	0	0	0
Litoria andiirrmalin	6,900	25	0	0	0	0	0	0	0	0	0	0	0
Litoria aruensis	10,250	0	0	0	0	0	0	0	0	0	0	0	0
Litoria capitula	3,675	0	0	0	0	0	0	0	0	0	0	0	0
Litoria congenita	47,550	0	0	0	0	0	0	0	0	0	0	0	0
Litoria cooloolensis	2,950	0	0	0	0	0	0	0	0	0	0	0	0
Litoria elkeae	1,900	0	0	0	0	0	0	0	0	0	0	0	0
Litoria louisiadensis	1,300	0	0	0	0	0	0	0	0	0	0	0	0
Litoria lutea	9,150	1,475	6,925	2,850	0	0	0	0	0	0	0	0	0
Litoria mystax	175	0	0	0	0	0	0	0	0	0	0	0	0
Litoria olongburensis	10,575	200	1,400	175	0	0	0	125	200	250	0	0	0

Litoria quadrilineata	150	0	0	0	0	0	0	0	0	0	0	0	0
Litoria vagabunda	425	150	350	300	0	0	0	0	0	0	0	0	0
Melanophryniscus dorsalis	9850	0	225	100	0	0	0	0	0	0	0	0	0
Melanophryniscus montevidensis	14,225	0	0	0	0	0	0	0	0	0	0	0	0
Melanophryniscus pachyrhynus	100	0	0	0	0	0	0	0	0	0	0	0	0
Mertensophryne howelli	50	0	0	0	0	0	0	0	0	0	0	0	0
Oophaga occultator	125	0	0	0	0	0	0	0	0	0	0	0	0
Oreophryne kapisa	2,550	0	0	0	0	0	0	0	0	0	0	0	0
Oreophryne loriae	350	0	0	0	0	0	0	0	0	0	0	0	0
Pelophylax cretensis	3,500	700	1,350	1,450	0	0	0	0	0	0	0	0	0
Peltophryne cataulaciceps	3,500	0	0	0	0	0	0	0	0	0	0	0	0
Peltophryne lemur	1,475	1,525	1,825	500	0	0	0	0	0	0	0	0	0
Petropedetes cameronensis	41,600	8525	10,275	4,250	0	0	0	0	0	0	0	0	0
Petropedetes johnstoni	25,300	1,850	8,150	3,300	0	0	0	0	0	0	0	0	0
Phrynobatrachus brevipalmatus	350	0	0	0	0	0	0	0	0	0	0	0	0
Phrynobatrachus pakenhami	225	0	0	0	0	0	0	0	0	0	0	0	0
Phrynobatrachus ungujae	275	0	0	0	0	0	0	0	0	0	0	0	0
Phrynomedusa bokermanni	200	50	0	0	0	0	0	0	0	0	0	0	0
Phyllobates terribilis	500	0	0	0	0	0	0	0	0	0	0	0	0

Phyllodytes brevirostris	150	0	0	0	0	0	0	0	0	0	0	0	0
Platymantis admiraltiensis	2,125	0	0	0	0	0	0	0	0	0	0	0	0
Platymantis latro	2,175	0	0	0	0	0	0	0	0	0	0	0	0
Platymantis parkeri	1,375	0	25	0	0	0	0	0	0	0	0	0	0
Platymantis pelewensis	450	0	0	0	0	0	0	0	0	0	0	0	0
Pseudacris kalmi	50,775	50	2,825	0	0	0	0	0	0	0	0	0	0
Rhinella pygmaea	21,750	1,925	1,325	1,025	0	0	0	0	0	0	0	0	0
Scinax agilis	31,100	300	825	600	0	0	0	0	0	0	0	0	0
Scinax jolyi	150	0	0	0	0	0	0	0	0	0	0	0	0
Scinax jureia	350	0	0	0	0	0	0	0	0	0	0	0	0
Stereocyclops parkeri	15,775	4,350	9,400	6,900	0	0	0	25	25	25	0	0	0
Stumpffia tetradactyla	500	300	2900	350	0	0	0	0	0	0	0	0	0
Tachycnemis seychellensis	175	0	0	0	0	0	0	0	0	0	0	0	0
Uperoleia aspera	24,925	0	0	0	0	0	0	0	0	0	0	0	0
Uperoleia daviesae	100	0	0	0	0	0	0	0	0	0	0	0	0
Uperoleia martini	16,625	150	1,250	425	25	25	25	50	75	75	50	50	50
Xenohyla truncata	14,875	75	250	150	0	0	0	0	0	0	0	0	0

Table S2. Anuran species assessed in the present study and their original distribution. Both taxonomy and geographic information were obtained from the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, version 2010.4 (IUCN 2010).

Taxa	Original distribution
Afrixalus sylvaticus	Kenya; Tanzania, United Republic of
Alsodes australis	Argentina; Chile
Alsodes kaweshkari	Chile
Amietophrynus pantherinus	South Africa (Western Cape Province)
Aplastodiscus eugenioi	Brazil
Aplastodiscus leucopygius	Brazil
Arenophryne rotunda	Australia
Arthroleptella lightfooti	South Africa (Western Cape Province)
Atelopus flavescens	French Guiana
Austrochaperina adelphe	Australia
Austrochaperina gracilipes	Australia; Papua New Guinea
Austrochaperina parkeri	Papua New Guinea
Babina holsti	Japan
Babina okinavana	Japan; Taiwan, Province of China
Babina subaspera	Japan
Barbourula busuangensis	Philippines
Barygenys exsul	Papua New Guinea
Batrachyla nibaldoi	Chile
Batrachylodes mediodiscus	Papua New Guinea
Batrachylodes trossulus	Papua New Guinea; Solomon Islands
Batrachylodes vertebralis	Papua New Guinea; Solomon Islands
Batrachylodes wolfi	Papua New Guinea; Solomon Islands
Boophis xerophilus	Madagascar
Breviceps macrops	Namibia; South Africa

Calluella brooksii	Indonesia; Malaysia
Calluella smithi	Malaysia
Callulops doriae	Papua New Guinea
Callulops kopsteini	Indonesia
Cardioglossa aureoli	Sierra Leone
Ceratobatrachus guentheri	Papua New Guinea; Solomon Islands
Ceratophrys stolzmanni	Ecuador; Peru
Chiasmocleis alagoanus	Brazil
Chiasmocleis capixaba	Brazil
Chiasmocleis carvalhoi	Brazil
Cophixalus verrucosus	Papua New Guinea
Copiula oxyrhina	Papua New Guinea
Craugastor yucatanensis	Mexico
Crinia insignifera	Australia
Crinia nimbus	Australia
Crinia remota	Australia; Indonesia; Papua New Guinea
Crinia tinnula	Australia
Cycloramphus juimirim	Brazil
Dendropsophus gaucheri	French Guiana; Suriname
Discodeles bufoniformis	Papua New Guinea; Solomon Islands
Discodeles guppyi	Papua New Guinea; Solomon Islands
Discodeles opisthodon	Papua New Guinea; Solomon Islands
Discodeles vogti	Papua New Guinea
Duttaphrynus valhallae	Indonesia
Elachistocleis surinamensis	Suriname; Trinidad and Tobago; Venezuela
Eleutherodactylus cavernicola	Jamaica
Eleutherodactylus cochranae	Puerto Rico; Virgin Islands, British; Virgin Islands, U.S.
Eleutherodactylus	Cuba

guanahacabibes	
Eleutherodactylus lentus	Virgin Islands, U.S.
Eleutherodactylus pinarensis	Cuba
Eleutherodactylus rogersi	Bahamas
Eleutherodactylus thomasi	Cuba
Fejervarya andamanensis	India
Fejervarya nicobariensis	India (Nicobar Is.)
Genyophryne thomsoni	Papua New Guinea
Hemisus perreti	Angola; Congo
Hylarana debussyi	Indonesia
Hylarana melanomenta	Philippines
Hylodes fredi	Brazil (Rio de Janeiro)
Hylomantis aspera	Brazil
Hyophryne histrio	Brazil
Hyperolius mariae	Congo, The Democratic Republic of the; Kenya; Tanzania, United Republic of; Zambia
Hyperolius puncticulatus	Tanzania, United Republic of
Incilius aucoinae	Costa Rica; Panama
Ingerana charlesdarwini	India
Ingerophrynus kumquat	Malaysia
Kalophrynus bunguranus	Indonesia
Leptobrachella natunae	Indonesia
Leptodactylus fallax	Dominica; Montserrat
Leptodactylus marambaiae	Brazil
Leptodactylus thomei	Brazil (Espírito Santo)
Lithobates okaloosae	United States
Lithobates sevosus	United States
Litoria andiirrmalin	Australia

Litoria aruensis	Indonesia
Litoria capitula	Indonesia
Litoria congenita	Indonesia; Papua New Guinea
Litoria cooloolensis	Australia
Litoria elkeae	Indonesia
Litoria louisiadensis	Papua New Guinea
Litoria lutea	Papua New Guinea; Solomon Islands
Litoria mystax	Indonesia
Litoria olongburensis	Australia
Litoria quadrilineata	Indonesia
Litoria vagabunda	Indonesia
Melanophryniscus dorsalis	Brazil
Melanophryniscus montevidensis	Brazil; Uruguay
Melanophryniscus pachyrhynus	Brazil
Mertensophryne howelli	Tanzania, United Republic of
Oophaga occultator	Colombia
Oreophryne kapisa	Indonesia
Oreophryne loriae	Papua New Guinea
Pelophylax cretensis	Greece
Peltophryne cataulaciceps	Cuba
Peltophryne lemur	Puerto Rico; Virgin Islands, British
Petropedetes cameronensis	Cameroon; Equatorial Guinea; Nigeria
Petropedetes johnstoni	Cameroon; Equatorial Guinea (Bioko)
Phrynobatrachus brevipalmatus	Angola
Phrynobatrachus pakenhami	Tanzania, United Republic of
Phrynobatrachus ungujae	Kenya; Tanzania, United Republic of
Phrynomedusa bokermanni	Brazil
Phyllobates terribilis	Colombia

Phyllodytes brevirostris	Brazil
Platymantis admiraltiensis	Papua New Guinea (Bismarck Archipelago)
Platymantis latro	Papua New Guinea (Bismarck Archipelago)
Platymantis parkeri	Papua New Guinea
Platymantis pelewensis	Palau
Pseudacris kalmi	United States
Rhinella pygmaea	Brazil
Scinax agilis	Brazil
Scinax jolyi	French Guiana
Scinax jureia	Brazil
Stereocyclops parkeri	Brazil
Stumpffia tetradactyla	Madagascar
Tachycnemis seychellensis	Seychelles
Uperoleia aspera	Australia
Uperoleia daviesae	Australia (Northern Territory)
Uperoleia martini	Australia
Xenohyla truncata	Brazil

CAPÍTULO 2

Oliveira et al.

Effects of climate change on biodiversity

Assessing Future Habitat Availability for Coastal Lowland Anurans in the Brazilian Atlantic Rainforest

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ABSTRACT

Climate change is expected to cause several modifications on physical environments and sea level rise is an assured consequence. However, the assessment on the potential impacts caused by sea level rise on biodiversity is still incipient. Therefore, we assessed the combined impact of climate change and sea level rise on the potential distribution of 19 coastal lowland anurans in the biodiversity hotspot Atlantic forest. We applied a correlative species distribution model (SDM) (BIOCLIM) and GIS-based spatial analyses. We evaluated the extent of changes of potential distributions under an extreme and a moderate climate change scenarios as well as two extreme sea level rise scenarios. Because the current potential distribution of these anuran species may be underestimated, we also analyzed their environmental niche under current conditions in order to provide a baseline for further field surveys. Our results suggest wide areas of suitable habitat for most species in the future. However, for 15 percent of these species the SDMs predict massive losses of range extent as a result of a combination of climate change and sea level rise. Such observations highlight an immediate need of considering the sea level rise potential effects in conservation action plans.

Key-words: Amphibian conservation; biodiversity hotspot; climate change; habitat suitability; species distribution model

RESUMO

As mudanças climáticas devem causar diversas alterações ambientais, incluindo o aumento do nível do mar como uma consequência inevitável. Apesar disso, estudos que avaliem os impactos potenciais do aumento do nível do mar sobre a biodiversidade ainda são escassos. Sendo assim, nós avaliamos os possíveis impactos das mudanças climáticas combinados com o aumento do nível do mar sobre a distribuição potencial de 19 espécies de anuros de áreas baixas costeiras na Mata Atlântica. Para tanto, utilizamos modelos de distribuição de espécies construídos com o algoritmo BIOCLIM. Em seguida, avaliamos as mudanças na distribuição de áreas potencialmente adequadas para as espécies em cenários climáticos moderados e extremos, juntamente com dois cenários extremos de aumento do nível do mar. Além disso, como a distribuição das espécies selecionadas pode ser subestimada, construímos modelos para avaliar habitats adequados nas condições climáticas atuais a fim de identificar áreas de amostragens para incentivar estudos em campo subsequentes. Nossos resultados revelaram extensas áreas adequadas para a maioria das espécies avaliadas. No entanto, para 15 por cento dos táxons nós identificamos perdas consideráveis de habitat adequado, como consequência, tanto das mudanças climáticas, quanto do aumento do nível do mar. Diante disso, sugerimos a inclusão de efeitos potenciais do aumento do nível do mar no planejamento de ações para a conservação.

INTRODUCTION

CLIMATE CHANGE IS A MAJOR THREAT TO BIODIVERSITY WORLDWIDE (Brook *et al.* 2008, Barnosky *et al.*, 2011). The increase of atmospheric CO_2 in recent decades is expected to affect several environmental parameters in a short term, mainly air temperature (IPCC 2007), and the implementation of action to mitigate predicted effects on biodiversity is paramount. Among several potential consequences, sea level rise (SLR) is particularly worrying for coastal terrestrial biota. In less than 100 years, water levels are expected to rise due to increased atmospheric warming (IPCC 2007, Bamber *et al.* 2009, Shepherd *et al.* 2012), changing worldwide costal shore-lines (Menon et al 2010). Although the Fourth Assessment Report (AR4) of the Intergovernmental Panel on Climate Change (IPCC) does not predict SLR to be above 60 cm (IPCC 2007), other studies focusing on SLR suggest much more alarming scenarios, with rising sea levels varying from 2 to 6 m by the year 2100 (Overpeck *et al.* 2006, Grinsted *et al.* 2010, Nicholls & Cazenave 2010). However, even though SLR is one of the most assured consequences of climate change (CC) in near future (Nicholls & Cazenave 2010), its effects on coastal terrestrial organisms remain largely understudied, hindering preventive conservation actions. Up to the present time, only few studies addressed potential consequences of SLR over terrestrial wildlife (*e.g.* Menon *et al.* 2010, Wetzel *et al.* 2012, Bellard *et al.* 2013). Consequently, a comprehensive assessment of the possible effects of SLR on terrestrial biodiversity is still needed.

Ecological communities and ecosystems related to shorelines (such as mangroves, saltmarshes, sandbanks, and estuaries) are undoubtedly the most threatened by SLR (Menon *et al.* 2010, Traill *et al.* 2011). Additionally, SLR may immediately affect terrestrial ecosystems through water intrusions (*e.g.* Rios-López 2008) or permanent flooding (Menon *et al.* 2010, Bellard *et al.* 2013), jeopardizing biodiversity and ecosystem services. Menon *et al.* (2010) conducted one of the first studies assessing potential future impacts of SLR on coastal fauna at the global scale, and identified regions most likely to be affected. Recently, Bellard *et al.* (2013) investigated how insular hotspots and endemic species may be affected in the near future under distinct SLR scenarios.

From the perspective of conservation management, a fail of conservation strategies is commonly observed as a result of the insufficient baseline information or ineffective implementation (James *et al.* 1999, Nóbrega & De Marco Jr 2011). The availability of resources for conservation in terms of time and money are often limited and prioritization of resources should be supported by theory to minimize biodiversity loss (Brooks *et al.* 2006). Thus, the scientific community should provide guidance in a comprehensive manner to facilitate resource allocation (Morais *et al.* 2013).

Although SLR is predicted to moderately affect Brazilian shoreline (Menon *et al.* 2010), this area includes part of the Atlantic forest, a biome that harbors astonishing biodiversity, rarity, and endemism levels (Ribeiro *et al.* 2011, Haddad *et al.* 2013, Toledo *et al*. 2014). However, humans have intensively disturbed the Atlantic forest over the past 500 years (Ribeiro *et al.* 2009). The impact of such disturbance, together with the fact that anurans are the most threatened vertebrates on Earth (Hoffman *et al.* 2011) and quite sensitive to future CC (Foden *et al.* 2013), raises concern about their conservation in the Atlantic forest. Thus, amphibian conservation assessment in this region is highly necessary and demand further studies (*e.g.* Lemes & Loyola 2013, Loyola *et al.* 2013).

Species distribution models (SDMs) have become a useful tool in ecology, evolution and conservation biology (*e.g.* Peterson & Nyári 2007, Thuiller *et al.* 2011, Capinha & Anastácio 2011). These models correlate information on a species' distribution with bioclimatic data in an attempt to predict areas providing suitable environmental conditions (i.e. which are part of the species' Grinnellian niche, see Soberon 2007). Owing to the many threats to biodiversity in the future, defining conservation priorities is urgent. In this context, mitigation of biodiversity loss needs to be performed with the data at hand, given that the time needed for gathering exhaustive information is impractical and impeditive (*e.g.* Pie *et al.* 2013, Pearson *et al.* 2007).

Therefore, we evaluate the future availability of suitable habitat for terrestrial coastal lowland species under different scenarios of CC and SLR. We applied a comprehensive modeling and GIS approach to 19 coastal lowland anuran species serving as biological models. Since distribution information for these species may be underestimated, we also explore the species' potential distribution under present conditions in order to guide and foster further field surveys.

MATERIAL AND METHODS

GEOGRAPHICAL EXTENT – The Brazilian Atlantic forest was one of the largest rainforests in the Americas, covering approximately 150 million ha in the past (Ribeiro *et al.* 2009). Nowadays it has less than 12 percent of its original cover but it is still one of the world's biodiversity hotspots owning a high number of threatened and endemic species (Ribeiro *et al.* 2011, Hadadd *et al.* 2013). Longitudinal, latitudinal, and elevational variation is largely responsible for high habitat heterogeneity in Atlantic forest. Longitude is correlated with the decrease of rainfall from the coast to the west causing distinct forest compositions. In regard to latitude, the tropical forest turns into subtropical from north toward south (Ribeiro *et al.* 2009). Such complexity may explain the high amphibian diversity (Toledo & Batista 2012) and level of endemism, which reaches about 90 percent in the Atlantic forest (Haddad *et al.* 2013). Besides this, the topographic complexity and elevation range (from sea level to about 3,000 m), increases the anuran rarity (Toledo *et al*. 2014). Thus, the Atlantic forest is a priority for wildlife conservation (Zachos & Habel 2011).

SPECIES DATA – We used anurans as biological models because they are highly sensitive to future environmental shifts (Loyola *et al.* 2013, Wake 2012). Besides, although this group is severely threatened (Hoffman *et al.* 2010), it is comparatively well known (Foden *et al.* 2013), which favors data access and the comprehension of potential effects.

Species were selected according to the following criteria: (1) only anurans endemic to the Atlantic forest; (2) with available information about altitudinal ranges; and (3) distributional range within coastal lowland areas. Although interesting for our aim, we exclude insular species because some islands have such a small extent that environmental information is not available. We selected exclusively Atlantic forest lowland coastal anurans based on those amphibians listed by Haddad *et al.* (2013). We considered as 'coastal lowland' those species with currently known altitudinal range distribution up to 60 m above sea level (asl) and no farther than 100 km from coastline. In total we considered 19 species (Table 1). We accessed altitudinal range information for each species at the IUCN website (IUCN 2013) and in Frost (2014). Although incomplete and often biased for several reasons (Loyola *et al.* 2013), occurrence points are valuable in SDMs approaches (*e.g.* Capinha & Anastácio 2011, Nóbrega & De Marco Jr 2011) and the use of range distribution maps to generate artificial points as surrogates may imply additional bias, since their accuracy needs to be reassessed in some regions, especially in South America (Ficetola *et al.* 2014). Additionally, there are no available range maps for some species present in our data set; therefore, the use of point locations was the only option to assemble the models.

For each previous selected species we primarily compiled occurrence records from the Specieslink online database (http://www.splink.org.br/), which allow access data from the following collections: Museu de Zoologia “prof. Adão José Cardoso”; Coleção “Célio F. B. Haddad”, Coleção Científica do Departamento de Zoologia e Botânica da Universidade Estadual Paulista (São José do Rio Preto), Coleção de Tecidos Animais do Departamento de Ciências Biológicas da Universidade Federal do Espírito Santo; and Coleção de Anfíbios do Museu de Biologia Mello Leitão. Since some selected species were only recently described, few or even no records were available for some of them. In such cases, and in order to increase the number of occurrence points as well, additional records were searched in GBIF (http://www.gbif.org/), in per reviewed literature and in the Frost’s website (Frost, 2014). All occurrence records were verified for possible geographical or altitudinal errors in ArcGIS 10 (ESRI 2011) and Google Earth.

Following our selection criteria our species dataset comprised a total of 19 species (Fig. 1). These species are allocated into seven families and have a total of 91 occurrence records (Table 1). Most of these species are not considered to be threatened, being classified as least concern (LC, *n*=3), data deficient (DD, *n*=7) or near threat (NT, *n*=1). Two of them are currently threatened, being classified as endangered (EN, *n*=1) or vulnerable (VU, *n*=1) (IUCN 2013). Additionally, seven species are reported to have decreasing populations, and six species have population trend assigned as unknown. Finally, five species have no additional information in regard to their distribution range, occurrence points available in online database, assessments for threats or population trends.

ENVIRONMENTAL DATA – We selected two extreme SLR scenarios of 3 and 6 m to simulate future potential loss of land of available habitat. We obtained SLR scenarios as raster files from the Center of Remote Sensing of Ice Sheets (https://www.cresis.ku.edu). Although, according to IPCC's AR4 (IPCC 2007) rising sea levels above 60 cm are not expected, several uncertainties are involved in this topic and it is possible that SLR may reach several meters (Overpeck *et al.* 2006, Bamber *et al.* 2009, Grinsted *et al.* 2010) in different parts of the world (Gomez *et al.* 2010).

The environmental variables used to generate the SDMs include 19 bioclimatic variables at a spatial resolution of 30 arc-second (approximately 1 km). For current conditions we obtained these climatic variables from the WorldClim homepage (http://www.worldclim.org); and future climatic scenarios were accessed from the CIAT (http://www.ccafs-climate.org/). In order to compare the resulting outputs, we generate models for two future distinctive scenarios for the mid-point of a 30-yr period (2071 to 2099), *i.e.* 2080; namely A2a, considered pessimistic, and B2a, optimistic (IPCC 2007). We used the three following climatic models projections for the year 2080: CCCMA-CGCM2, CSIRO-MK2, and HCCPR-HadCM3 developed by IPCC AR4 (IPCC 2007). We calculated the arithmetic mean of each climatic variable among the three climate models to reduce the uncertainty of forecasted climates that arises from variability among distinct climate models.

We avoid to subjectively select variables since the specific bioclimatic variables differ in type, magnitude and significance for each analyzed species (Lawling & Polly 2011). However, since the variables describe means and extremes of temperatures and precipitation values, it is required to take into account the multicollinearity among the bioclimatic variables. To solve this issue we performed a Principal Component Analysis (PCA), removing the collinearity and reducing the dimensionality of the climatic data. We used the four principal components (PCs) produced by PCA that encompassed the greatest cumulative variance (92%) through the data as input in each SDM.

SPECIES DISTRIBUTION MODEL – We assemble SDMs for the year 2080 to assess potential effects provided by future climate conditions and future SLR. We investigated expected potential effects of SLR on future habitat availability under CC by combining climatic scenarios and water levels in a logic manner. We explored a reasonable upper bound of a 3 m SLR (Hansen 2007) and an extreme scenario of SLR up to 6 m (Overpeck *et al*. 2006, Menon *et al*. 2010, Wetzel *et al*. 2012). We used this last extreme scenario in order to detect potential losses caused by sea level variations (e.g. lunar effects, marine inundation or storms), since the horizontal intrusions are difficult to predict (Wetzel *et al*. 2012, Bellard *et al*. 2013). We coupled the 3 m SLR with the B2a climatic scenario, and the 6 m with the A2a. Furthermore, we built SDMs for all species under current climatic conditions to provide additional information and also a starting point for future field survey in view to increase available information for such species.

Although there are a plethora of methods to assess potential distributions (Franklin 2009), we used the BIOCLIM algorithm implemented in the free software DIVA-GIS 7.5 (available at http://www.diva-gis.org/) to assemble the SDMs. BIOCLIM is a useful correlative presence-only modeling tool that summarizes a species' climatic envelope to predict its potential distribution (Beaumont *et al.* 2005, Araújo & Peterson 2012). It calculates the similarity between conditions by associating the values of climatic variables at any location of the study area to a percentile distribution of the values at previous known occurrences, ascribing suitability according to the distance to the 50th percentile (the median), *i.e.*, the closer to the median (Hijmans & Elith 2013) (http://cran.r-project.org/web/packages/dismo/vignettes/sdm.pdf). In addition, BIOCLIM is largely used in SDM approaches (*e.g.* Guisan *et al.* 2007, Lawling & Polly 2011), particularly when the aim is to evaluate potential distributions rather than the occupied distributional area (Jiménez-Valverde *et al.* 2011, Araújo & Peterson 2012).

We established distinct thresholds for each species in the SDMs, based on the ROC (Receiver Operating Characteristic) curve plot-based approach to derive binary vector models (0/1). In this case, the threshold corresponds to the "most northwestern" point in the plot (Liu *et al.* 2005, Jiménez-Valverde *et al.* 2011). We opted for this method to minimize omission and commission errors, producing potential range maps with lower uncertainty while also reducing the risk of underestimating the extent of suitable sites. The same threshold criterion was used to generate binary range maps under current climatic conditions.

We evaluated the fit of all SDMs by assessing the area under the ROC curve (AUC). Although controversial (Lobo *et al.* 2008), model evaluation based on the AUC values are commonly used (*e.g.* Nóbrega & De Marco Jr 2011), and offers a statistical estimate of the model's performance. AUC values vary between 0 and 1, and values around or below 0.5 suggest that the predictive capacity of the model is similar to random. Values above 0.8 are desirable (Swets 1988). We analyzed 95 models, three SDMs outputs (current, B2a and A2a) and two SLR scenarios implemented for 19 species.

QUANTIFYING AVAILABLE SUITABILITY AND THE MAGNITUDE OF POTENTIAL IMPACTS – We first calculated the total extent of predict climate suitability (SDMs outputs) in number of grid cells and then converted them in square kilometers to assess the potential suitability and evaluate the magnitude of potential consequences of CC and SLR. After that, we extracted the potential loss of land by flood caused by SLR by overlapping and calculating the aggregate intersection in square kilometers (Fig. 2). Consequently, we could assess the combined impact of CC and SLR over potential suitable habitat. Then, we tested the significance of the dissimilarities observed in the range shifts among the two CC scenarios, as well as the potential effects provided by SLR on predicted suitable habitat availability, by the application of a simple paired Wilcoxon test, after Shapiro-Wilk normality test.

RESULTS

CURRENT HABITAT SUITABILITY – Under current climatic conditions we notice several distinct patterns among the taxa (Table S1). The potential distribution for the family Microhylidae (five species) was generally larger (2 x 10^4 to 1.5 x 10^5 km^2) than the other families (see details in supporting information). In addition, SDMs showed potential distributions ranging between 1 and 5 x 10^3 km^2 for four species (*Melanophryniscus setiba*, *Phyllodytes punctatus*, *Crossodactylus lutzorum*, and *Chiasmocleis sapiranga*) and ranging from 5 x 10^3 to 1 x 10^4 km^2 for other three species (*Aparasphenodon arapapa*, *Physalaemus atlanticus*, and *Scinax cretatus*), whereas for additional three species (*A. bokermanni*, *Gastrotheca megacephala*, and *Xenohyla truncata*) the potential distributions reached values between 1 and 2 x 10^4 km^2. Finally, three species (*Dendrophryniscus skuki*, *Haddadus plicifer*, and *Leptodactylus hylodes*) apparently have a restricted potential suitable habitat. For instance, for the Craugastoridae *H. plicifer* the potential distribution covered less than 600 km^{2}and for two other species (*Dendrophryniscus skuki* and *Leptodactylus hylodes*) the size of suitable habitats is expected to be about100 km^2 (Table S1).

FUTURE SUITABLE HABITAT AVAILABILITY – We obtained good model fit across all SDMs, with AUC values relatively high for most species (global average ± standard deviation (SD) = 0.95 ± 0.06) and none of the models exhibited AUC value below 0.79 (Table 1). Therefore, all SDMs were used for further analyses (Girardello *et al.* 2009).

No cases of complete loss of future climatically suitable areas owing to CC or either SLR were detected. We observed an increase in the extent of suitable areas for 10 species and a decrease for nine in each future climatic scenario (Table 2). Differences concerning the magnitude of changes in suitable area extent between CC scenarios were significant (p = 0.018), with A2a scenario producing greater changes than the B2a scenario (Fig. 3). Yet, the A2a scenario suggested larger potential distributions (26,662 km^2 ± 32,194) as were suggested by the B2a scenario (12,904 km^2 ± 15,410). SLR decreased future availability for suitable habitats in all cases. We also observed significant differences between SLR scenarios (p = 0.0001) (Fig. 3), with the 6 m scenario affecting the potential distributions to a greater extent (1,881 ± 2,246) than the 3 m scenario (675 ± 770). However, the combination of CC and SLR revealed different patterns in terms of final habitat suitability (Table 2). The B2a scenario combined with SLR of 3 m showed relatively lower impacts with five species presenting approximately 10 percent and two over than 30 percent potentially suitable area loss (see an example in Fig. 4). The A2a scenario coupled with SLR of 6 m revealed greater potential losses for the taxa in general, with ten species presenting approximately 10 percent, and other four species with over 20 percent suitable area loss (Table 2). For this scenario one species (*Crossodactylus lutzorum*) loses more than 40 percent of the suitable area (Fig.4D, E, and F). Nevertheless, on average the A2a scenario suggested larger potential distributions (24 781.12 ± 30 226.37) than the B2a scenario (12 228.6 ± 14 751.8).

DISCUSSION

Amphibians are facing high extinction risk (Hoffman *et al.* 2010, Wake 2012) that is likely to severely decrease its biodiversity in the group at alarming rates (Wake 2012). Even worse, we hereby reveal an additional threat to be considered together with the other claimed threats. Understanding and quantifying future potential CC and SLR impacts on terrestrial fauna synergistically is still challenging. For instance, Bernardo-Silva *et al*. (2012) identified priority areas for the conservation of two endangered red-bellied toads (*Melanophryniscus dorsalis* and *M. montevidensis*) in Brazil and Uruguay based on their climatic requirements. However, at least *M. dorsalis*, which is restricted to environments as coastal dunes, is likely to suffer from SLR. Therefore, since available resources for implementing Conservation Units are limited, we argue that potential effects of SLR need to be considered in conservation strategies.

Although we identified 19 taxa likely to potentially suffer suitable area loss, we stress out that the actual number of Atlantic forest species under SLR threat is underestimated. For example, exclusively insular anurans were excluded (e.g. *Cycloramphus faustoi*, *Scinax alcatraz, S. faivovichi* and *S. peixotoi*, all assigned as CR) owing to data limitation. Moreover, even though dispersal overseas is a possibility for amphibians (Vences et al. 2013), we lack evidence showing that this is common. Yet, species isolated on islands possess environmental requirements and physiological constraints (Wells 2007), representing a special challenge for forecasting future distributions.

Our modeling approach may also improve categorization of endangerment of some species, as in the case of *Haddadus plicifer* and *Leptodactylus hylodes*. Morais *et al.* (2013) provided an overview on the risk of extinction and categorization in regard to data deficient (DD) species. These authors considered the extent of occurrence and the time passed since the description of the species to infer the threat category of DD species. According to their criteria, both species assigned as DD (IUCN 2013) are in fact CR. Conversely, even after discounting losses caused by future SLR, *L. hylodes* is still predicted to have an increase in the extent of climatically suitable areas. However, *H. plicifer* is predicted to have losses caused by CC and SLR, with only less than a half of its potential current suitable habitat remaining. These two species are among those that have the most restrictive habitat constraints, and based on the long time passed since their description, it is likely that they are rare (Morais *et al.* 2013).

The A2a scenario predicts a greater amount of atmospheric CO_2 and higher air temperatures in comparison to B2a (IPCC 2007). However, our results showed significant larger potential distributions under the A2a scenario, even with potential effects of SLR accounted. Moreover, comparing both scenarios, SDMs for the B2a suggest suitable habitats exclusively outside conservation units for further species. In fact, climate change may provide increased habitat suitability for few taxa and decrease for others (Erasmus *et al.* 2012). Nevertheless, we highlight that models do not consider other factors such as biotic interactions or barriers to dispersal and projected habitat suitability is an estimate of the realized distribution.

Concerning the current habitat availability, our assessment provides a starting point for future field surveys. Because several species have only been recently described (Frost, 2014), their real distributions are potentially broader than currently known. In addition, models revealed climatic suitability in mountainous regions for some species (*e.g. Chiasmocleis atlantica, C.*

capixaba and *C. lacrimae*), and such species may not be restricted to coastal areas. On the other hand, several species showed restricted potential habitat ranges, including some described a long time ago (which suggest that they are truly rare) and, in such cases, development of further field surveys is necessary to improve the existing knowledge about their distribution range.

There are several factors that can bias SDMs, such as spatial autocorrelation and non-uniform data samples. Species with restrictive distributional range represent a special challenge to be overcome in SDM approaches, since few records spatially clustered tend to reduce statistical power (Wisz *et al.* 2008). Nonetheless, cases in which the number of occurrence records can be negatively correlated to the model performance (*e.g.* Girardello *et al.* 2009) highlight how complex is to evaluate the models (Liu *et al.* 2005, Lobo *et al.* 2008). Although SDM predictions still require better evaluation approaches (Diniz-Filho *et al.* 2012), understanding factors that can jeopardize the conservation of species is also urgent, and cannot wait for the accumulation of complete knowledge (Pie *et al.* 20113). In this sense, our results stresses potential events that may severely impact habitat availability for coastal lowland anuran species, and provide a starting point for further investigations in the Atlantic forest. In agreement to the recommendations of the Brazilian Amphibian Conservation Action Plan (Verdade *et al.* 2012) we suggest long-term population monitoring, including coastal lowland species, since this practice may enable the detection of population fluctuations, declines or local effects owing to CC and especially the SLR.

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TABLES

Table 1. Model efficiency based on the AUC value for prediction on potential habitat suitability extent for 19 coastal lowland anurans from the Brazilian Atlantic forest.

Species	**Year of description**	**Number of records**	**AUC values**
Aparasphenodon arapapa	2009	5	0.97
Aparasphenodon bokermanni	1993	5	0.97
Chiasmocleis alagoana	1999	4	0.97
Chiasmocleis atlantica	1997	4	0.97
Chiasmocleis capixaba	1997	11	0.85
Chiasmocleis lacrimae	1997	10	0.83
Chiasmocleis sapiranga	2007	3	0.98
Crossodactylus lutzorum	1993	4	0.99
Dasypops schirchi	1924	5	0.89
Dendrophryniscus skuki	2012	2	1
Gastrotheca megacephala	2009	3	0.89
Haddadus plicifer	1888	4	1
Leptodactylus hylodes	1862	5	1
Melanophryniscus setiba	2012	2	0.97
Phyllodytes punctatus	2004	5	1
Physalaemus atlanticus	2004	5	0.97
Scinax cretatus	2011	5	0.98
Sphaenorhynchus palustris	1966	5	0.91
Xenohyla truncata	1959	4	1
Average ± standard deviation		4.78 ± 2.25	0.95±0.051

Table 2. Estimated suitable area for the present and future climatic conditions, and potential losses of habitat availability by future sea level rise for 19 lowland anuran species in the Brazilian Atlantic forest.

	Current	**B2a**			**A2a**		
Taxa	**Estimated suitable area (km^2)**	**Future suitability (km^2)**	**Loss by 3 m sea level rise (%)**	**Final suitable area (km^2)**	**Future suitability (km^2)**	**Loss by 6 m sea level rise (%)**	**Final suitable area (km^2)**
Aparasphenodon arapapa	8,160	10,863	5	10,318	17,596	7	16,287
Aparasphenodon bokermanni	15,305	16,455	5	15,571	13,152	3	12,710
Chiasmocleis alagoana	20,630	21,364	4	20,476	87,965	8	80,715
Chiasmocleis atlantica	71,126	28,767	0.1	28,726	58,980	0.8	58,504
Chiasmocleis capixaba	79,804	65,538	5	62,131	82,505	6	76,864
Chiasmocleis lacrimae	145,014	24,922	5	23,514	92,463	5	87,464
Chiasmocleis sapiranga	2,649	7,607	6	7,108	2,794	25	2,094
Crossodactylus lutzorum	976	748	33	495	631	42	360
Dasypops schirchi	27,169	10,434	11	9,215	24,886	7	23,114
Dendrophryniscus skuki	113	829	5	780	1,220	9	1,106

Gastrotheca megacephala	16,245	14,229	5	13,480	26,386	8	24,208
Haddadus plicifer	537	190	31	130	430	26	315
Leptodactylus hylodes	101	2,464	13	2,133	1,475	26	1,077
Melanophryniscus setiba	4,571	1,680	1	1,663	2,507	6	2,349
Phyllodytes punctatus	1,333	2,410	13	2,096	7,553	13	6,545
Physalaemus atlanticus	5,342	6,186	7	5,737	4,579	11	4,066
Scinax cretatus	5,182	3,171	9	2,855	10,299	12	8,964
Sphaenorhynchus palustris	20,861	9,025	9	8,201	58,586	9	52,830
Xenohyla truncata	10,153	18,289	3	17,705	12,574	10	11,260

FIGURE LEGENDS

FIGURE 1. Occurrence records obtained for the 19 coastal lowland anuran species in the Brazilian Atlantic forest.

FIGURE 2. Flowchart of analyses used in our study. From left to right, metrics and techniques used to evaluate potential future suitable habitat available under climate change and sea level rise for lowland coastal anurans in the Brazilian Atlantic forest.

FIGURE 3. Different expected consequences on distribution range. Bar plots showing the potential effects caused by: A) two distinctive climatic scenarios in which the A2a scenario is predicted to provide greater amount of suitable habitats in the future (in average) compared to current conditions and B2a scenario; B) two different sea level rise (SLR) scenarios, showing 6m in rising sea levels decreasing more severely available suitable habitats.

FIGURE 4. Suitable habitat availability and potential losses by sea level rise for two lowland anuran species in Atlantic forest, namely *Haddadus plicifer* ((A) location, (B) potential habitat in the B2a climatic scenario, (C) potential effects of 3 m sea level rise); and *Crossodactylus lutzorum* ((D) location, (E) potential habitat in the A2a climatic scenario, (F) potential effects of 6 m sea level rise).

Figures

Figure 1

Figure 2

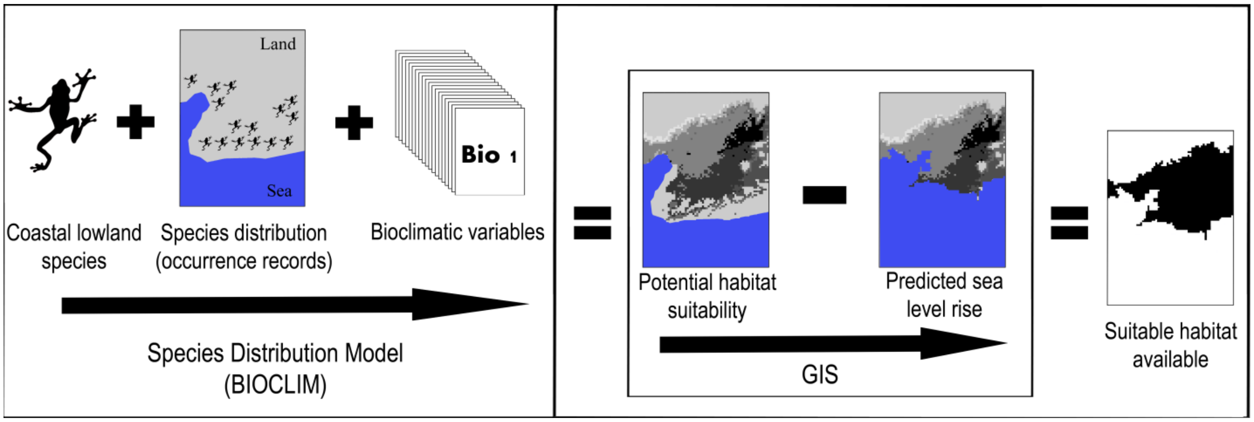

Land
Sea
Bio 1
Coastal lowland species
Species distribution (occurrence records)
Bioclimatic variables
Species Distribution Model (BIOCLIM)
Potential habitat suitability
Predicted sea level rise
GIS
Suitable habitat available

Figure 3

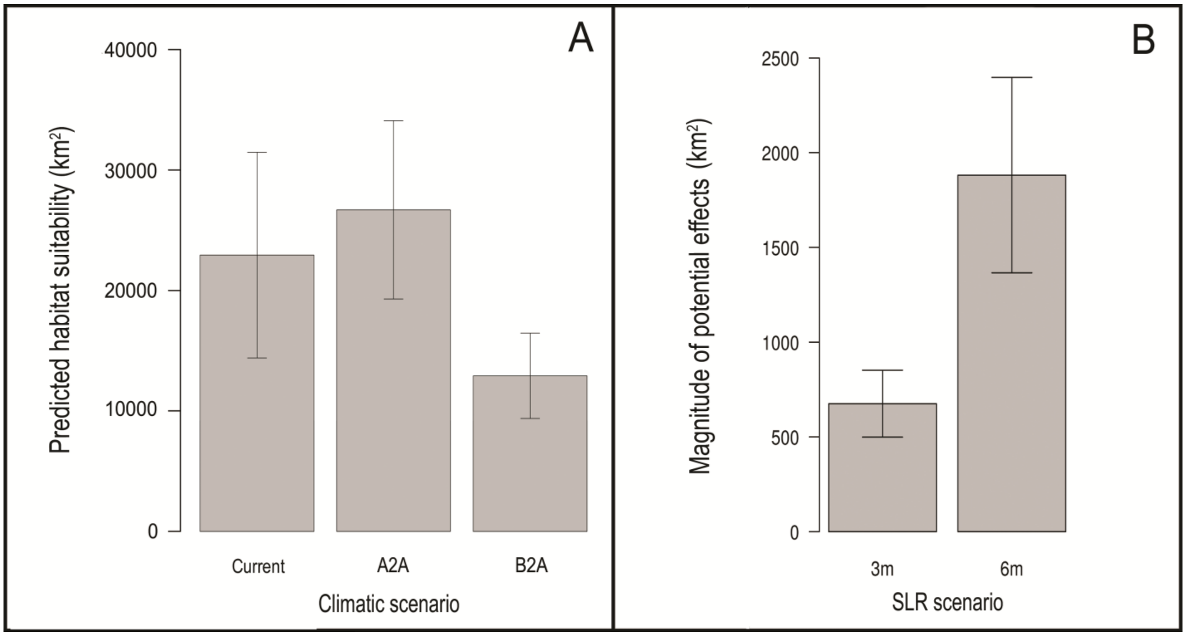
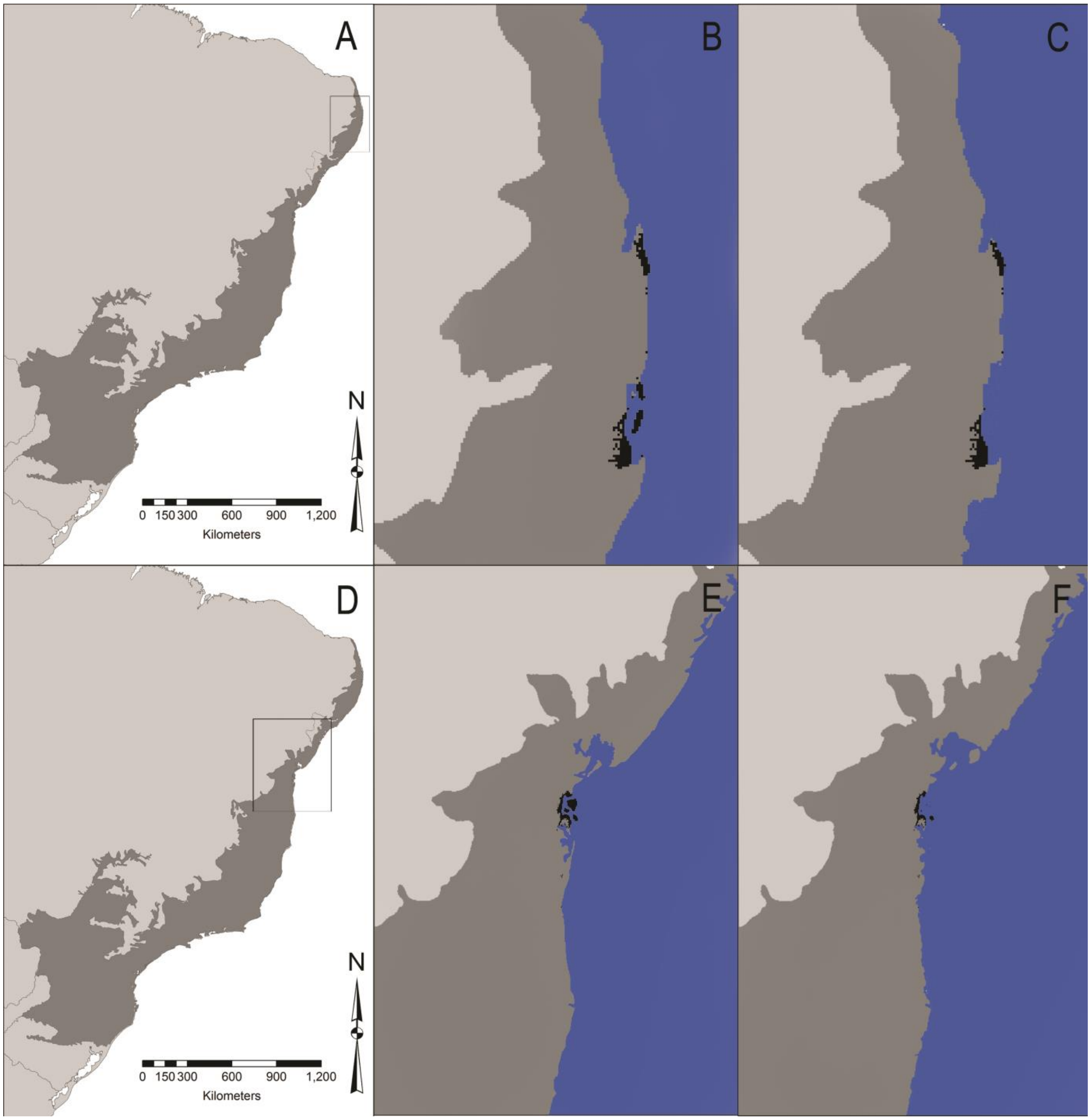

A
Predicted habitat suitability (km²)
40000
30000
20000
10000
0
Current
A2A
B2A
Climatic scenario
B
Magnitude of potential effects (km²)
2500
2000
1500
1000
500
0
3m
6m
SLR scenario

Figure 4


A
B
C
D
E
F
N
0 150 300 600 900 1,200
Kilometers
N
0 150 300 600 900 1,200
Kilometers

SUPPORTING INFORMATION

Assessing Future Habitat Availability for Coastal Lowland Anurans in the Brazilian Atlantic Rainforest

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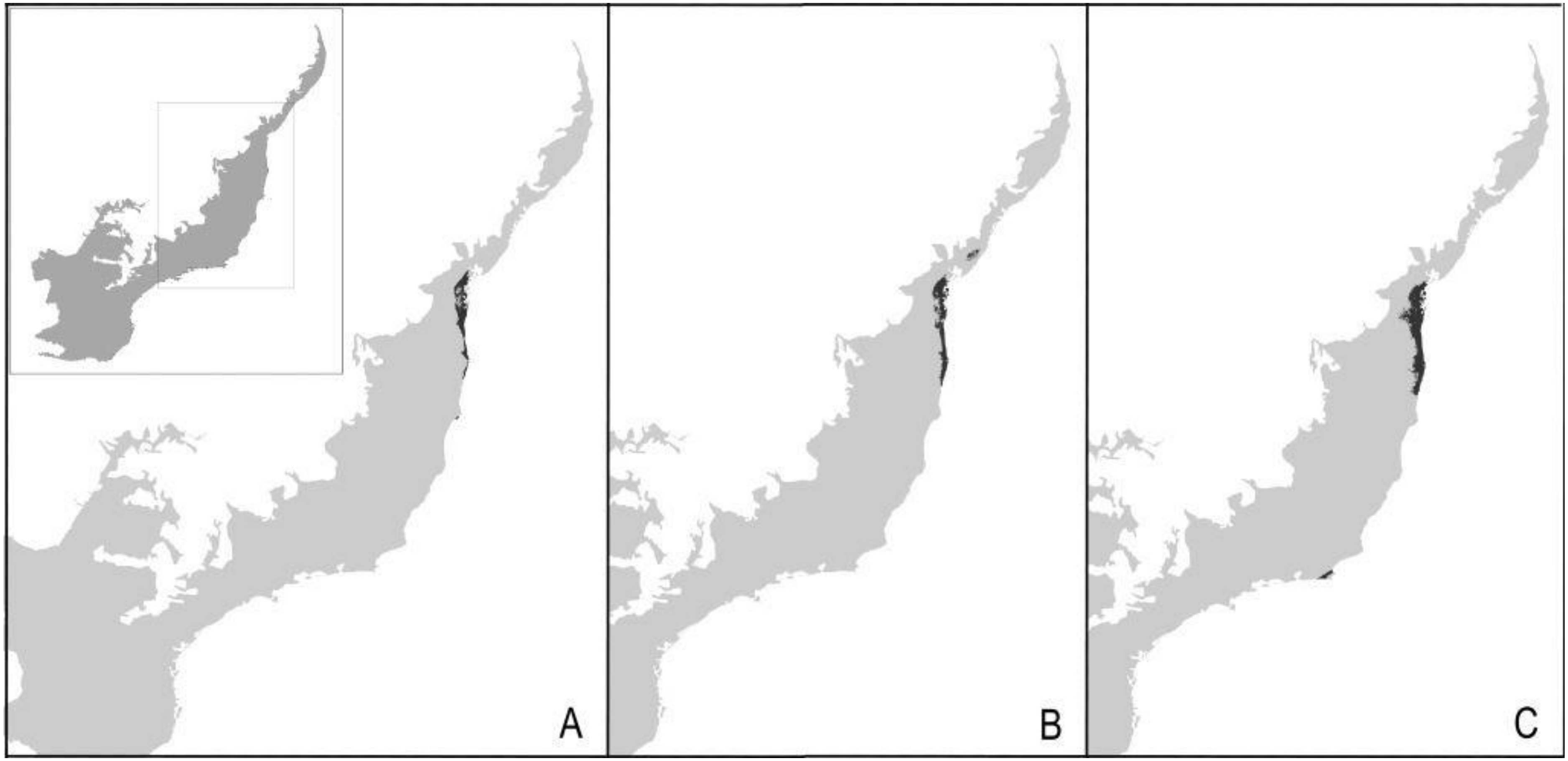

FIGURE S1: Estimated current (A) and future habitat suitability in the B2A (B) and A2A (C) climatic scenario for the year 2080 in the Brazilian Atlantic forest for *Aparasphenodon arapapa*.

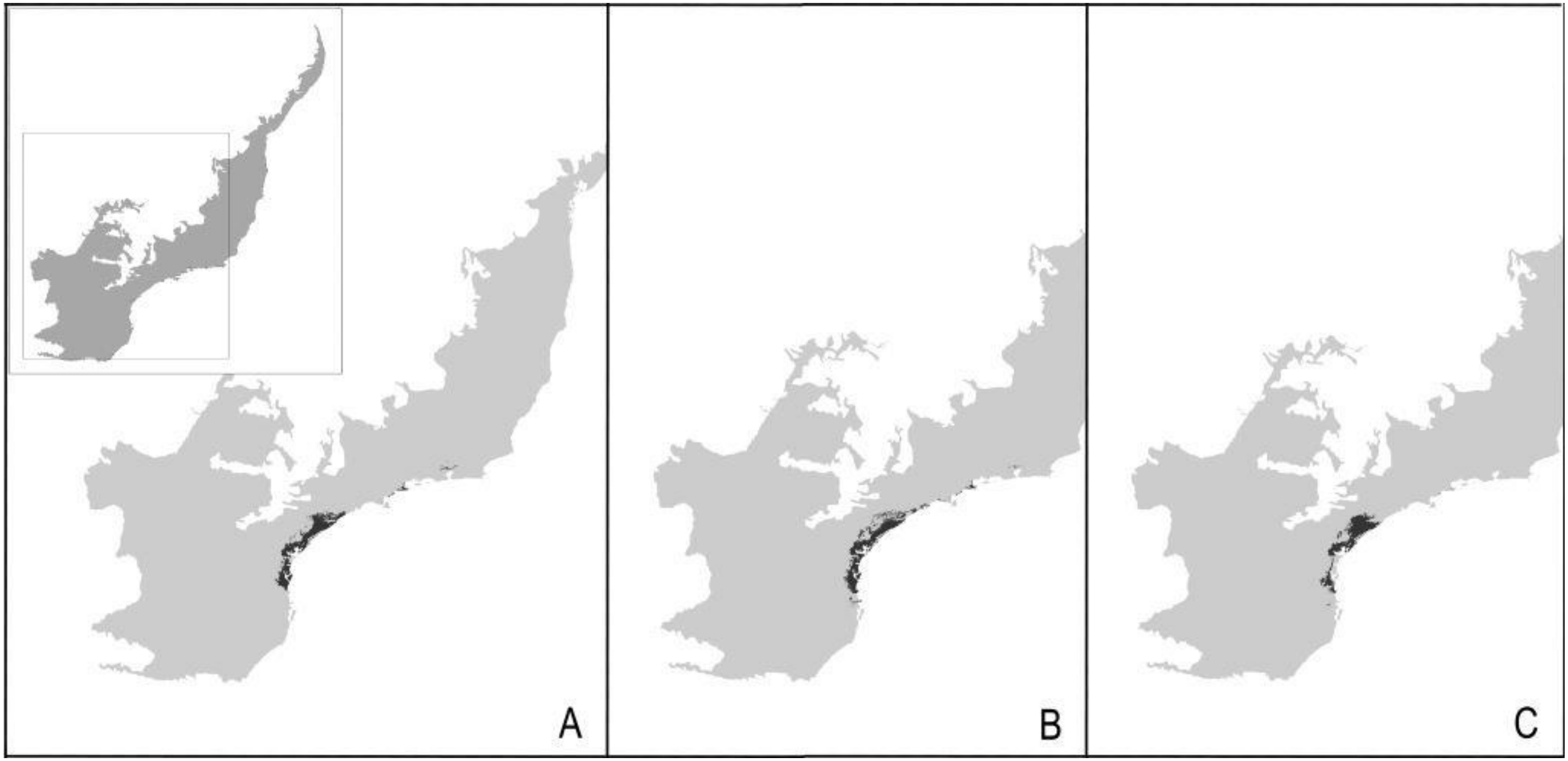

FIGURE S2: Estimated current (A) and future habitat suitability in the B2A (B) and A2A (C) climatic scenario for the year 2080 in the Brazilian Atlantic forest for *A. bokermanni*.

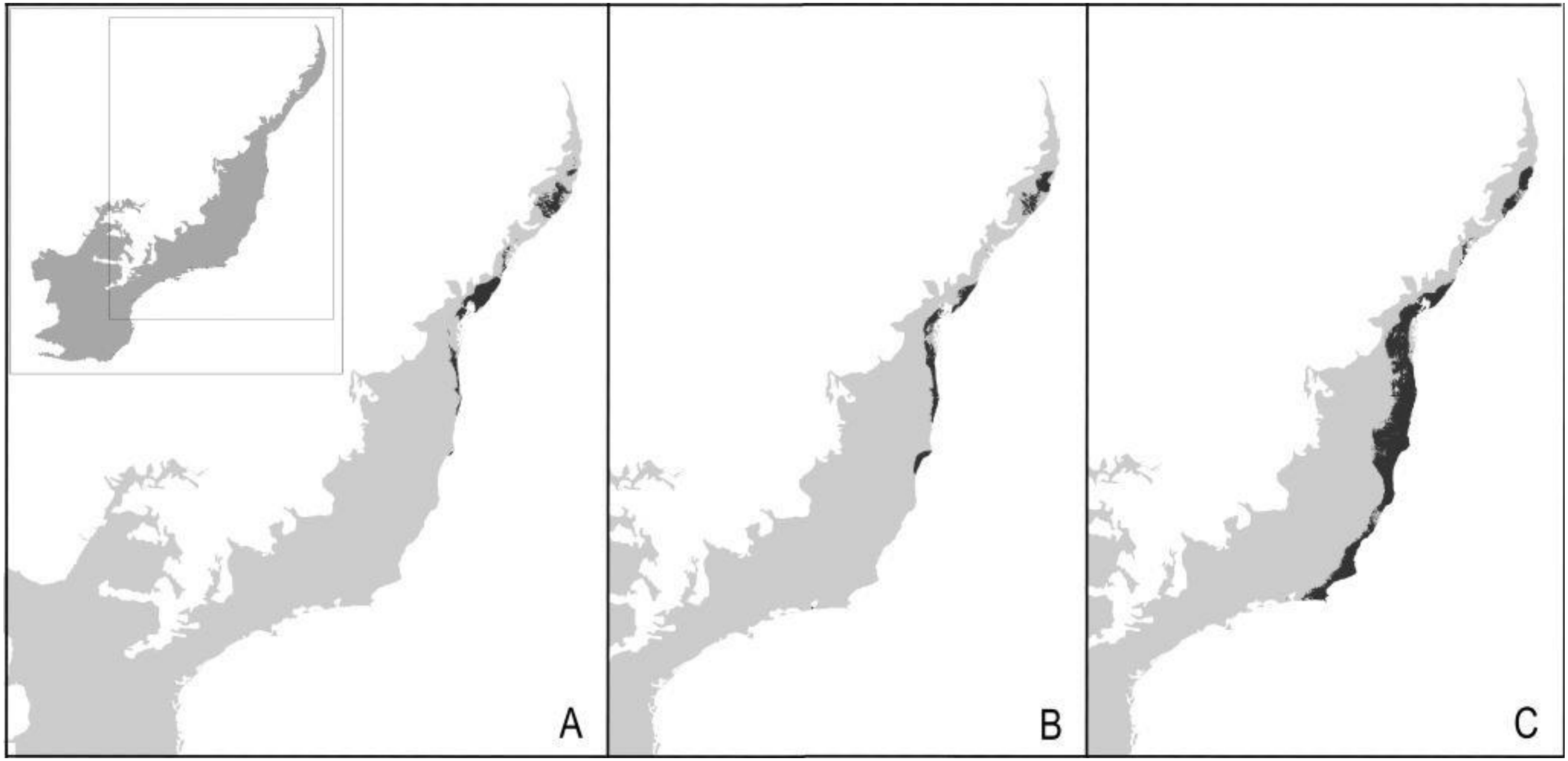

FIGURE S3: Estimated current (A) and future habitat suitability in the B2A (B) and A2A (C) climatic scenario for the year 2080 in the Brazilian Atlantic forest for *Chiasmocleis alagoana*.

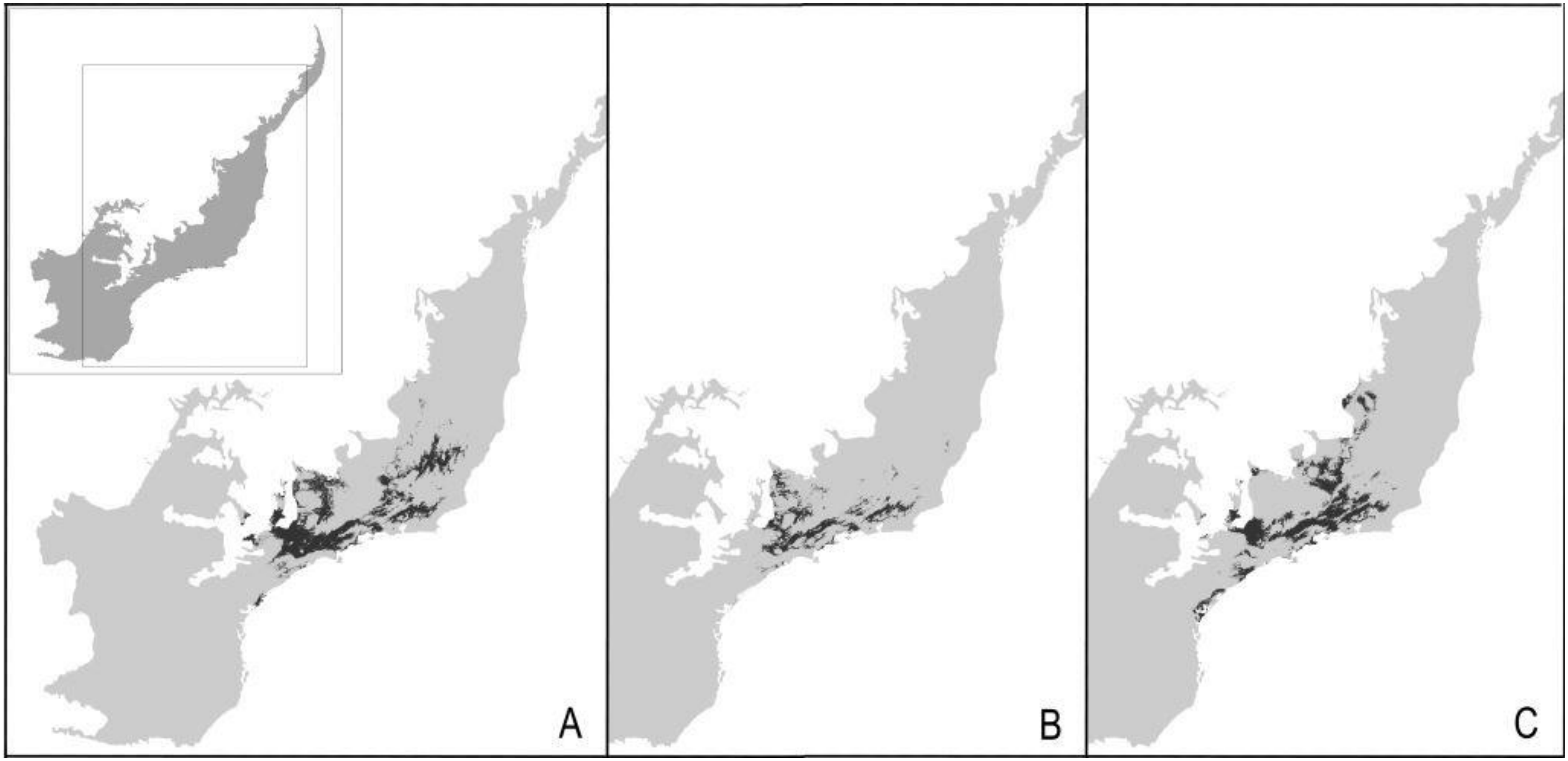

FIGURE S4: Estimated current (A) and future habitat suitability in the B2A (B) and A2A (C) climatic scenario for the year 2080 in the Brazilian Atlantic forest for *C. atlantica*.

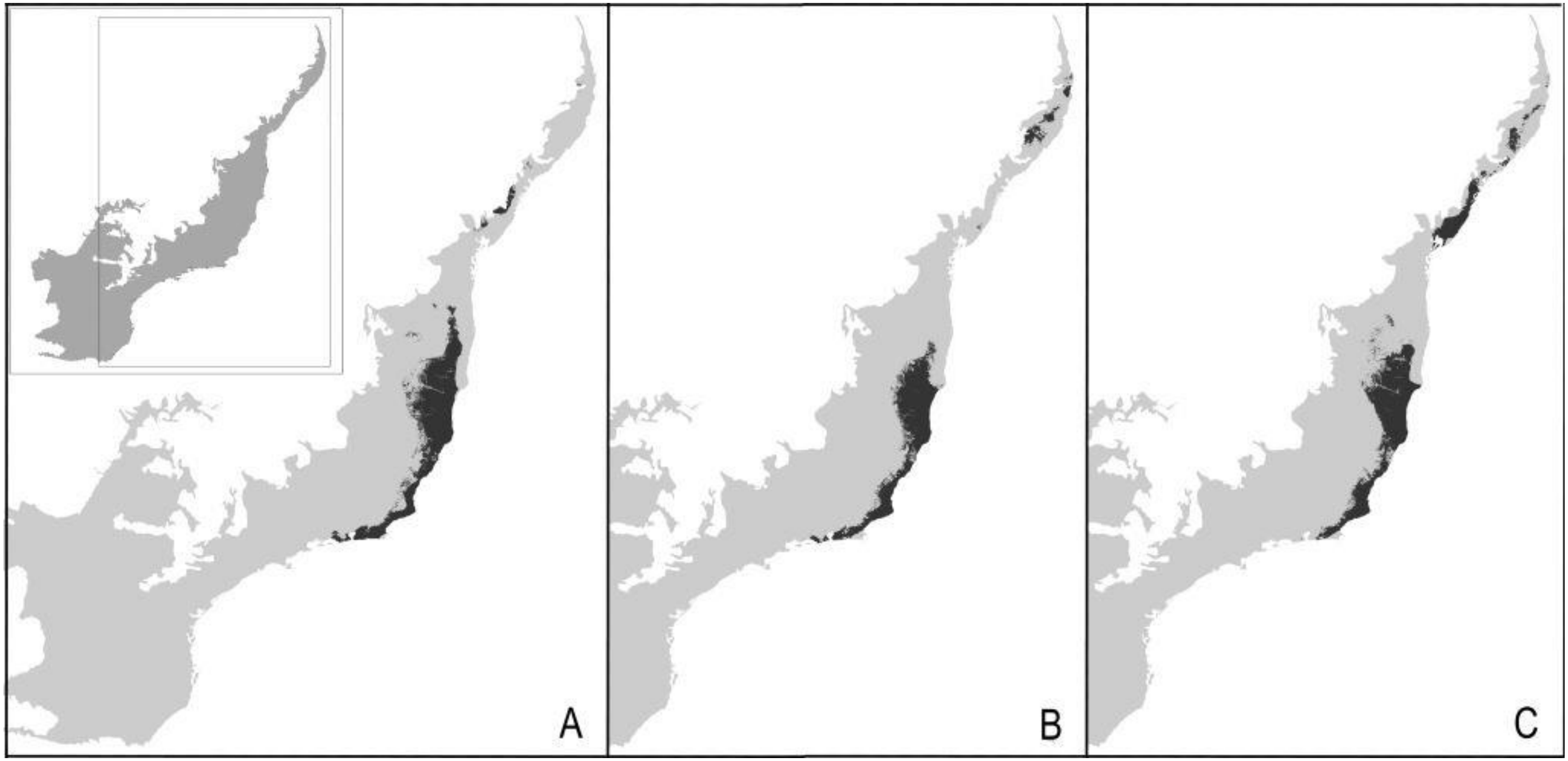

FIGURE S5: Estimated current (A) and future habitat suitability in the B2A (B) and A2A (C) climatic scenario for the year 2080 in the Brazilian Atlantic forest for *C. capixaba*.

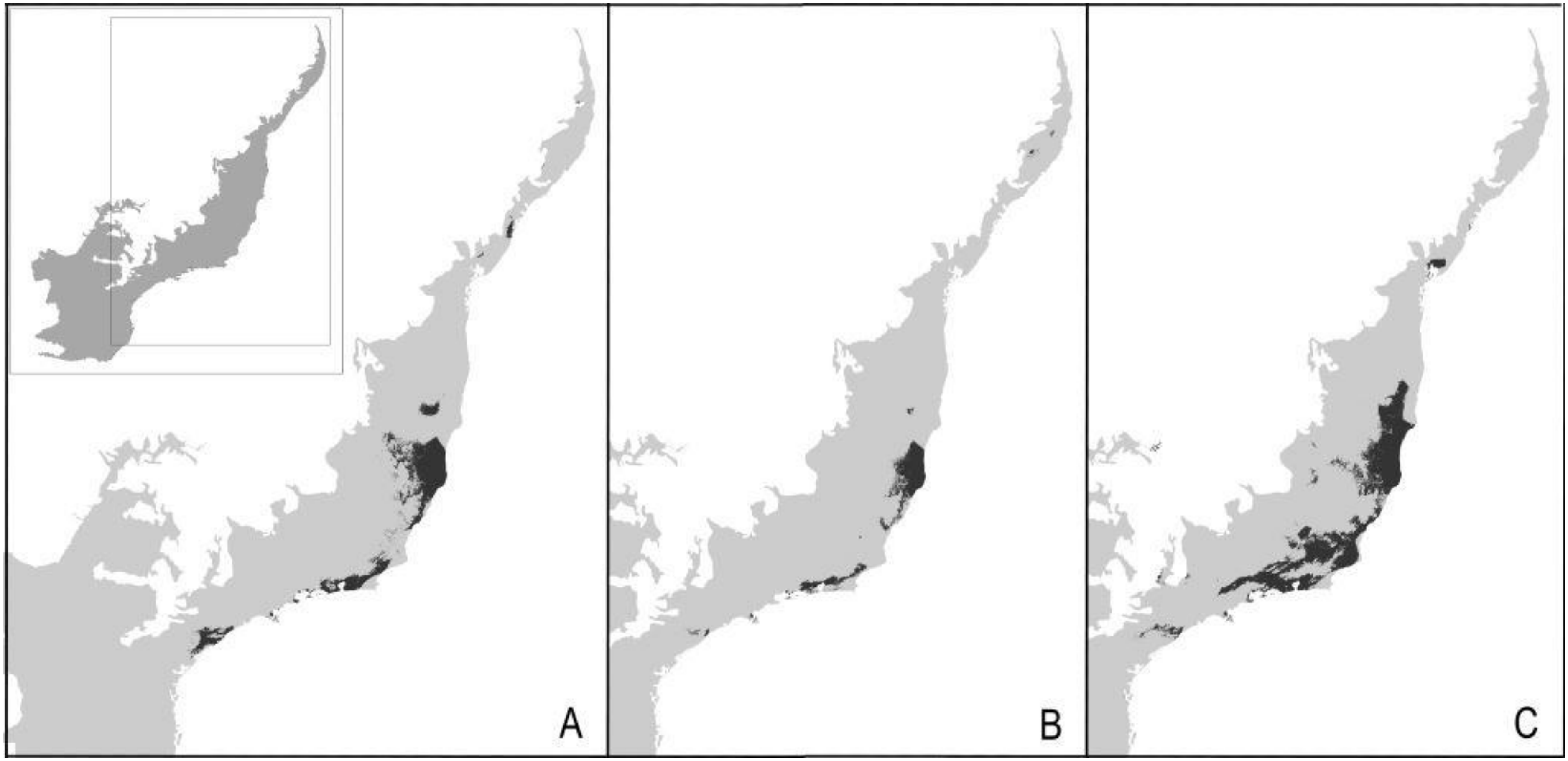

FIGURE S6: Estimated current (A) and future habitat suitability in the B2A (B) and A2A (C) climatic scenario for the year 2080 in the Brazilian Atlantic forest for *C. lacrimae*.

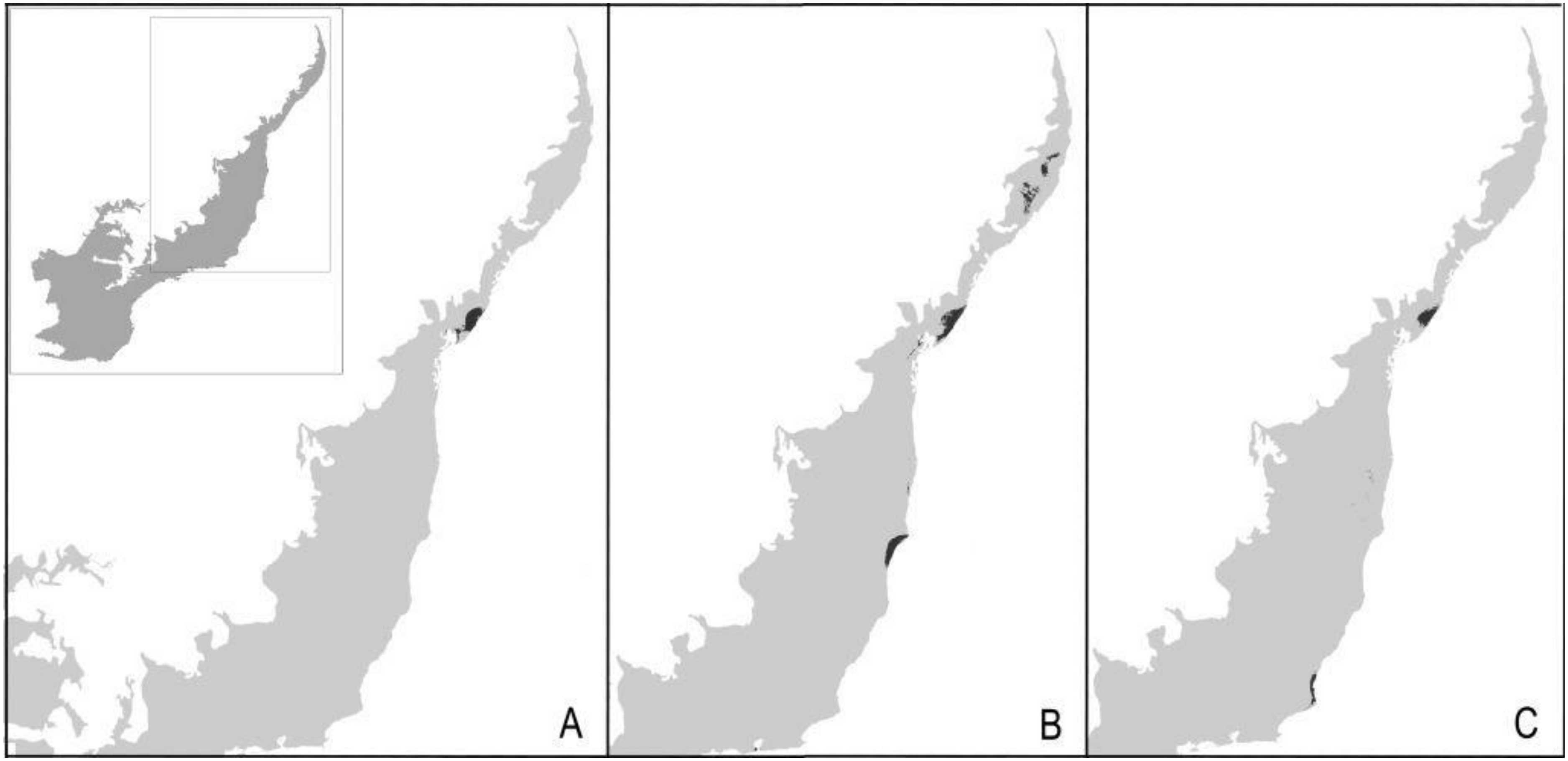

FIGURE S7: Estimated current (A) and future habitat suitability in the B2A (B) and A2A (C) climatic scenario for the year 2080 in the Brazilian Atlantic forest for *C. sapiranga.*

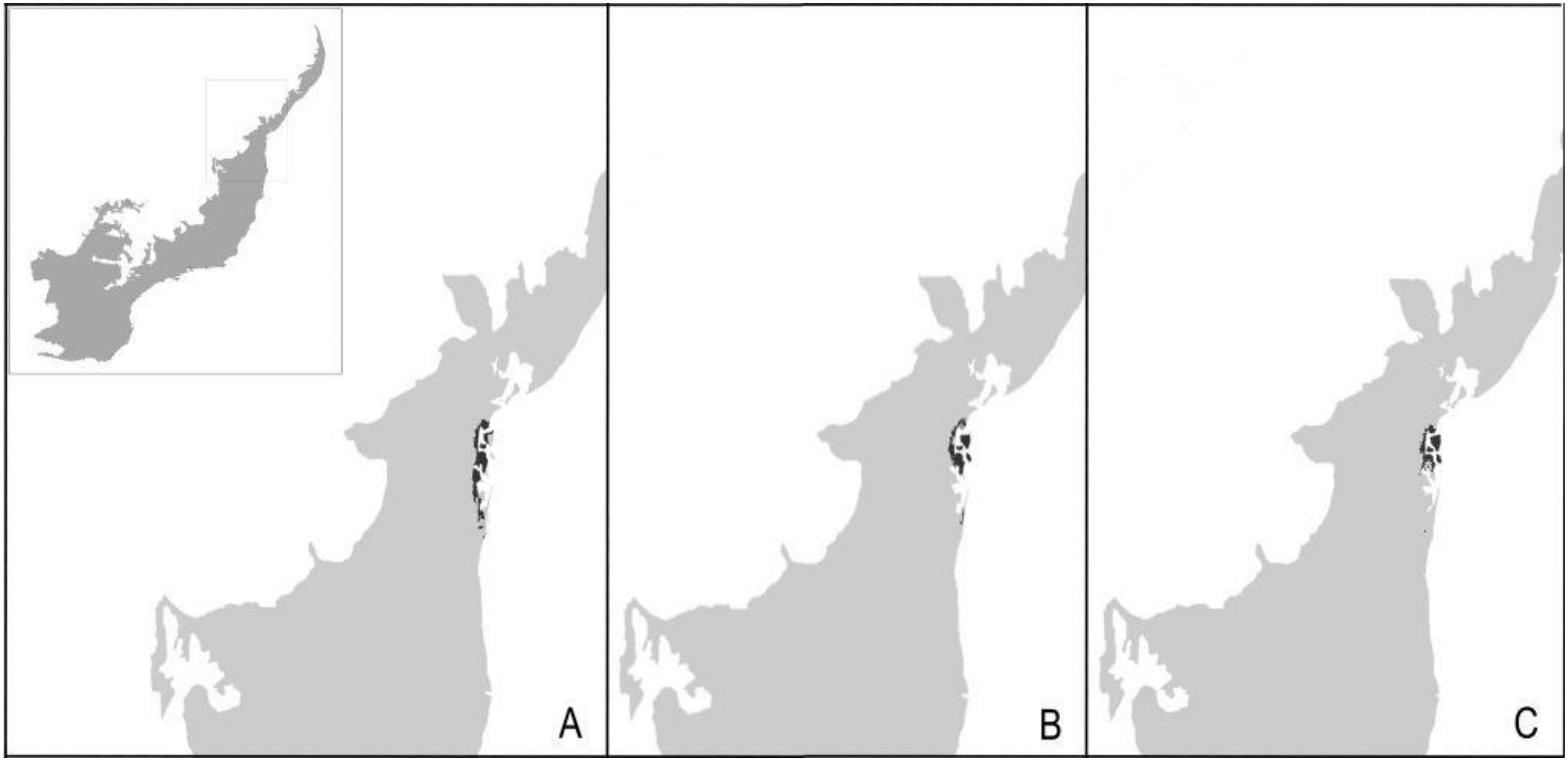

FIGURE S8: Estimated current (A) and future habitat suitability in the B2A (B) and A2A (C) climatic scenario for the year 2080 in the Brazilian Atlantic forest for *Crossodactylus lutzorum*.

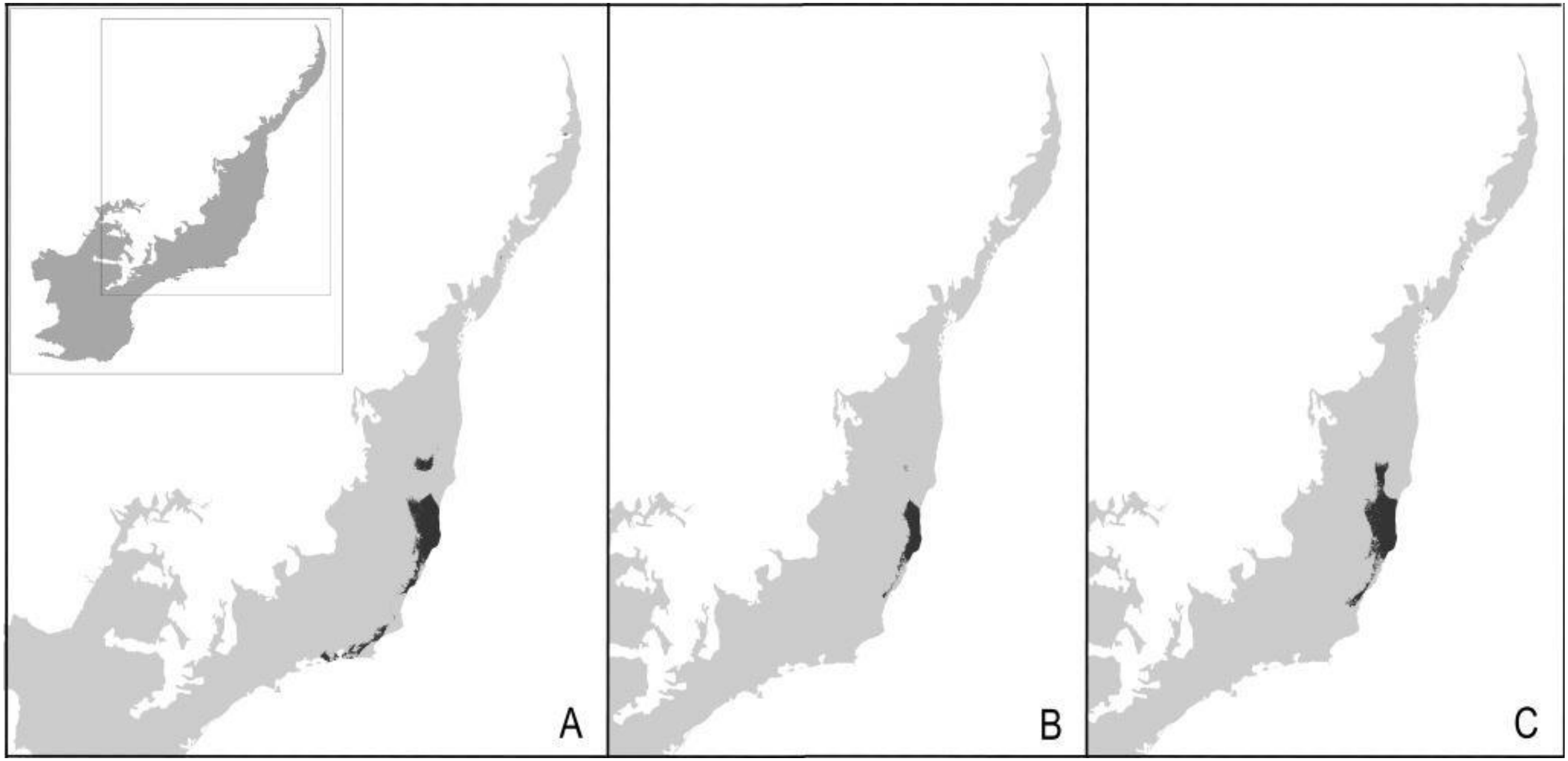

FIGURE S9: Estimated current (A) and future habitat suitability in the B2A (B) and A2A (C) climatic scenario for the year 2080 in the Brazilian Atlantic forest for *Dasypops schirchi*.

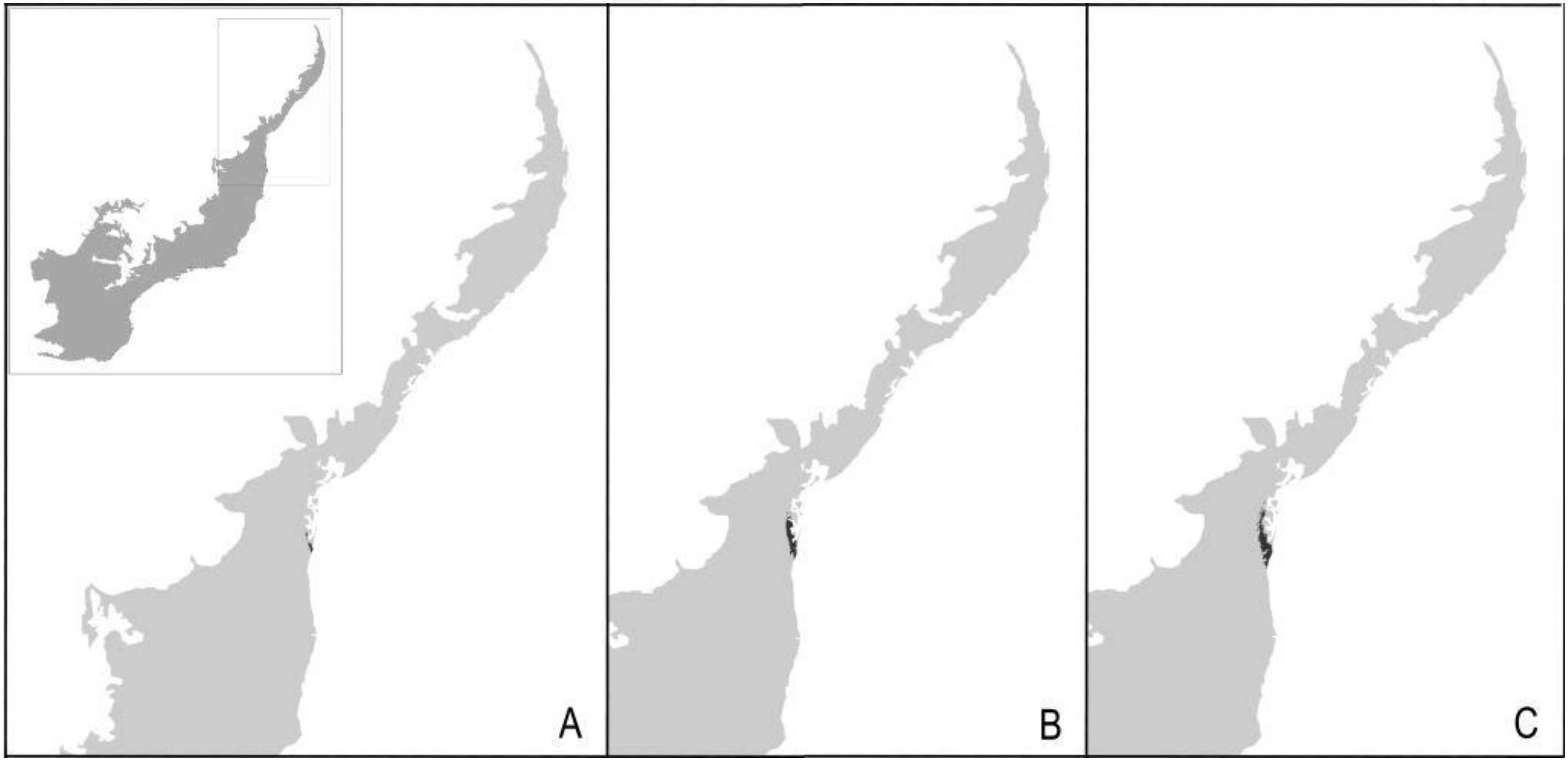

FIGURE S10: Estimated current (A) and future habitat suitability in the B2A (B) and A2A (C) climatic scenario for the year 2080 in the Brazilian Atlantic forest for *Dendrophryniscus skuki*.

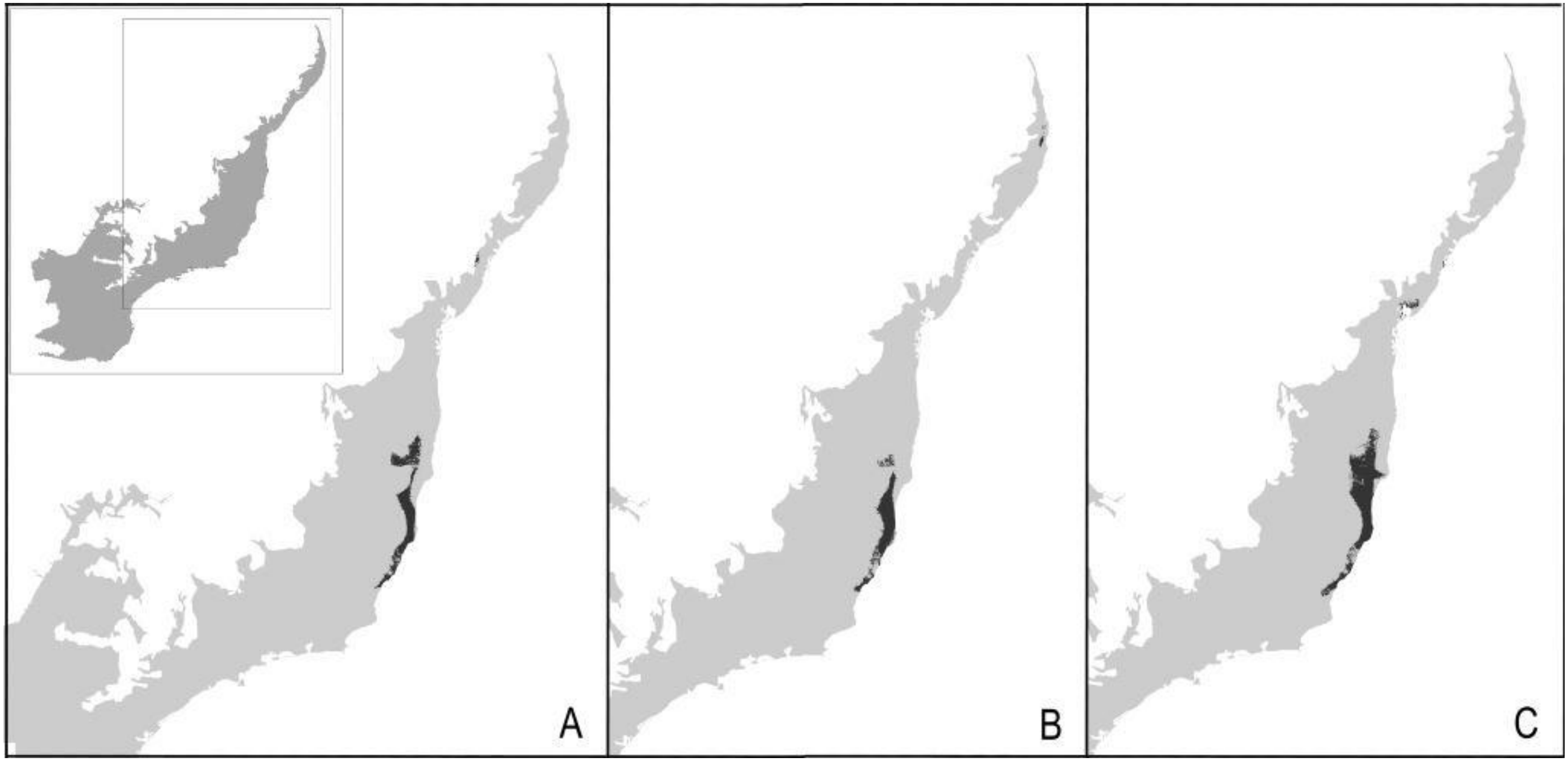

FIGURE S11: Estimated current (A) and future habitat suitability in the B2A (B) and A2A (C) climatic scenario for the year 2080 in the Brazilian Atlantic forest for *Gastrotheca megacephala*.

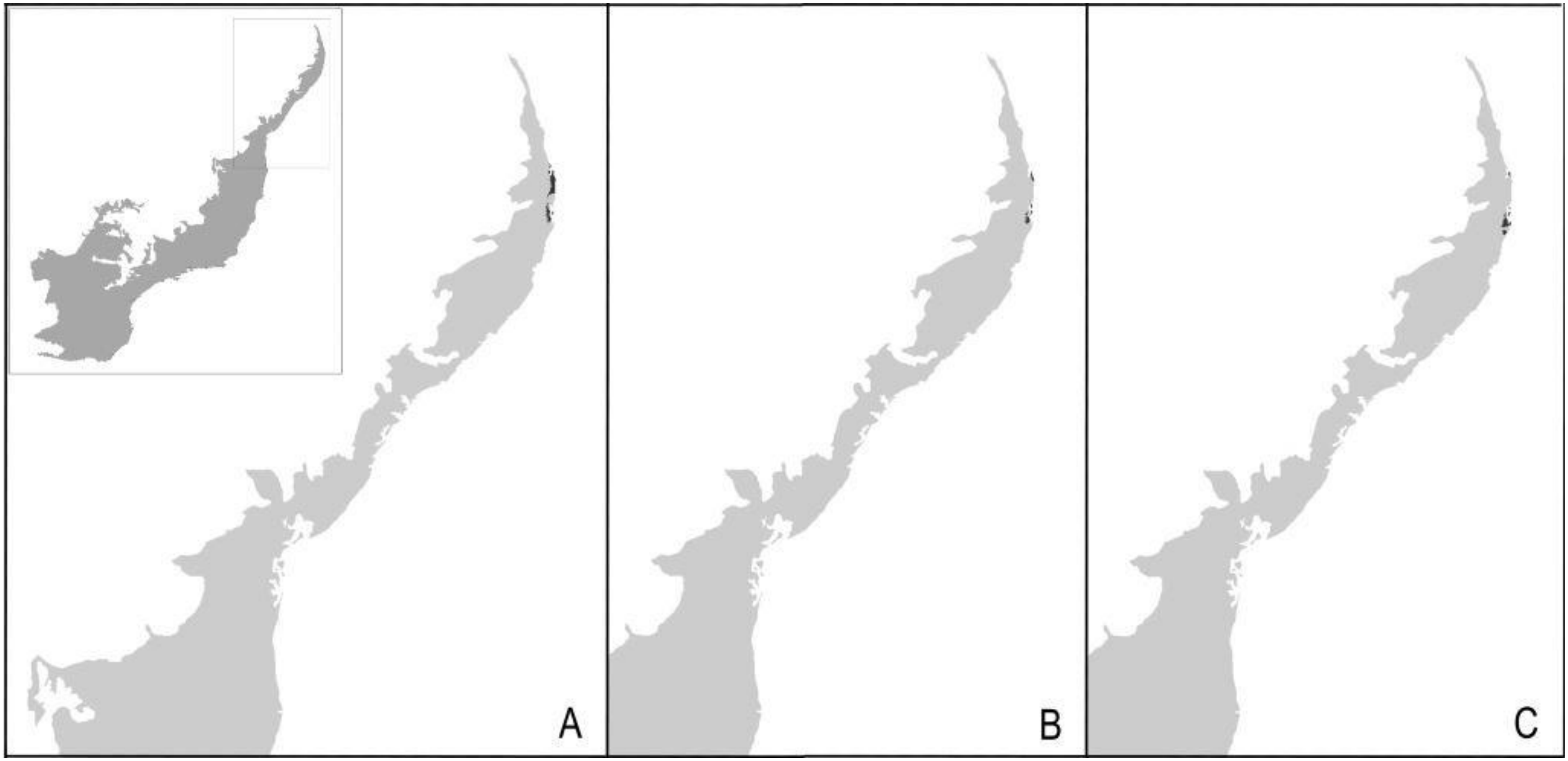

FIGURE S12: Estimated current (A) and future habitat suitability in the B2A (B) and A2A (C) climatic scenario for the year 2080 in the Brazilian Atlantic forest for *Haddadus plicifer*.

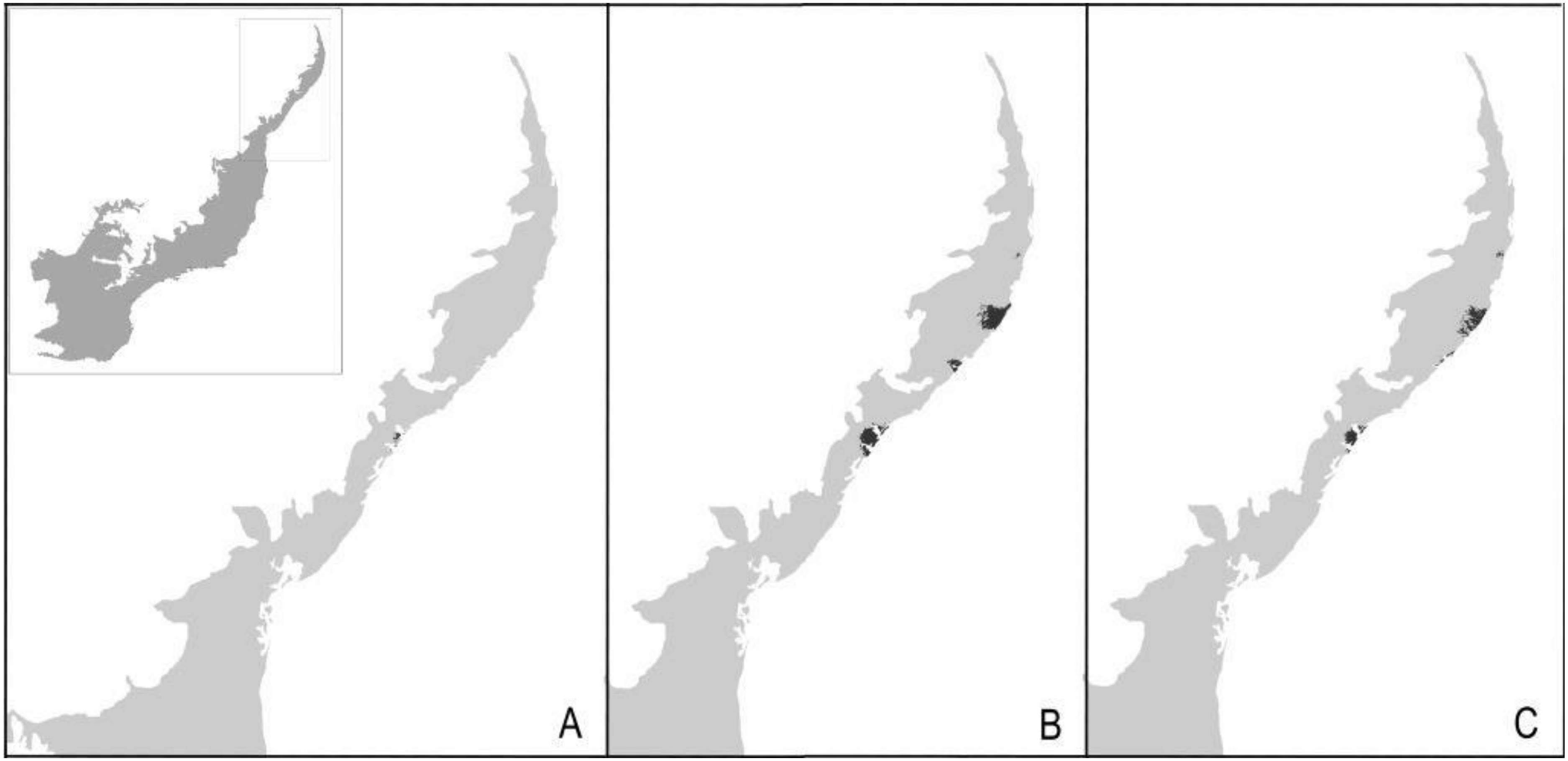

FIGURE S13: Estimated current (A) and future habitat suitability in the B2A (B) and A2A (C) climatic scenario for the year 2080 in the Brazilian Atlantic forest for *Leptodactylus hylodes*.

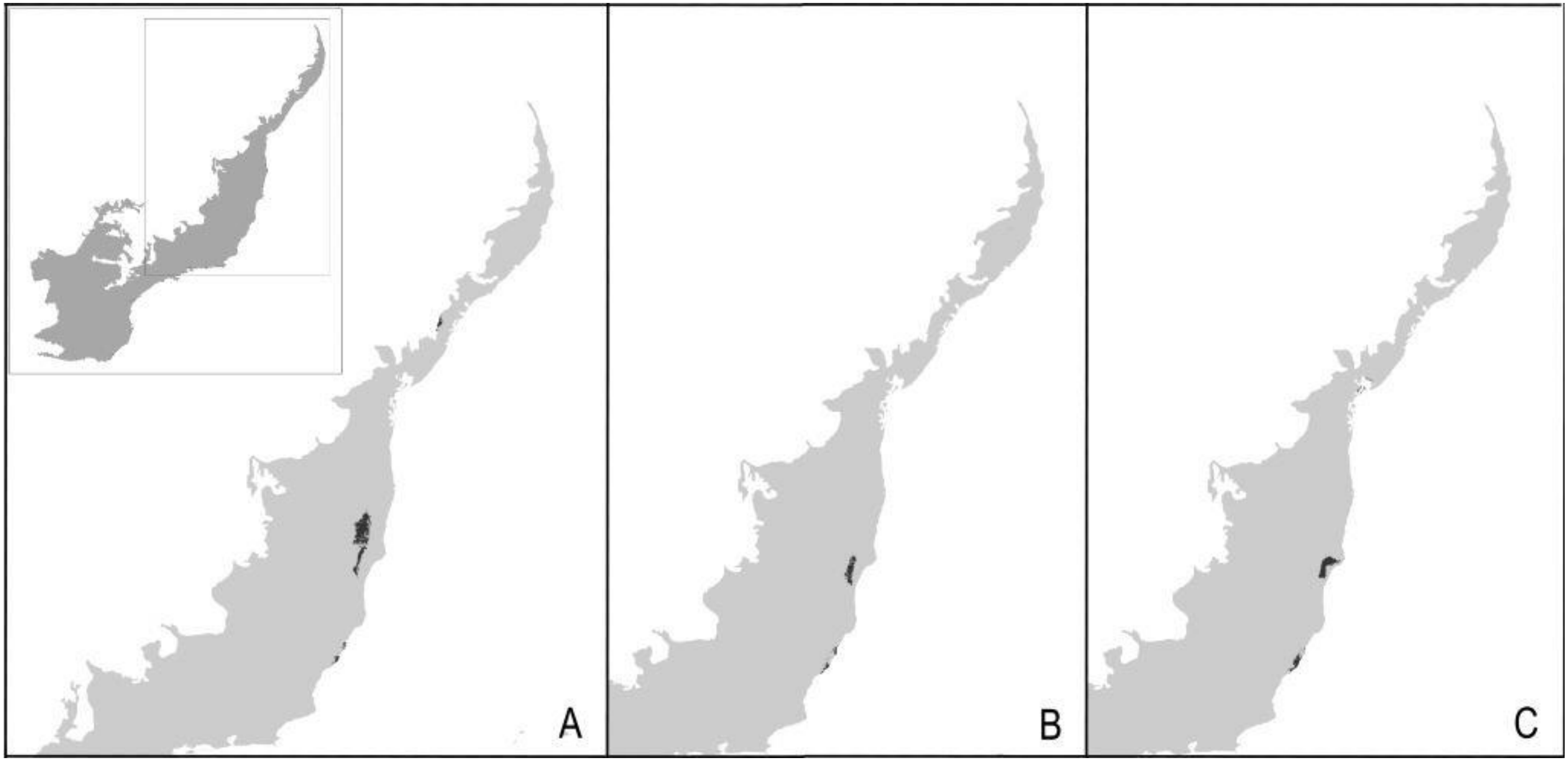

FIGURE S14: Estimated current (A) and future habitat suitability in the B2A (B) and A2A (C) climatic scenario for the year 2080 in the Brazilian Atlantic forest for *Melanophryniscus setiba*.

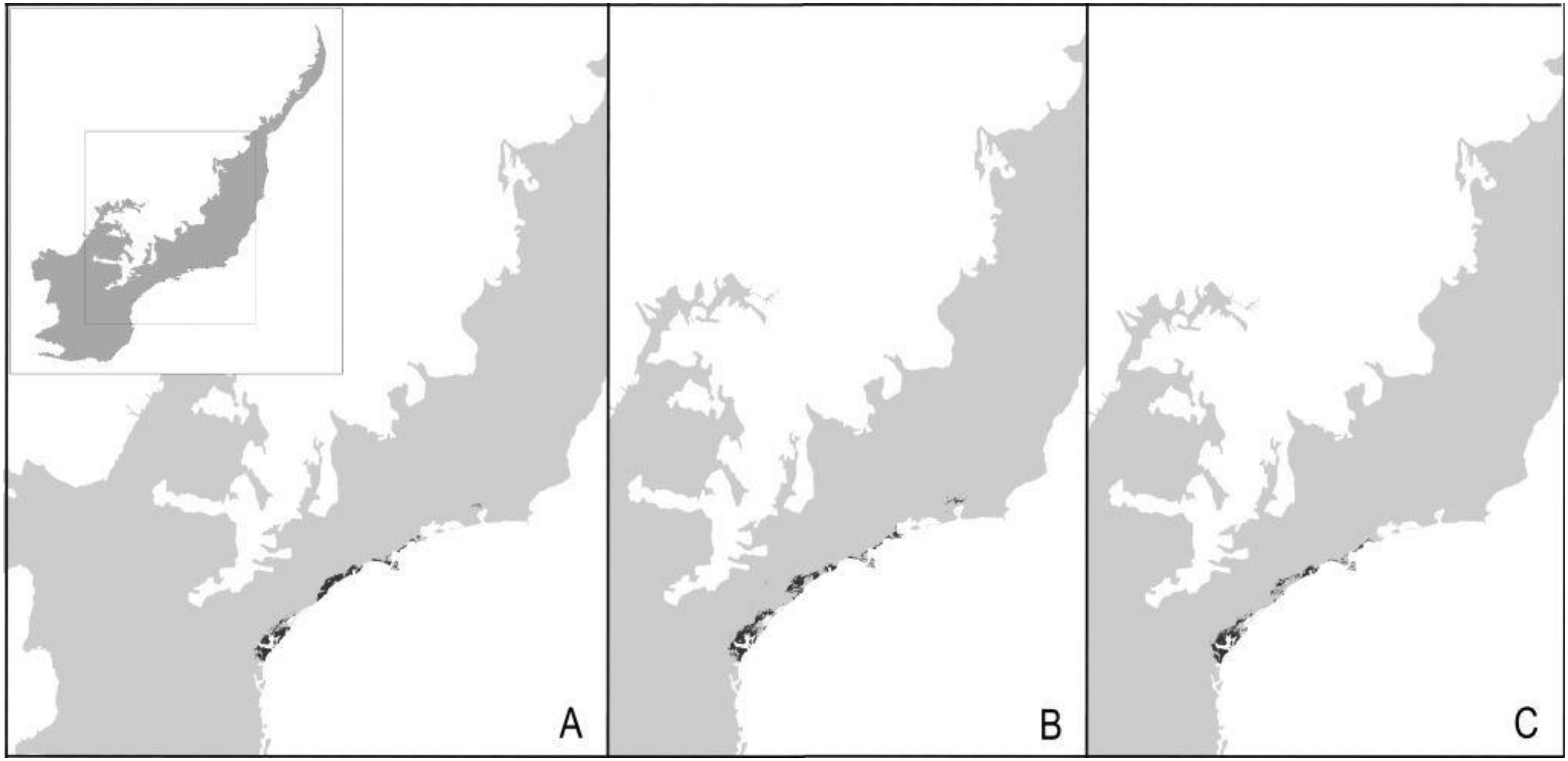

FIGURE S15: Estimated current (A) and future habitat suitability in the B2A (B) and A2A (C) climatic scenario for the year 2080 in the Brazilian Atlantic forest for *Physalaemus atlanticus*.

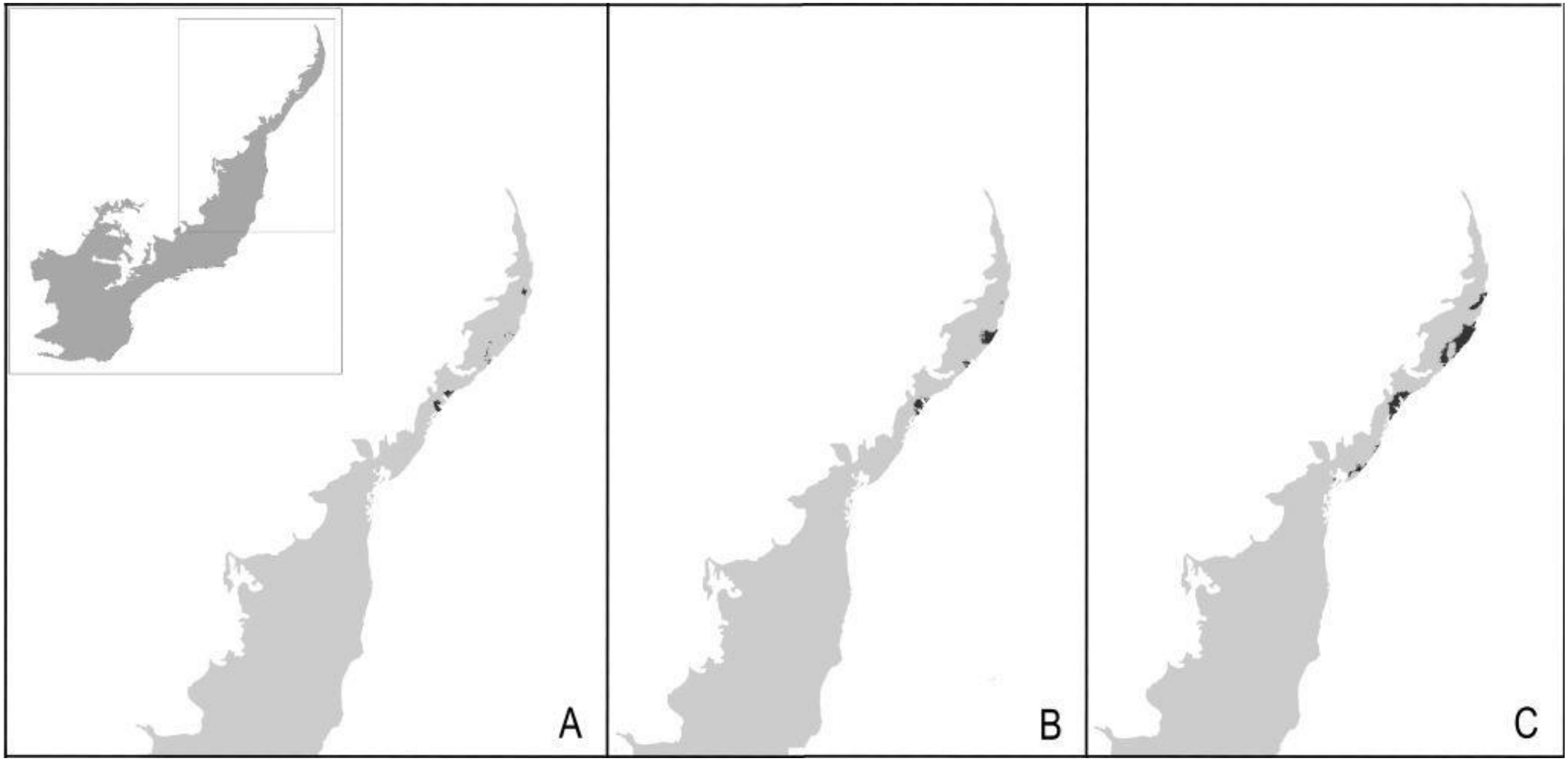

FIGURE S16: Estimated current (A) and future habitat suitability in the B2A (B) and A2A (C) climatic scenario for the year 2080 in the Brazilian Atlantic forest for *Phyllodytes punctatus*.

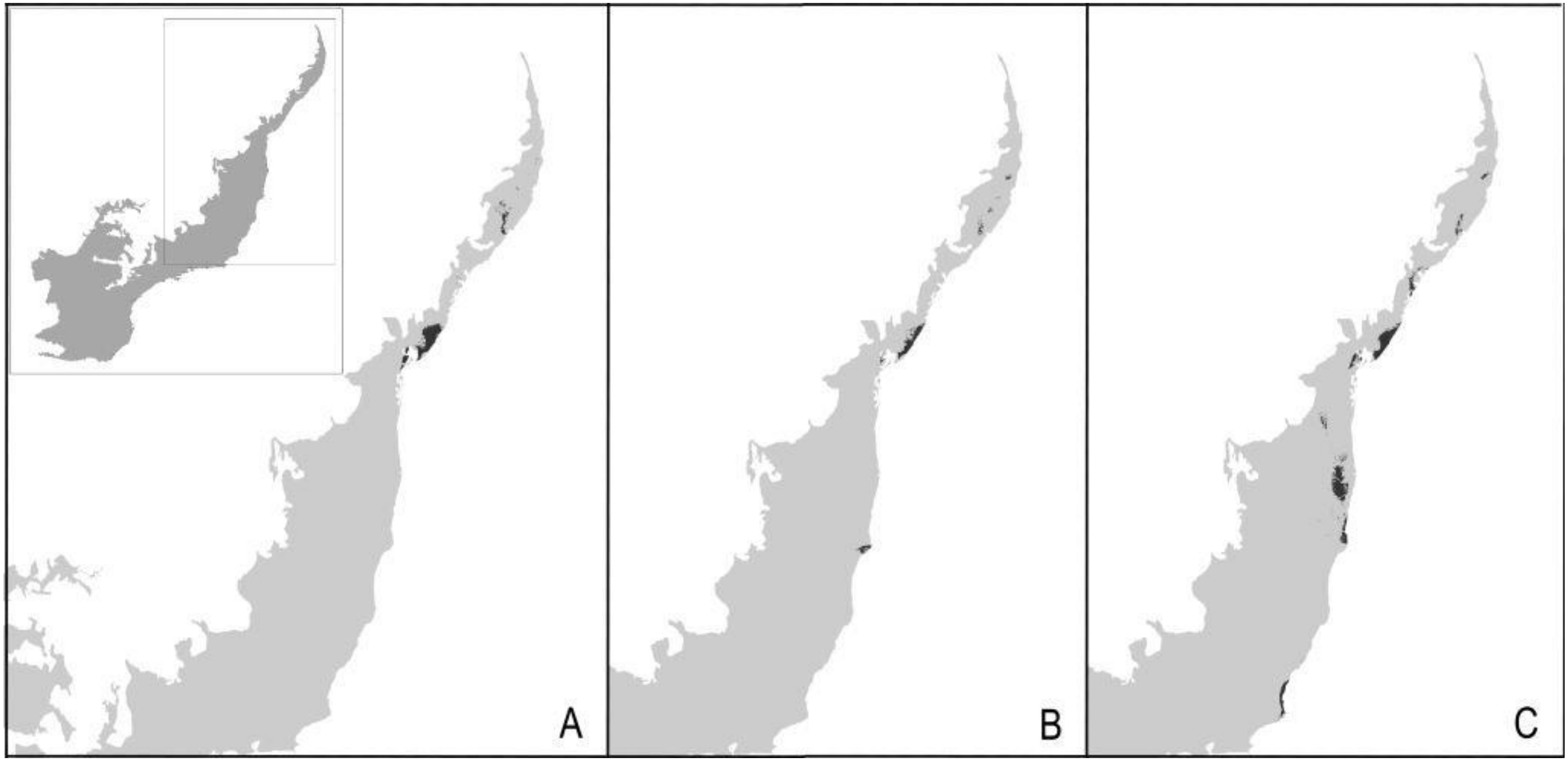

FIGURE S17: Estimated current (A) and future habitat suitability in the B2A (B) and A2A (C) climatic scenario for the year 2080 in the Brazilian Atlantic forest for *Scinax cretatus*.

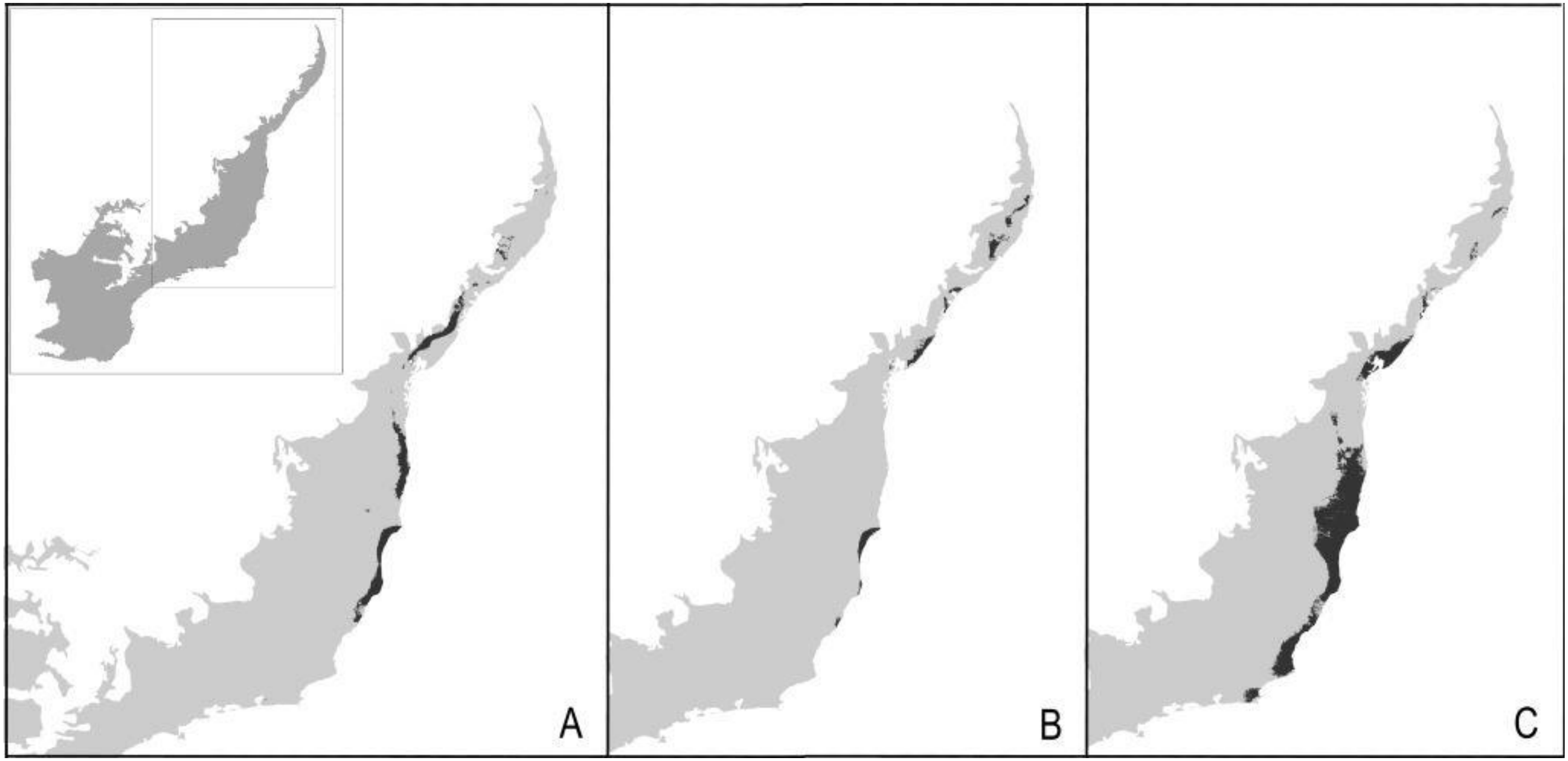

FIGURE S18: Estimated current (A) and future habitat suitability in the B2A (B) and A2A (C) climatic scenario for the year 2080 in the Brazilian Atlantic forest for *Sphaenorhynchus palustris*.

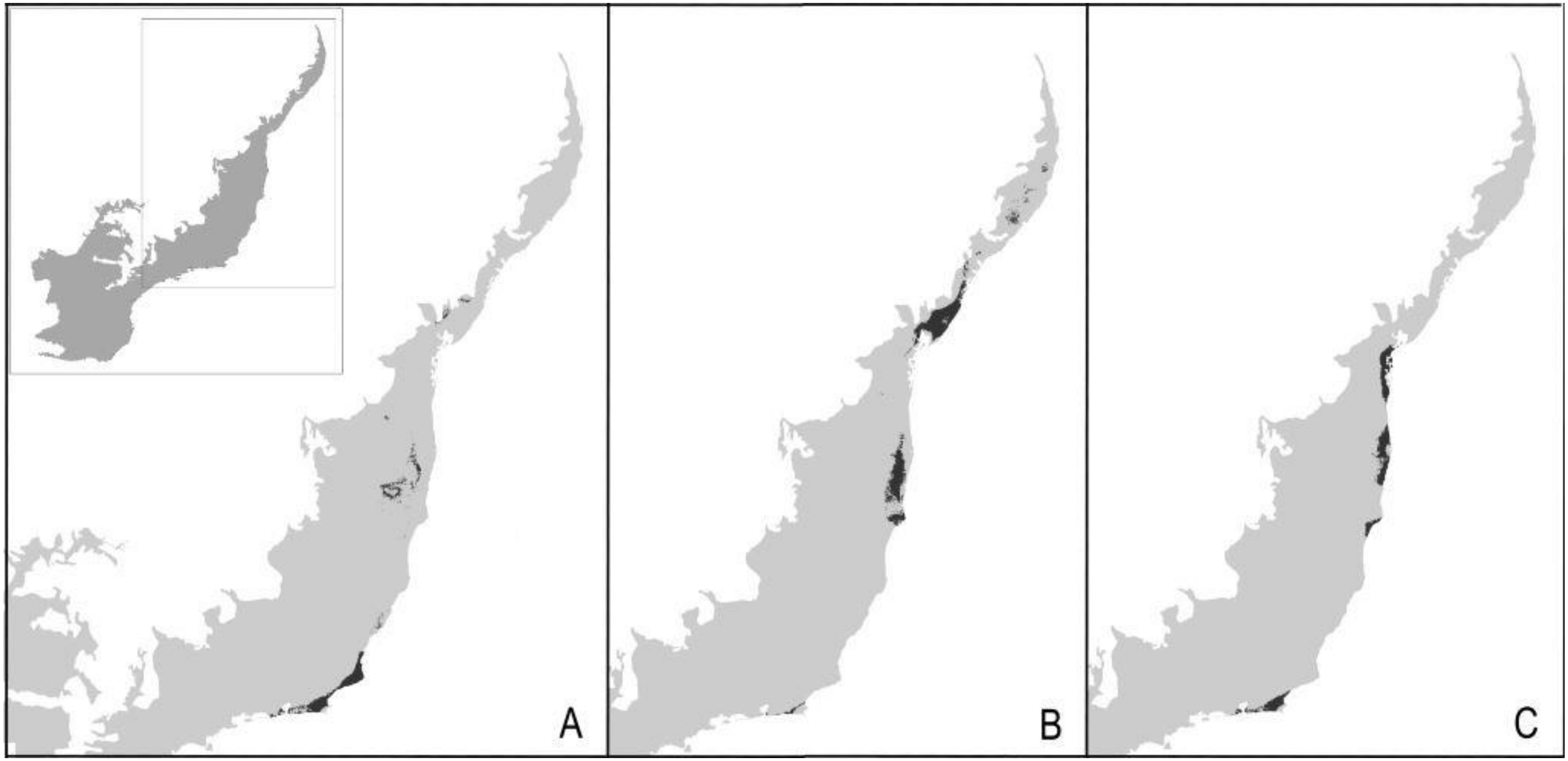

FIGURE S19: Estimated current (A) and future habitat suitability in the B2A (B) and A2A (C) climatic scenario for the year 2080 in the Brazilian Atlantic forest for *Xenohyla truncata*.

CAPÍTULO 3

Shedding light on data-deficient amphibian species

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Manuscrito formatado segundo o periódico Biological Conservation

Abstract

The IUCN system for the categorization of threatened species is a powerful tool broadly applied in wildlife conservation. However, for some evaluated species there is insufficient information available, and therefore, they are assigned as data deficient (DD). That's especially the case of amphibians, for which a fourth of its diversity lacks information, preventing or hindering actions for their appropriate conservation as a whole. Thus, the development of alternative systems that allow species prioritization for research in order to gather sufficient information may serve as a useful tool to overcome the current lack of data. Herein we developed a method to rank DD species in order to identify and prioritize those species that could be facing a higher set of threats, and consequently higher chances of extinction. We combined 12 factors related to amphibian population declines to estimate a relative risk index (I_{dd}) with range values between zero and one. I_{dd} consists in organize different data into standardized numeric values by the application of different methods, offering as a final result a numeric index which serves to rank the species. We identified 38 amphibian species currently assigned as DD to be considered high priority for research in order to gather sufficient information to allow their change of category. Our index seems to work properly and reasonably when compared to other classification systems, since several species assigned as priority by I_{dd}, also are highlighted as important for conservation by other methods. The advantage of I_{dd} is that multiple factors are considered in its calculation, working in order to balance the final index. Although we selected the Atlantic forest amphibians as a focal group, we advocate the use of I_{dd} for other groups, since its principles are applicable to any organism with minimum information available.

Key-words: Biodiversity hotspot, amphibian conservation, species prioritization, distribution model, IUCN red list, extinction risk

1. Introduction

The International Union for Conservation of Nature (IUCN) Red List of Threatened Species is undoubtedly the most widely applied categorization system in the field of conservation (Butchart et al., 2005; Rodrigues et al., 2006), which generally is the first step towards preservation of species. This system follows an objective framework based on population characteristics such as size, trend, distributional range and occupancy to quantitatively assign species into categories related to their escalated extinction risk (IUCN, 2012). Since the 1950s, first with Red Data Books and then with Red Lists (Butchart et al., 2005), IUCN developed and serve as a generalized baseline for actions related to conservation. The proposal of ranked classes as Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), or Critically Endangered (CR), reflecting increasing orders of threat, provides the information of which taxa might need to be firstly targeted by conservation programs. Likewise the development of regional or national lists is also encouraged (IUCN, 2010), increasing the network and accuracy of information.

At the same time that categorization offers a valuable approximation of the extinction risks species are facing, there is the Data Deficient (DD) category. Taxa are considered DD when there is insufficient information to clearly assess their extinction risk after evaluation, especially appropriate data on abundance and distribution (IUCN 2012). This clearly justifies the inclusion of certain taxa into such category, even when apparently there is sufficient biological information available. Moreover, some situations favor the assignment as DD, such as in the circumstances of recent descriptions (i.e., there were insufficient time to gather information), species described long time ago, but rarely reencountered (e.g. rare, cryptic taxa or located in remote areas), or cases of species that were insufficiently studied. As a result, a large proportion of species of different groups fall into this category (Howard and Bickford, 2014; IUCN, 2014; Teixeira et al., 2014). Indeed, DD species could be allocated in any of the IUCN categories, from LC to EX (Extinct in the wild), including all threatened ones (Howard and Bickford, 2014), if sufficient information were reached. In spite of that, DD species are usually ignored in fundraising and resource investment (Hoffmann et al., 2010; Morais et al., 2013; Teixeira et al., 2014), and therefore these species remain as a gap that may bias conservation plans (Butchart and Bird, 2010). Thus, the existence of a great proportion of DD species hinders enhancements in conservation practices (Morais et al., 2013; Howard and Bickford, 2014). Additionally, management of biodiversity conservation is a challenge because it demands an adequate balance between application of limited funds and time in an effective conservation framework (Brooks et al., 2006; Nóbrega and De Marco, 2011). Thus, multifarious techniques for prioritization (e.g. Brooks et al., 2006; Lemes and Loyola, 2013; Weinmann et al., 2013) are desirable as they help to select targets for the resource allocation, increasing species' information, and improving biodiversity protection.

With such concern in mind, the number of studies concerning the DD species has recently increased (e.g. Butchart and Bird, 2010; Morais et al., 2013; Howard and Bickford, 2014; Teixeira et al., 2014). Such efforts are valuable since they offer different approaches in attempt to include DD species into conservation actions. For example, Butchart and Bird (2010) highlighted countries with large number of DD bird species, as well as, their habitat type, whereas Howard and Bickford (2014) identified global regions where research priority is needed for amphibians. Likewise, Teixeira et al. (2014) propose a method to gather information on geographic distribution for DD taxa using a bat as model, and Morais et al. (2013) assessed the current extinction risk for Atlantic forest DD amphibians based on their geographic distribution and on the time passed since their description. Thus, there is an increasing acknowledgement that DD species and its associated tools have the potential to guide fundamental actions. Therefore, it is clear that DD species need attention, not only by theoretical perspectives, but also those to amplify their biological knowledge in terms of population ecology and distributional ranges, enabling us to assess their current extinction risk status. Hence, straightforward methods able to indicate which DD species should be prioritized may help to properly allocate time, money, and efforts.

Following this rationale, we hereby propose a classification system, ranking DD species based on fragmented available information. Such ranking provides a feasible structure applicable to every organism for which there is a minimum set of information. Our proposal is driven by the guideline question: which DD species might be prioritized in primary research? In attempt to answer this question we used Brazilian Atlantic forest (AF) amphibians as models. The AF is one of the world's biodiversity hotspots (Myers, 2000, 2003) severely impacted along history (Ribeiro et al., 2011) and likely to be vulnerable to future climate change (Colombo and Joly, 2010; Lemes et al., 2013). Consequently, this domain is a significant focus to conservation efforts (Ribeiro et al., 2011). Similarly, although amphibians are highly diverse in the AF (Haddad et al., 2013), the group is severely threatened (Hoffmann et al., 2010), rather sensitive to environmental changes (Hof et al., 2011; Foden et al., 2013), and possess a high proportion of DD species in this biome (Haddad et al., 2013; IUCN, 2014). Besides this, amphibians are currently the tetrapods (terrestrial vertebrates) with higher percentage of DD species (IUCN, 2014). Therefore, this scenario makes the AF amphibians a high priority for wildlife conservation worldwide and a model to be explored within our purpose.

2. Material and Methods

2.1. Data compilation

We delimited our geographical scale to the Brazilian Atlantic forest and used amphibians as biological models. We considered AF amphibians those listed by Haddad et al. (2013) and DD species those recognized by IUCN (2014). We did not use the Brazilian red list of threatened amphibians (Haddad, 2008), because, although it is mentioned the existence of 90 data deficient amphibians species, the list was not showed in the book, since the focus is on threatened taxa. We then selected a set of 12 factors (F_n) (Table 1), currently acknowledged as correlated with amphibian population declines, to calculate the prioritization index (referred hereafter as I_{dd}). For each F_n we provided values minimizing lack of information and preventing underestimations of the I_{dd}.

As the resulting matrix contained several non-numerical categorical variables, we established classes with values between zero and one for each categorical variable (Table 1). We attributed values to the factors based on the precautionary principle, which states that when a hypothesis is plausible, it does not mean it is probable, but if such scenario comes true, it could imply in population declines (UNESCO, 2005). In other words, numeric values were credited in order to avoid under or overestimations based on amphibians biological traits. Besides that, missing information should encourage improving knowledge (Howard and Bickford, 2014). Therefore, if there was lack of information for one factor we interpreted as more risk toward to extinction risk and attributed values of one. On the other hand, certain traits are likely to increase individual fitness, such as higher tolerance to environmental changes (e.g. diversity of reproductive modes, or a measure of resilience). Hence, for species with these characteristics we attributed value of zero for the specific F_n. The only exception was the F_6 (Table 1), for which we assumed null value for the absence of data (unknown), even though we know that there are no confirmed cases of *Batrachochytrium dendrobatidis* absence.

2.2. Estimating climatic suitability

We used Ecological Niche Modeling (ENM) (Peterson and Soberón, 2012) to estimate the range of climatic suitability for each species in order to explore suitable niche instead the realized. Therefore, we intentionally overestimate species' distributions owing to the exploratory nature of our proposal. We applied the Maximum Entropy algorithm (Phillips et al., 2006) implemented in the software MaxEnt version 3.3.3k (http://www.cs.princeton.edu). Maximum Entropy is largely used in distribution model approaches and generally presents good performance (Pearson et al., 2007; Mendoza-González et al., 2013; Zank et al., 2014). It build models of environment suitability by the use of presence-only species records to project probability densities in covariate space (Elith et al., 2011). In addition, MaxEnt usually show high success rate with few presence-points (Pearson et al., 2007), which is common when dealing with DD species. To evaluate the model performance we verified the AUC (Area Under the Receiver Operating Characteristic Curve) values. Based on the AUC value each model was considered acceptable or not (Swets, 1988; Girardello et al., 2009). In order to minimize potential bias resulted from transferability (Liu et al., 2005; Peterson et al., 2007), and also to intentionally produce a flexible estimation of suitable areas, we selected low values of threshold to generate binary maps of suitability (Nenzén and Araújo, 2011; Peterson et al., 2007).

Occurrence records were obtained from the Global Biodiversity Information Facility (http://www.gbif.org/) and from the SpeciesLink (http://splink.cria.org.br/) websites. We built ENMs under current and future climatic conditions for each taxa using nine bioclimatic variables in order to avoid bias by collinearity (e.g. Nori et al., 2011; Zank et al., 2014). Interpolated bioclimatic conditions (from 1950 to 2000) at a grid cell resolution of 30 arc-second (~1 km) were obtained from WorldClim (http://www.worldclim.org). We projected climatic suitability to the year 2080 under climate change in the B2 emission scenario (IPCC, 2007) using the CCCMA-CGCM2, CSIRO-MK2, and HCCPR-HadCM3 models, arithmetically merged by map algebra in ArcGIS 10 (ESRI, 2011), obtained from the Research Program on Climate Change, Agriculture and Food Security website (http://www.ccafs-climate.org).

3.Calculation

3.1 Designing the prioritization index

To create the I_{dd}, based on multiple F_n (Table 1), we designed a score system to systematically rank DD species according the number of possible handicaps that could be potentially deleterious to amphibian populations. Thus, I_{dd} can be interpreted as a prioritizing index, where species with the highest I_{dd} are those that may be the first targets of gathering information or conservation related research. We fractionated the ranked index results into classes of prioritization using quartiles. The first quartile was labeled “low”, the second and third were “moderate”, and the fourth quartile was considered “high” in terms of priority. Finally, we used a simple arithmetic average to calculate I_{dd} by the following equation:

$$I_{dd} = \frac{1}{F_n} \sum_{n=1}^{\infty} f(n)$$

4. Results

Our final data set encompassed 153 DD amphibian species (4 Gymnophiona and 149 Anura) within the Brazilian AF. The threshold values for the quartiles were: 0.457 (first), 0.458 and 0.539 (second and third), and 0.540 (fourth) (Fig. 1). Thus, the fourth quartile contained 38 species considered as high priority for primary research (Table 2). *Leptodactylus hylodes* presented the highest value for the I_{dd} score (0.768), whereas *Hysiboas exastis* showed the lowest score number (0.268).

The ENMs we built to estimate habitat suitability presented a general good fit with acceptable to high AUC values ranging from 0.73 to 1 (mostly higher than 0.9) (Table A1); therefore, all models were considered. According to the output maps, although no case of total unsuitability was detected (i.e. extinction risk by unsuitable climate), when projecting the models to future climate conditions, around 45% (n = 70) of species presented some level of decrease in their range of suitable habitat (Table A2). In terms of spatial distribution, the assessment of the occurrence of all DD species and the high priority DD species highlight a large number of DD taxa in the southeastern portion of the Atlantic forest, with up to 31 (for all DDs) or 8 (high priority) DD species in the same grid cell (Fig. 2).

5. Discussion

We developed an index to rank DD species in order to facilitate their prioritization for research, hoping to encourage further gathering of sufficient information, which will allow their future reclassification into one of the other IUCN categories, starting to those that might be more vulnerable to extinction. Our I_{dd} seems to work properly in indicating high priority DD species for research. For example, showing that the rationale behind I_{dd} is reasonable, nine of high priority DD amphibians present in our study were assigned as VU, EN or CR by Morais et al. (2013), emphasizing I_{dd} efficiency and the urgency to assess those species. Furthermore, one advantage of I_{dd} is that it considers several attributes and balances positive and negative numeric features to produce an interpretable final score value. Examining additional details in the study of Morais et al. (2013) it is noticeable that some species were not considered as threatened (e.g. *Chiasmocleis sapiranga*, *Cycloramphus asper* or *Scinax ranki*); because these species were recently described (this is an important premise of their method). However, I_{dd} stresses these same species as high priority, because I_{dd} takes into account additional features (such as population trend, rarity, presence within conservation unit) that may affect future of populations (Toledo et al., 2014). The opposite situation is also true, with several species assigned as threatened by Morais et al. (2013), but not considered high priority by I_{dd}. This is also related to the balance among different population factors, in which, although some species may be threatened because the conjunction of time since species discovery and its extent of occurrence, there are other characteristics that disfavor potential population declines, such as abundance or habitat suitability. Thus, disregarding differences in methods and aims, I_{dd} can be considered a step forward in regard to studies focused on DD species, and the I_{dd} scores result presented here are promptly to use.

Moreover, Howard and Bickford (2014) stressed AF as a world target region for primary research on amphibians due to the proportion of DD species occurring in this biome, and we identified the southeastern region of AF as a “DD hotspot of occurrence” using mapping techniques, and this may help to focus future research. As a matter of fact, the entire AF currently faces several sources of threats (Ribeiro et al., 2011) and additional pressures are predicted for the near future with climate change (Colombo and Joly, 2010; Lemes et al., 2013), making basic research and increase of knowledge urgent. Consequently, I_{dd} may be a useful tool since it be used to guide future research. In addition, surprisingly, the southeastern part of AF is not only where several DD taxa are located, but also the most sampled region in Brazil in regard to herpetological studies (Toledo and Batista, 2012). This pattern suggest how difficult is to assess information about some of the Neotropical DD species, emphasizing the necessity of planned and organized research to save time, effort and funds.

Usually DD species issues are not a leading topic in conservation, but the general interest on them has increased (e.g. Butchart and Bird, 2010; Morais et al., 2013; Howard and Bickford, 2014). In this sense, I_{dd} is innovative, because it is an additional and functional easy tool that can be applied to any organism. It also uses simple principles and structure that can be adjusted as more information arises or by adding new columns (features) to its basic structure. Thus, by recalculating I_{dd} as more information on a given species is gathered, its I_{dd} score tend to gradually decrease as the same time that sufficient information is reached to correctly assign it into a different category, and then such taxa will finally no longer be DD.

Although functional, we acknowledge some limitations in I_{dd}. For instance, I_{dd} is not sensitive to the intensity of some factors used in its calculation as the amount of potential losses by an eventual sea level rise, intensity of catastrophic events, shift rates between current and future projected climate scenarios or connectivity among suitable habitats. Additionally, I_{dd} does not take into account difficulties to find the species in the natural environment or level of crypsis as well. Nevertheless, I_{dd} may be a first step to organize priority DD taxa, but it could be further developed by adding complexity to its basic formula or increasing the number of factors with available information. This shows that I_{dd} is also flexible. Furthermore, although the method provides a ranked order according to their reached I_{dd} scores, moderate or low priority DD species still must be considered targets for basic research and conservation actions, even with less emphasis. In fact, species' I_{dd} scores should be continuously reassessed in order to verify the current rank order of species. In consonance, Butchart and Bird (2010) argued that DD species should be treated with precaution in the conservation context, and that focused research is priority for these taxa, independently of the taxonomic group, in order to reduce uncertainties inherent of extinction risk estimates; therefore, conservation plans should include DD species indiscriminately.

Despite innumerous barriers to overcome, especially limited time and money (Brooks et al., 2006), difficulties in logistic and accesses, as well as number of specialists, fostering population information is a key step for successful conservation (Howard and Bickford, 2014). As raised by Morais et al. (2013) and Howard and Bickford (2014) theoretical assessments on DD species shall not be used as a shortcut to avoid the formal IUCN assessment, but may serve to encourage the focus on the ongoing data collection. Thus, prioritization systems such as the one presented here may be a reasonable option to embrace and may indicate target species as a starting point. We hope our contribution could be directly applied in the Atlantic forest and also embraced by other regions of the globe. We also hope our approach may be an useful tool in future studies by encouraging further research on DD species, disentangling their gaps in knowledge, and consequently providing more solid basis for effective and accurate conservation planning and implementation henceforth.

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Tables

Table 1. Structure of conceptual criteria organization used to calculate each factor (F_n) of the DD prioritization index (I_{dd}).

Code	Factors (F_n)	Original categories	Equation	Values	Rationale	Source of information
F_1	Number of years since the species description	Year of description	$F_1 = (Y - D/Y - D_f)$	Y = current year; D = year of description of the species D_f = year of description of the first living amphibian	We used this equation to adjust this factor to float between zero and one. Though the division by the maximum possible value, we ensure that all values are within our established range. In the case of amphibians the year of description of the first living species is 1758 (Frost, 2014).	Frost (2014)
F_2	Tolerance to disturbed habitats	Yes, no, unknown		Yes = 0 No = 1 Unknown = 1	Species able to survive in disturbed habitats are expected to be less sensitive to environmental changes than those that cannot.	IUCN (2014)
F_3	Population trend	Stable, decline, unknown		Stable = 0 Decline = 1 Unknown = 1	Population decline is one of the causes of the amphibian biodiversity crisis (Barnosky et al., 2011) and a clear step toward to potential extinction.	IUCN (2014)
F_4	Habitat	Open area, cocoa plantation and forest, open area and forest, natural grassland, shrubby dunes, forest, swamp,		Open area = 0 Cocoa plantation and forest = 0 Open area and forest = 0 Natural grassland = 1 Shrubby dunes = 1 Forest = 1 Swamp = 1 High altitudinal grassland = 1	Deforestation is massive in the Atlantic forest, while open areas increased (Ribeiro et al., 2011). Therefore, species able to survive in open areas may be benefited with deforestation, while those that inhabit forested or rare environments may be handicapped.	IUCN (2014)

		high altitudinal grassland				
F_5	Rarity score	1 (very rare), 2 (rare), 3 (common), and 4 (very common)	$F_5 = 1/R$	R = original rarity category	Toledo et al. (*in prep*.) provided data on the eight forms of rarity (joining geographic range, habitat specificity and population size) for the AF anurans.	Toledo et al. (2014)
F_6	Confirmed positive infection of *Batrachochitrium dendrobatidis* (*Bd*)	Yes or unknown		Yes = 1 Unknown = 0	The presence of this pathogen is known to be the causative agent of several population declines worldwide (Berger et al., 1998; Louca et al., 2014). Hence, we attributed the value one for Bd^+ species. On the other hand, species absence of positive cases cannot be considered uninfected, therefore, they were considered unknown.	Anyelet et al. (*in prep*)
F_7	Number of reproductive modes	One or more		One = 1 More than one = 0	We assumed that species with more than one reproductive mode may have alternative options (e.g., microhabitats or egg laying sites) to breed and, consequently, resist to possible environmental changes (Toledo et al., 2011).	Haddad et al. (2013)
F_8	Evolutionary distinctiveness (ED)	ED	F_8 = ED/100	ED = evolutionary distinctiveness calculated to each species.	We adopted the rationale proposed by Isaac et al. (2007) divided per 100 to fit into the desirable index range.	Isaac et al. (2007); and Pyron and Wiens (2011)
F_9	Estimation of the current habitat suitability	1 ($E_s <$ 5.10^3 km^2), 2 ($5.10^3 <$	$F_9 = 1/E_s$	E_s = Binary estimation of the range for the	We used the concepts of extent of occurrence and the B1 criteria (IUCN, 2012) to establish categories that fit in a	Ecological Niche Modeling (present study)

		$E_s < 2.10^4$), 3 ($E_s > 2.10^4$)		current habitat suitability per species	range from zero to one.	
F_{10}	Estimation of the future habitat suitability	1 ($E_f < 5.10^3$ km^2), 2 ($5.10^3 < E_f < 2.10^4$), 3 ($E_f > 2.10^4$)	$F_{10} = 1/E_f$	E_f = Binary estimation of the range for the future habitat suitability per species	The same concept of F_9 to project habitat suitability to the future under climate change based on current trends.	Ecological Niche Modeling (present study)
F_{11}	Record of occurrence within a conservation unit	Yes and no		Yes = 0 No = 1	Occurrence in protected areas may reduce the overall potential risk of extinction.	Geographic Information Systems
F_{12}	Potential loss of suitable habitats by future sea level rising	Yes and no		Yes = 1 No = 0	Species occurring close to coastal areas are expected to have their habitat suitability reduced by marine intrusions or submersion in the future (Bellard et al., 2014; Menon et al., 2010; Oliveira et al. in prep.).	Oliveira et al. (*in prep*)

Table 2. Data deficient amphibian species of Brazilian Atlantic forest and respective prioritization index (I_{dd}) scores (approximate values) for primary research.

Priority categories							
Low		**Moderate**				**High**	
Taxa	***Idd***	**Taxa**	***Idd***	**Taxa**	***Idd***	**Taxa**	***Idd***
Hypsiboas exastis	0.268	*Bokermannohyla gouveai*	0.458	*Cycloramphus mirandaribeiroi*	0.508	*Brachycephalus alipioi*	0.540
Scinax kautskyi	0.276	*Hylodes charadranaetes*	0.459	*Paratelmatobius poecilogaster*	0.509	*Brachycephalus izecksohni*	0.540
Leptodactylus jolyi	0.277	*Crossodactylus grandis*	0.459	*Bokermannohyla langei*	0.515	*Crossodactylus lutzorum*	0.543
Physalaemus jordanensis	0.282	*Dendropsophus ruschii*	0.459	*Aplastodiscus musicus*	0.515	*Brachycephalus pernix*	0.543
Adenomera ajurauna	0.355	*Ischnocnema erythromera*	0.460	*Aplastodiscus sibilatus*	0.518	*Phyllodytes gyrinaethes*	0.546
Ischnocnema sambaqui	0.359	*Crossodactylus aeneus*	0.461	*Paratelmatobius lutzii*	0.520	*Zachaenus carvalhoi*	0.548
Cycloramphus lutzorum	0.362	*Megaelosia lutzae*	0.461	*Physalaemus maximus*	0.522	*Cycloramphus eleutherodactylus*	0.549
Bokermannohyla ahenea	0.370	*Aplastodiscus flumineus*	0.461	*Gastrotheca fulvorufa*	0.522	*Holoaden luederwaldti*	0.549
Sphaenorhynchus bromelicola	0.371	*Physalaemus bokermanni*	0.462	*Proceratophrys paviotii*	0.523	*Hylodes magalhaesi*	0.549
Leptodactylus viridis	0.372	*Gastrotheca ernestoi*	0.464	*Bokermannohyla claresignata*	0.523	*Ischnocnema verrucosa*	0.563
Physalaemus barrioi	0.372	*Scinax ariadne*	0.464	*Bokermannohyla feioi*	0.523	*Cycloramphus stejnegeri*	0.569
Bokermannohyla lucianae	0.385	*Xenohyla eugenioi*	0.464	*Phyllodytes edelmoi*	0.524	*Melanophryniscus spectabilis*	0.576
Frostius erythrophthalmus	0.396	*Cycloramphus juimirim*	0.464	*Chiasmocleis crucis*	0.524	*Hylodes glaber*	0.577
Hypsiboas latistriatus	0.431	*Physalaemus moreirae*	0.464	*Ischnocnema randorum*	0.525	*Chiasmocleis gnoma*	0.579
Aparasphenodon bokermanni	0.436	*Cycloramphus migueli*	0.465	*Cycloramphus granulosus*	0.525	*Phasmahyla timbo*	0.581
Melanophryniscus simplex	0.438	*Cycloramphus bandeirensis*	0.466	*Hylodes mertensi*	0.525	*Physalaemus irroratus*	0.581
Dendropsophus studerae	0.438	*Proceratophrys moehringi*	0.467	*Crossodactylus dispar*	0.526	*Crossodactylus cyclospinus*	0.582

Ischnocnema izecksohni	0.438	*Brachycephalus ferruginus*	0.471	*Physalaemus angrensis*	0.526	*Dendropsophus dutrai*	0.582
Ischnocnema spanios	0.439	*Brachycephalus nodoterga*	0.471	*Megaelosia boticariana*	0.527	*Hylodes sazimai*	0.583
Trachycephalus lepidus	0.439	*Crossodactylus dantei*	0.473	*Chthonerpeton noctinectes*	0.527	*Mimosiphonops vermiculatus*	0.584
Leptodactylus cupreus	0.441	*Cycloramphus diringshofeni*	0.475	*Bokermannohyla clepsydra*	0.528	*Dendrophryniscus stawiarskyi*	0.584
Hylodes heyeri	0.442	*Chiasmocleis cordeiroi*	0.475	*Physalaemus caete*	0.528	*Siphonops insulanus*	0.589
Scinax jureia	0.442	*Holoaden pholeter*	0.479	*Phyllodytes brevirostris*	0.528	*Cycloramphus cedrensis*	0.591
Physalaemus camacan	0.443	*Cycloramphus bolitoglossus*	0.480	*Cycloramphus izecksohni*	0.529	*Cycloramphus valae*	0.591
Adelophryne pachydactyla	0.444	*Ischnocnema nigriventris*	0.480	*Crossodactylodes pintoi*	0.530	*Megaelosia massarti*	0.604
Bokermannohyla ibitipoca	0.445	*Crossodactylus trachystomus*	0.491	*Cycloramphus duseni*	0.530	*Hypsiboas freicanecae*	0.605
Sphaenorhynchus pauloalvini	0.445	*Melanophryniscus alipioi*	0.491	*Crossodactylus bokermanni*	0.531	*Paratelmatobius gaigeae*	0.610
Physalaemus obtectus	0.448	*Phyllodytes wuchereri*	0.498	*Paratelmatobius cardosoi*	0.534	*Scinax ranki*	0.610
Hypsiboas secedens	0.451	*Scinax heyeri*	0.499	*Cycloramphus catarinensis*	0.536	*Cycloramphus ohausi*	0.616
Ischnocnema holti	0.452	*Brachycephalus vertebralis*	0.500	*Ischnocnema gehrti*	0.536	*Cycloramphus asper*	0.619
Hylodes fredi	0.454	*Melanophryniscus cambaraensis*	0.501	*Scinax arduous*	0.536	*Chiasmocleis sapiranga*	0.620
Ischnocnema pusilla	0.454	*Megaelosia bocainensis*	0.501	*Chiasmocleis mantiqueira*	0.536	*Dendropsophus limai*	0.622
Hylodes dactylocinus	0.456	*Hylodes babax*	0.502	*Hylodes pipilans*	0.537	*Phyllodytes punctatus*	0.622
Megaelosia apuana	0.456	*Hylodes vanzolinii*	0.502	*Hylodes uai*	0.537	*Chthonerpeton viviparum*	0.635
Brachycephalus pombali	0.457	*Phrynomedusa bokermanni*	0.502	*Phyllodytes tuberculosus*	0.538	*Stereocyclops histrio*	0.650
Scinax atratus	0.457	*Phrynomedusa vanzolinii*	0.503	*Phyllodytes maculosus*	0.538	*Hylodes amnicola*	0.662
Scinax melloi	0.457	*Hylodes regius*	0.503	*Phasmahyla spectabilis*	0.539	*Haddadus plicifer*	0.728
Brachycephalus brunneus	0.457	*Paratelmatobius mantiqueira*	0.506			*Leptodactylus hylodes*	0.768

Figures

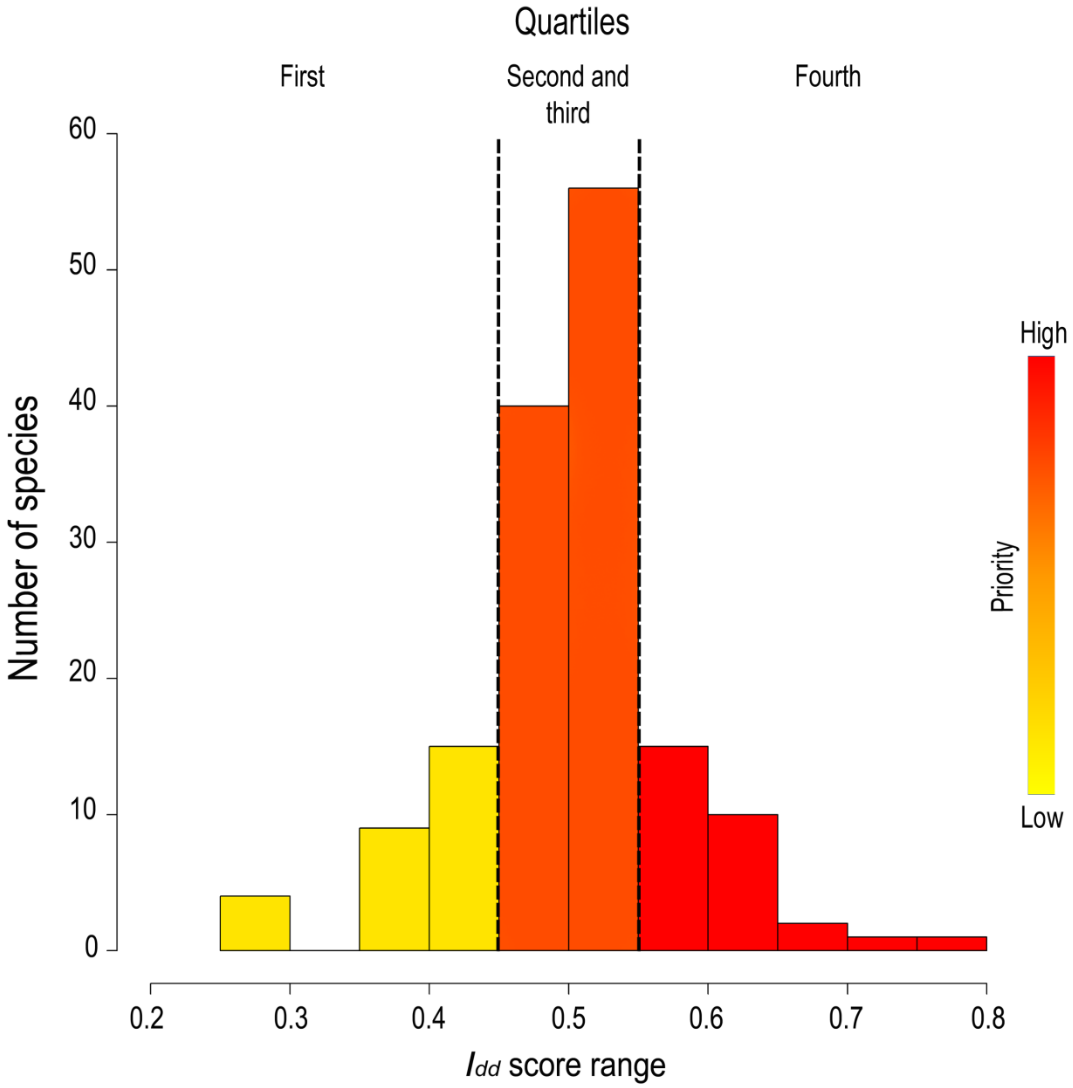

Fig. 1. Number of data deficient species per quartile according to the Idd scores. Heat colors indicate priority for research.

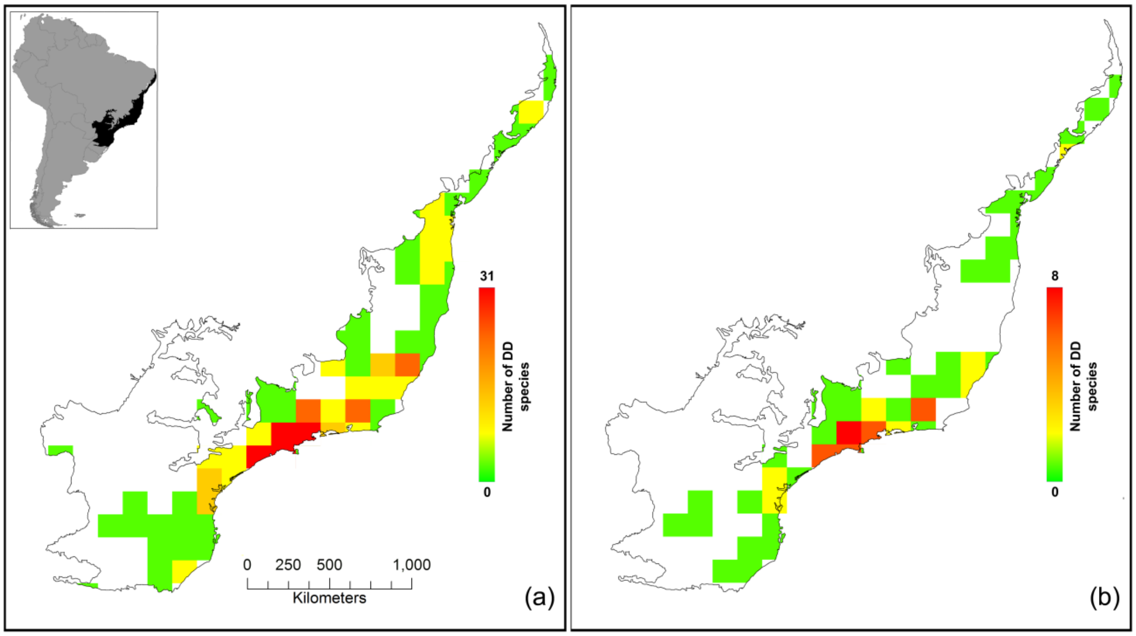

Fig. 2. Distribution map of data deficient (DD) species within Brazilian Atlantic forest (AF) showing (a) current location of all DD species, and (b) DD species considered as high priority for research based on the I_{dd} scores. Both maps highlight clustered spatial pattern in southeastern part of AF. Heat colors indicate number of DD species per grid.

Supplementary material

Table A1. Ecological Niche Model's AUC values.

Taxa	**AUC**
Adelophryne pachydactyla	0.99
Adenomera ajurauna	0.99
Aparasphenodon bokermanni	0.99
Aplastodiscus flumineus	0.99
Aplastodiscus musicus	0.99
Aplastodiscus sibilatus	0.99
Bokermannohyla ahenea	0.91
Bokermannohyla claresignata	0.93
Bokermannohyla clepsydra	0.98
Bokermannohyla feioi	0.98
Bokermannohyla gouveai	0.99
Bokermannohyla ibitipoca	0.99
Bokermannohyla langei	0.97
Bokermannohyla lucianae	0.98
Brachycephalus alipioi	0.99
Brachycephalus brunneus	0.99
Brachycephalus ferruginus	0.99
Brachycephalus izecksohni	0.99
Brachycephalus nodoterga	0.97
Brachycephalus pernix	0.84
Brachycephalus pombali	0.99
Brachycephalus vertebralis	0.99
Chiasmocleis cordeiroi	0.98
Chiasmocleis crucis	0.99
Chiasmocleis gnoma	0.99
Chiasmocleis mantiqueira	0.98
Chiasmocleis sapiranga	0.99
Chthonerpeton noctinectes	0.99
Chthonerpeton viviparum	0.99
Crossodactylodes pintoi	0.99
Crossodactylus aeneus	0.98
Crossodactylus bokermanni	0.99
Crossodactylus cyclospinus	0.99
Crossodactylus dantei	0.99
Crossodactylus dispar	0.91
Crossodactylus grandis	0.98
Crossodactylus lutzorum	0.92
Crossodactylus trachystomus	0.99
Cycloramphus asper	0.97
Cycloramphus bandeirensis	0.99

Cycloramphus bolitoglossus	0.96
Cycloramphus carvalhoi	0.97
Cycloramphus catarinensis	0.99
Cycloramphus cedrensis	0.99
Cycloramphus diringshofeni	0.96
Cycloramphus duseni	0.97
Cycloramphus eleutherodactylus	0.92
Cycloramphus granulosus	0.95
Cycloramphus izecksohni	0.99
Cycloramphus juimirim	0.93
Cycloramphus lutzorum	0.99
Cycloramphus migueli	0.99
Cycloramphus mirandaribeiroi	0.99
Cycloramphus ohausi	0.94
Cycloramphus stejnegeri	0.98
Cycloramphus valae	0.91
Dendrophryniscus stawiarskyi	0.96
Dendropsophus dutrai	0.99
Dendropsophus limai	0.99
Dendropsophus ruschii	0.82
Dendropsophus studerae	0.99
Frostius erythrophthalmus	0.99
Gastrotheca ernestoi	0.98
Gastrotheca fulvorufa	0.94
Haddadus plicifer	0.99
Holoaden luederwaldti	0.99
Holoaden pholeter	0.95
Hylodes amnicola	0.99
Hylodes babax	0.97
Hylodes charadranaetes	0.92
Hylodes dactylocinus	0.96
Hylodes fredi	0.99
Hylodes glaber	0.91
Hylodes heyeri	0.89
Hylodes magalhaesi	0.97
Hylodes mertensi	0.99
Hylodes pipilans	0.99
Hylodes regius	0.98
Hylodes sazimai	0.99
Hylodes uai	0.95
Hylodes vanzolinii	0.99
Hypsiboas exastis	0.99
Hypsiboas freicanecae	0.98

Hypsiboas latistriatus	0.99
Hypsiboas secedens	0.97
Ischnocnema erythromera	0.96
Ischnocnema gehrti	0.99
Ischnocnema holti	0.99
Ischnocnema izecksohni	0.97
Ischnocnema nigriventris	0.98
Ischnocnema paranaensis	0.97
Ischnocnema pusilla	0.98
Ischnocnema randorum	0.98
Ischnocnema sambaqui	0.98
Ischnocnema spanios	0.96
Ischnocnema verrucosa	0.96
Leptodactylus cupreus	0.78
Leptodactylus hylodes	0.93
Leptodactylus jolyi	1
Leptodactylus viridis	0.96
Megaelosia apuana	0.97
Megaelosia bocainensis	0.97
Megaelosia boticariana	0.99
Megaelosia lutzae	0.98
Megaelosia massarti	0.98
Melanophryniscus alipioi	0.95
Melanophryniscus cambaraensis	0.98
Melanophryniscus simplex	0.99
Melanophryniscus spectabilis	0.99
Mimosiphonops vermiculatus	0.93
Paratelmatobius cardosoi	0.96
Paratelmatobius gaigeae	0.99
Paratelmatobius lutzii	0.97
Paratelmatobius mantiqueira	0.99
Paratelmatobius poecilogaster	0.97
Phasmahyla spectabilis	0.99
Phasmahyla timbo	0.95
Phrynomedusa bokermanni	0.99
Phrynomedusa vanzolinii	0.99
Phyllodytes brevirostris	0.99
Phyllodytes edelmoi	0.99
Phyllodytes gyrinaethes	0.98
Phyllodytes maculosus	0.97
Phyllodytes punctatus	0.96
Phyllodytes tuberculosus	0.93
Phyllodytes wuchereri	0.99

Physalaemus angrensis	0.99
Physalaemus barrioi	0.99
Physalaemus bokermanni	0.98
Physalaemus caete	0.96
Physalaemus camacan	0.97
Physalaemus irroratus	0.92
Physalaemus jordanensis	0.91
Physalaemus maximus	0.87
Physalaemus moreirae	0.95
Physalaemus obtectus	0.73
Proceratophrys moehringi	0.92
Proceratophrys paviotii	0.95
Scinax arduous	0.82
Scinax ariadne	0.99
Scinax atratus	0.97
Scinax heyeri	0.96
Scinax jureia	0.99
Scinax kautskyi	0.97
Scinax melloi	0.99
Scinax ranki	0.97
Siphonops insulanus	0.96
Sphaenorhynchus bromelicola	0.99
Sphaenorhynchus pauloalvini	0.99
Stereocyclops histrio	0.99
Trachycephalus lepidus	0.98
Xenohyla eugenioi	0.98
Zachaenus carvalhoi	0.89

CAPÍTULO 4

Historical habitat suitability shifts may explain the rare current occurrence of the most ancestral and endemic amphibian-killing chytrid lineage

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Abstract

The killing chytrid fungus *Batrachochytrium dendrobatidis* (*Bd*) causes an infectious disease and has led to amphibian population declines. It is currently widespread throughout the world and is considered one of the major threats to amphibian conservation. Recent findings demonstrated that *Bd*'s evolutionary history is more complex than previously thought, and thus, investigate *Bd*'s historical processes and patterns are pivotal to understand its evolution. To investigate past potential distribution and distributional range shifts through time, we built Ecological Niche Models (ENMs) with different algorithms to evaluate distinct possibilities. Also, to assess potential niche overlap in the environmental space between *Bd*-Brazil and *Bd*-GPL, we used a PCA based analysis to model environmental niche. ENMs indicate the existence of available past suitable habitat for *Bd*-Brazil establishment, supporting the endemicity hypothesis of *Bd*-Brazil in South America. However, some ENMs suggest decreasing habitat suitability for *Bd*-Brazil through time, which could explain the rarity of *Bd*-Brazil. In addition, we found low levels of niche overlap, and then replacement of *Bd*-Brazil by *Bd*-GPL is a possible ongoing event that could explain the rarity of the Brazilian lineage. Such replacement can jeopardize native amphibians, as the *Bd*-GPL lineage is the one related to population declines and extinctions in other parts of the world.

Key Word: Emerging infectious disease, ecological niche modeling, niche overlap, amphibian conservation, competition

Introduction

The chytrid fungus *Batrachochytrium dendrobatidis* (*Bd*) is an emerging infectious disease related to amphibian declines worldwide (Berger et al., 1998; Bosch et al., 2001; Garner et al., 2006; Cheng, 2011). This fungus infects keratinized body portions of amphibians (Berger et al., 1998, 2005), potentially leading to a disease called chytridiomycosis, killing the most susceptible individuals as a consequence of osmotic imbalance through loss of electrolytes (Voyles et al., 2007, 2012; Fites et al., 2013).

Besides its occasional extreme virulence (Fisher et al., 2009) and potential to cause extinctions (Crawford et al., 2010), another alarming characteristic of the *Bd* is its broad current distributional range of occurrence, extending to all continents inhabited by amphibians (Olson et al., 2013). Although there is still much uncertainty about how *Bd* disperses in the wild, it has been suggested that such spread can also be promulgated by the international amphibian trade (Weldon et al., 2004; Schloegel et al., 2010, 2012).

The cause for global emergence of *Bd* is still controversial and unclear (Rachowicz et al., 2005). However, the hypothesis that suggesst *Bd* (or genotypes of *Bd*) have recently expanded in geographic area (novel pathogen hypothesis) has been supported by several studies (Lips et al., 2008; Kilpatrick 2009; Rosenblum et al., 2010; Cheng, 2011). On the other hand, genetic diversity studies suggest that the evolutionary history of *Bd* is more complex than previously estimated (Rosenblum et al., 2013; Rodriguez et al., 2014;). *Batrachochytrium dendrobatidis* comprises multiple lineages (Farrer et al., 2011b; Schloegel et al., 2012; Rosenblum et al., 2013) including, among others, a widespread global hypervirulent enzootic lineages (*Bd*-GPL) (Farrer et al., 2011), divergent endemic lineages, such as *Bd*-Brazil and *Bd*-Korea (Schloegel et al., 2012; Bataille et al., 2013), and hybrids (Schloegel et al., 2012; Rodriguez et al., 2014). Moreover, it was recently suggested that *Bd*-Brazil diverged before the other lineages of *Bd*, implying that *Bd* is older, more diverse, and possesses more complex evolutionary history than previously believed (Rosenblum et al., 2013). These recent discoveries suggest that some lineages are endemic, while the *Bd*-GPL lineage appears to be a clonal, epizootic and recently spread lineage (Morehouse et al., 2003).

The distinct lineages differ for example in DNA copy number (e.g., Longo et al., 2013), phenotype and virulence (Fisher et al., 2009). They also present different distributions, where *Bd*-Brazil seems to be naturally restricted to the southern Brazilian Atlantic forest, whereas *Bd*-GPL is widespread over the globe, also co-occurring with *Bd*-Brazil (Schloegel et al., 2012). Therefore, the lineages could also have different environmental requirements and compete for hosts (Goka et al., 2009; Schloegel et al., 2012). These two hypotheses are plausible, not mutually exclusive, and could explain differences in their current distribution in the wild. Here, we assessed climatic niche availability over the time for both lineages to investigate patterns of distribution. We addressed that by means of Ecological Niche Modeling (ENM) (Peterson and Soberón, 2012), implementing algorithms of different complexities in order to assess different possibilities of habitat availability through time. We also tested the hypothesis that *Bd*-Brazil possesses different environmental niche and tested whether it is nested or not within the *Bd*-GPL niche, by the use of niche overlap analysis based on PCA (Broennimann et al., 2012).

Methods

Study area

For the assessments on *Bd*-Brazil's temporal potential distribution we limited the ENM analyzes to Brazilian borders since this lineage is putatively an endemic lineage of the country and to the Atlantic forest (AF) (Rosenblum et al., 2013; Rodriguez et al., 2014). At the same time, although we calibrated the modeling algorithms with the world range distribution of *Bd*-GPL, we present ENMs on its potential distribution within Brazilian borders as well, in order to allow comparisons between the niche requirements of each lineage.

Occurrence data

Occurrence records of *Bd*-Brazil lineage were obtained by genotyping pure cultures isolated from wild frogs and also from the supplementary material related to the contribution of Rodriguez et al. (2014). Point locations of *Bd*-GPL were obtained from The Global *Bd*-Mapping Project (available at http://www.bd-maps.net/). We verified the distribution of records in order to inspect and eliminate bias possible caused by data clustering (e.g. Hernandez et al., 2006). We limited our occurrence input database to one record per square kilometer per strain. This filtering is important when assessing species' environmental niche via climate data in a GIS framework to avoid pseudo-replication in densely sampled areas (Rödder et al., 2013). We processed the distributional data with the software ArcGIS 10 (ESRI, 2011) and R (R Development Core Team, 2014, version 3.1.0). Since the Brazilian chytrid lineage is naturally rare (Rodriguez et al., 2014), the final data set for *Bd*-Brazil had nine occurrence records (Fig 1), whereas for the *Bd*-GPL data set was composed of 2,428 locations worldwide, of which 13 were within the Atlantic forest.

Models for *Bd*-GPL were calibrated with the entire data set available after treatment, and subsequently projected to the area of interest.

Climatic data

We computed the ENMs and also compared niche overlap of the two *Bd* lineages by the use of six bioclimatic variables (e.g. Rödder et al., 2009): annual mean temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, precipitation of the wettest month and precipitation of the driest month (Hijmans et al., 2005). These variables were selected based on the known environmental requirements and biological traits of *Bd* as a species (Rödder et al., 2009), as range and tolerance of temperature variation and moisture limitations (Berger et al., 1998; Piotrowski, 2004; Rosenblum et al., 2010). Also, the choice of meaningful variables for a given organism aids to avoid issues regarding multicollinearity (e.g. Nori et al., 2011). Bioclimatic variables were downloaded from the WorldClim Global Climate Data homepage (available at http://www.worldclim.org) at a resolution of 10 arcmin (~ 20 km) for the following time frame periods: ~ 120-140,000 (last inter-glacial), 22,000 (last glacial maximum) and 6,000 (mid Holocene) years ago, and current (1950-2000). The last inter-glacial period coincides with the probable period of divergence between *Bd*-Brazil and *Bd*-GPL lineages. Variables used to compute ENMs were originally generated by MIROC-ESM, a global climate model MIROC (Model for Interdisciplinary Research on Climate), which comprehensively incorporates an atmospheric general circulation model (AGCM), ocean (GCM) with ice-sea component (COCO), land surface (MATSIRO), and atmospheric chemistry components (CHASER), among others (details in Watanabe et al., 2011).

Ecological Niche Models

We computed ENMs following proper time frames for each lineage (Rosenblum et al., 2013) for the different climatic scenarios using three modeling algorithms: DOMAIN (Carpenter et al., 1993), implemented in the free software DIVA-GIS, version 7.5 (available at http://www.diva-gis.org); Maximum Entropy (Phillips et al., 2004), through the use of the software MaxEnt, version 3.3.3.k (http://www.cs.princeton.edu/~schapire/maxent); and alpha-shapes, generated in R, version 3.1.0 (R Development Core Team, 2014), by the free code provided by Capinha and Pateiro-López (2014).

The DOMAIN algorithm is an environmental envelope method that uses point-to-point similarity to assign classification values to locations according to the proximity with the most similar record site in environmental space (Carpenter et al., 1993). Conversely, the learning machine MaxEnt process presence-only species location as input together with a set of environmental predictors across a defined landscape, from which it extracts a sample of background locations to contrast against presence locations (Merow et al., 2013). Finally, alpha-shape is a flexible envelope fitting procedure recently introduced to distribution modeling by Capinha & Pateiro-López (2014). This method makes no previous assumption about the shape of the niche in the environmental space (Edelsbrunner et al., 1983; Capinha and Pateiro-López, 2014), and its ability to draw non-convex boundaries is an advantage since it allows the definition of a more precise geometric delimitation of a species' climatic requirements, avoiding overprediction (Capinha and Pateiro-López, 2014). Following information provided by Rosenblum et al. (2013) regarding to time since divergence for each lineage, we built four time frame models for the *Bd*-Brazil lineage, and three for the lineage *Bd*-GPL.

To estimate suitability we converted the ENM's outputs into binary prediction maps through thresholds derived from the ROC (Receiver Operating Characteristic) curve (e.g. Nóbrega and De Marco 2011; Serra et al., 2012). The generation of binary prediction of species' range requires the choice of an appropriate value of threshold (Elith et al., 2006) to minimize omission and commission errors (Nóbrega and De Marco, 2011). We adopted the true skill statistics (TSS) to evaluate model fit (Allouche et al., 2006). TSS values range from – 1 to + 1, where more close to – 1 is the value imply weak performance, i.e, the model is not better than expected by random; whereas TSS values close to + 1 suggest good discrimination power, i.e., minimized overprediction and omission errors (Allouche et al., 2006).

Measure of niche overlap

Evaluation of current niche overlap between lineages in the environmental space was performed by the application of the PCA-env approach, following the statistical framework proposed by Broennimann et al. (2012) and also the "ecospat" R package (Broennimann et al., 2014). This is a multivariate method to measure niche overlap from occurrence and environmental information. In this framework, environmental range of a pair of selected species is used to compute a principal component analysis (PCA). Subsequently, the two most representative principal components are used as measure to project records of both species into the environmental space, and a Kernel density function is applied to balance unequal samples. Lastly, measurement of niche overlap is calculated by the *D* metric (Schoener, 1970), and then statistically tested in terms of similarity and equivalency (Warren et al., 2008; Broennimann et al., 2012). All niche overlap analyzes were performed in R (R Development Core Team, 2014) versions 3.1.0 and 3.1.2, and adjusted according to Di Cola et al. (2014, available at http://www.unil.ch).

Results

Ecological Niche Models

All ENMs exhibited good or acceptable discrimination capacity (*Bd*-Brazil TSS = 0.65, 1, and 0.96; and *Bd*-GPL TSS = 0.99, 0.91, 0.66, for DOMAIN, MaxEnt, and alpha-shapes, respectively). The algorithms showed considerable variation in their outputs (Fig 2 and 3), i.e., different magnitudes of prediction of suitability for the *Bd*-Brazil in terms of extension range, which is expected owing to their different complexity and procedures. Additionally, the TSS values indicate statistical reliability, allowing us to proceed with the analysis without discarding any model (Girardello et al., 2009).

ENMs indicate suitable habitat for both lineages in all time frames considered (Fig 2 and 3). For *Bd*-Brazil, DOMAIN indicates a large suitable area in the last inter-glacial (~ 120-140,000 years ago) (Fig 2). However, for the same time frame, models resulted from MaxEnt show more restricted suitable areas in Southern regions, while alpha-shapes indicate few suitable spots available. Nonetheless, the models were congruent showing a decrease in *Bd*-Brazil habitat suitability, although it could also be interpreted as moderate habitat stability, from the Holocene to the current scenario. Besides this, and in spite of discontinuous distributions, all ENMs show the existence of suitable habitats predominantly within the AF for current climatic conditions. On the other hand, while DOMAIN and MaxEnt show a substantial decrease from the last glacial maximum to the Holocene, the alpha-shapes model showed an increase of habitat suitability in the same period (Fig S1).

Moreover, *Bd*-Brazil ENMs generated by DOMAIN predict larger potential suitable areas for all climatic scenarios (Fig 2A-D) when compared to the other algorithms (Fig 2E-L). These models suggest the existence of extensive climatically suitable areas since the last inter-glacial, as well as, current potential suitability for *Bd*-Brazil beyond AF, in adjacent biomes, such as the Pampas, Cerrado and Caatinga. Similarly, MaxEnt shows suitable areas mostly in Southern region for the last glacial maximum (Fig 2D). In addition, ENMs generated by MaxEnt indicates habitat suitability related to the AF since the Holocene to current (Fig. 2E-F), and also MaxEnt is the only model that indicates suitable habitats in scattered areas in the Amazonia. Finally, the alpha-shapes was the most conservative model indicating suitable areas almost exclusively within the AF since the last glacial period, being also the model showing the most environmental stability in such region (Fig 2G-I).

On the other hand, ENMs generated by DOMAIN for *Bd*-GPL (Fig 3) indicate relatively decreasing distribution of suitable areas from glacial to Holocene and stability from Holocene to current, while Alpha-shapes indicate an increase in range suitability, and subsequent decrease for the same periods of time. In turn, MaxEnt models show a decrease in availability of suitable habitat for the time glacial-Holocene frame, and stability after that to current (Fig S1).

Niche Overlap

Our results on multivariate analysis in the environmental space using PCA showed low niche overlap (D = 0.131) between *Bd*-Brazil and *Bd*-GPL (Fig 4), indicating the existence of different requirements in the environment dimension for each lineage. Furthermore, niche equivalency test rejected the null hypothesis (p = 1) of equivalency of geographical ranges of these two lineages (i.e. there are distinctive niches between lineages), whereas niche similarity test was non-significant in two directions (p = 1).

Discussion

Distribution of *Bd* through time

We show the existence of suitable past climatic conditions for the occurrence of *Bd*-Brazil in the Brazilian territory. Thus, we provide additional evidence for the potential long-term presence of this lineage within the AF and surrounding biomes as previously suggested (Rosenblum et al., 2013; Rodriguez et al., 2014).

Moreover, these results are consistent with the recent findings on the evolutionary history of *Bd*-Brazil strain, which diverged from the ancestor lineage over approximately 100,000 years ago (Rosenblum et al., 2013). Therefore, our ENMs backdating 120-140,000 years ago showed the existence of habitat suitable climate for *Bd*-Brazil, further corroborating the suggestion of its origins in Brazil (Rodriguez et al., 2014). Besides that, it also revealed a narrow habitat suitability, supporting the idea of endemicity of this lineage (Rosenblum et al., 2013; Rodriguez et al., 2014).

It is currently unknown how long either *Bd*-Brazil or *Bd*-GPL lineages actually have co-existed in the Atlantic forest. However, these models in the historical context show a potential coevolution between amphibians (hosts) and *Bd* (pathogen). One possible result of evolution between host and pathogen organisms together is resistance through co-evolution (Svensson and Råberg, 2010; Schulze-Lefert and Panstruga, 2011; Antonovics et al., 2013). The chytrid fungus is largely distributed within the country (Carnaval et al., 2006; Valencia-Aguilar et al., in press), and resistance could explain the lack of recent declines reportedly attributed to *Bd* infection in Brazil (Eterovick et al., 2005). Coevolution is also supported by long term refugia for hosts based on amphibian past distribution, which shows that the *Bd*-Brazil past potential distribution (this study) is likely to be largely overlapping with the past distribution of some amphibians species (see Carnaval and Moritz, 2008; Thomé et al., 2010; Porto et al., 2013).

Another fruitful avenue revealed by ENMs for *Bd*-Brazil is the shrinking range of habitat suitability. DOMAIN and MaxEnt showed a decrease in terms of habitat suitability for *Bd*-Brazil over time, whereas alpha-shapes demonstrated a relatively constrained and stable suitable range area in the last 6,000 years. Moreover, alpha-shapes suggest suitable range not larger than 15,000 km^2 under present climatic conditions (Fig 4). This scenario may explain in part why *Bd*-Brazil displays very low frequency in the nature as evidenced by Rodriguez et al. (2014), since persistence in the natural environment may have not been constrained by host occurrence (as we can see by the coevolution hypothesis), but by the constrain of habitat suitability, since *Bd* possess a free living stage in its life cycle (Berger et al., 2005).

Environmental niche requirements

Environmental niches of the two *Bd* lineages are significantly distinct, rejecting the niche equivalency hypothesis (Fig 3) (Broennimann et al., 2012). The niche overlap hypothesis states that when resources are abundant to support two different organisms (in this case lineages), competition tends to be low, even with high niche overlap (Pianka, 1974). Our analyses indicate low niche overlap, but this itself may be due to the opposite situation, i.e., under competitive process. It is hypothesized that *Bd*-GPL has been replacing the endemic *Bd* lineages (Schloegel et al., 2012), and the low frequency of *Bd*-Brazil in nature can be due to a competitive exclusion process, since the co-occurrence of both strains in the AF is acknowledge to be historical (Rodriguez et al., 2014). The current distribution may reflect ancestral interference competition, which may arise when resource overlap among entities is high (Case and Gilpin, 1974), ending in exclusion (e.g. Tannerfeldt et al., 2002) or equilibrium (e.g. Vance, 1984). On the other hand, the low environmental niche overlap observed between the two *Bd* strains may suggest absence of current competition, not supporting the hypothesis of replacement of endemic *Bd* lineages (Schloegel et al., 2012). In addition, the existence of hybrids of *Bd*-Brazil and *Bd*-GPL strains (Rodriguez et al., 2014) can be interpreted as an evidence of coexistence, minimizing possibility of competition and replacement. Conversely, ENMs indicate suitable habitat for *Bd*-GPL totally overlapped with *Bd*-Brazil, diminishing the idea of eventual competition as a primary role in the present.

Climatic conditions are determinant of species' distribution (Araújo and Pearson, 2005; Munguía et al., 2012) and environmental variables within suitable geographic regions can be understood as an abundant requirement for organisms (*Bd* lineages in this case), unless changes in climate comply organisms to their physiological boundaries (e.g. Duarte et al., 2012). Furthermore, amphibians as the primary host are abundant in the geographic region considered, and both *Bd* lineages utilize the same substrate (host's tadpole mouthparts, tadpole and post-metamorphic skin) to grow (Berger et al., 2005; Voyles et al., 2007). In this case, amphibians can also be interpreted as an abundant resource in the Brazilian AF, since they are abundant and species rich, facilitating infection by the chytrid fungus (Becker et al., 2014). Thus, given the low niche overlap we observed and based on the niche overlap hypothesis (Pianka, 1974), our results seems reasonable to the assumption that interference by *Bd*-GPL may be replacing *Bd*-Brazil (Schloegel et al., 2012), at least since its arrival (Rodriguez et al., 2014). Exclusion by *Bd*-GPL combined with a decrease of habitat suitability cannot be discarded as a possible and plausible explanation for the rarity of *Bd*-Brazil in nature.

Finally, we address that our results should be used as a starting point for searching additional sites where *Bd*-Brazil may occur, especially in western regions of the Brazilian states of São Paulo and Paraná, or even eastern Argentina. These regions are contiguous but outside of the range of confirmed records of the endemic lineage. Finding such sites would shed light into *Bd* evolution, strains competition, delimitation of the hybrid zone, and the effects of long-term host-pathogen interactions. These findings could be fundamental to understand this disease dynamics, ultimately improving the necessary amphibian conservation efforts.

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Figure Legends

Fig 1 – Current known distribution of the lineages of the chytrid fungus *Batrachochytrium dendrobatidis* in South America. Red dots represent distribution of *Bd*-GPL, blue dots are the current distribution of *Bd*-Brazil, and green dots correspond to the distribution of *Bd*-Hybrid. The darker shade within Brazil corresponds to the original distribution of the Brazilian Atlantic rainforest.

Fig 2 – Three different Ecological Niche Models (ENMs) algorithms (Domain, MaxEnt, and Alpha-shapes) showing potential habitat suitability (in blue) for *Bd*-Brazil in four different climatic scenarios: last inter-glacial (120-140,000 y.a.), last glacial maximum (22,000 y.a.), Holocene (6,000 y.a.), and current (1950-2000).

Fig 3 – Three different Ecological Niche Models (ENMs) algorithms (Domain, MaxEnt, and Alpha-shapes) showing potential habitat suitability (in red) for *Bd*-GPL in three different climatic scenarios: last glacial maximum (22,000 y.a.), Holocene (6,000 y.a.), and current.

Fig 4 – Environmental niche overlap between *Bd*-Brazil (blue) and *Bd*-GPL (red). Darker areas in the PCA-env plot indicate high density of species records, whereas the available climate spaces within the general area of occurrence are indicated by solid (100%) and dashed lines (50%).

Figures

Fig 1

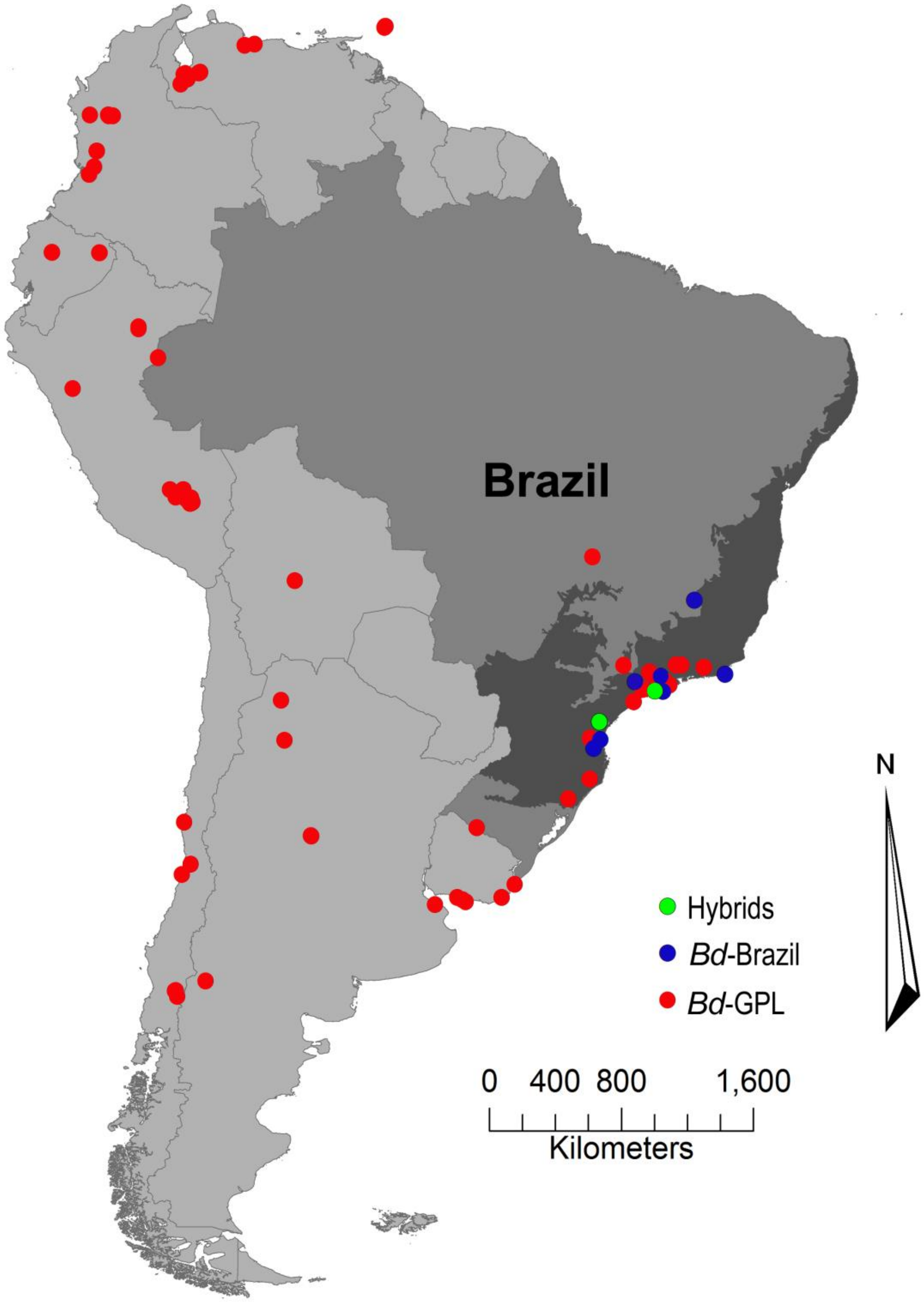
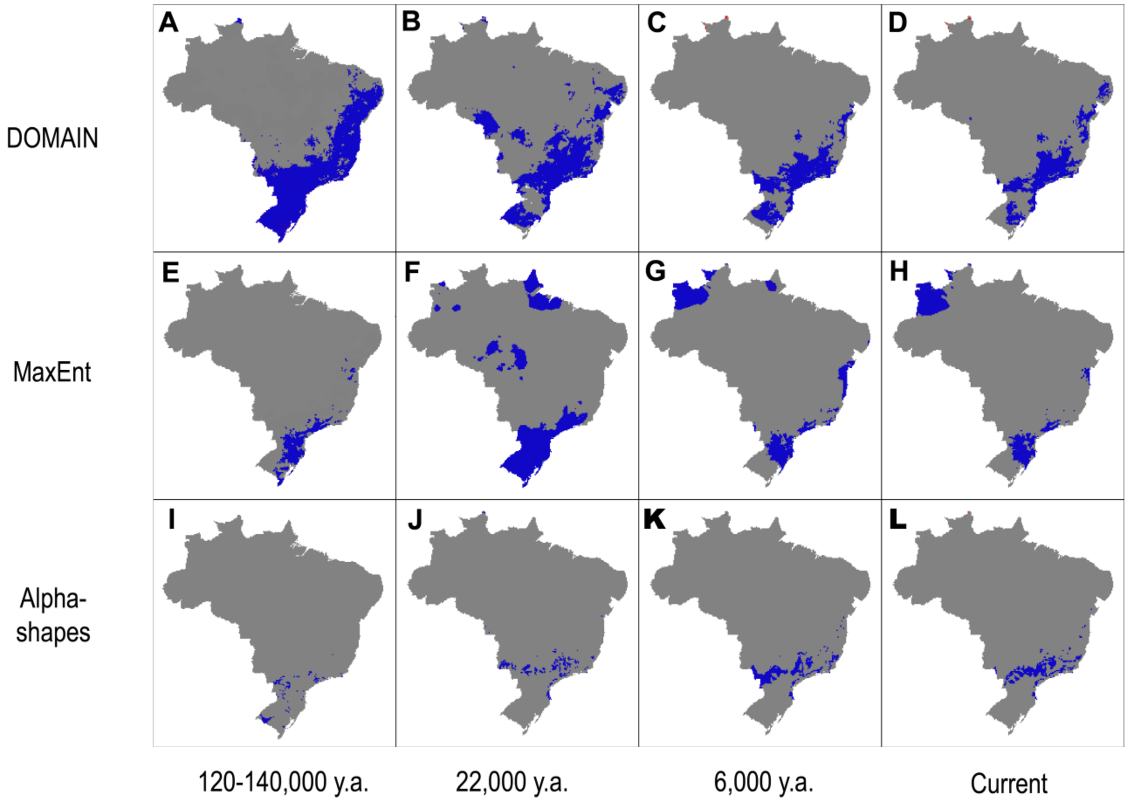


Fig 2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Current

Fig 3

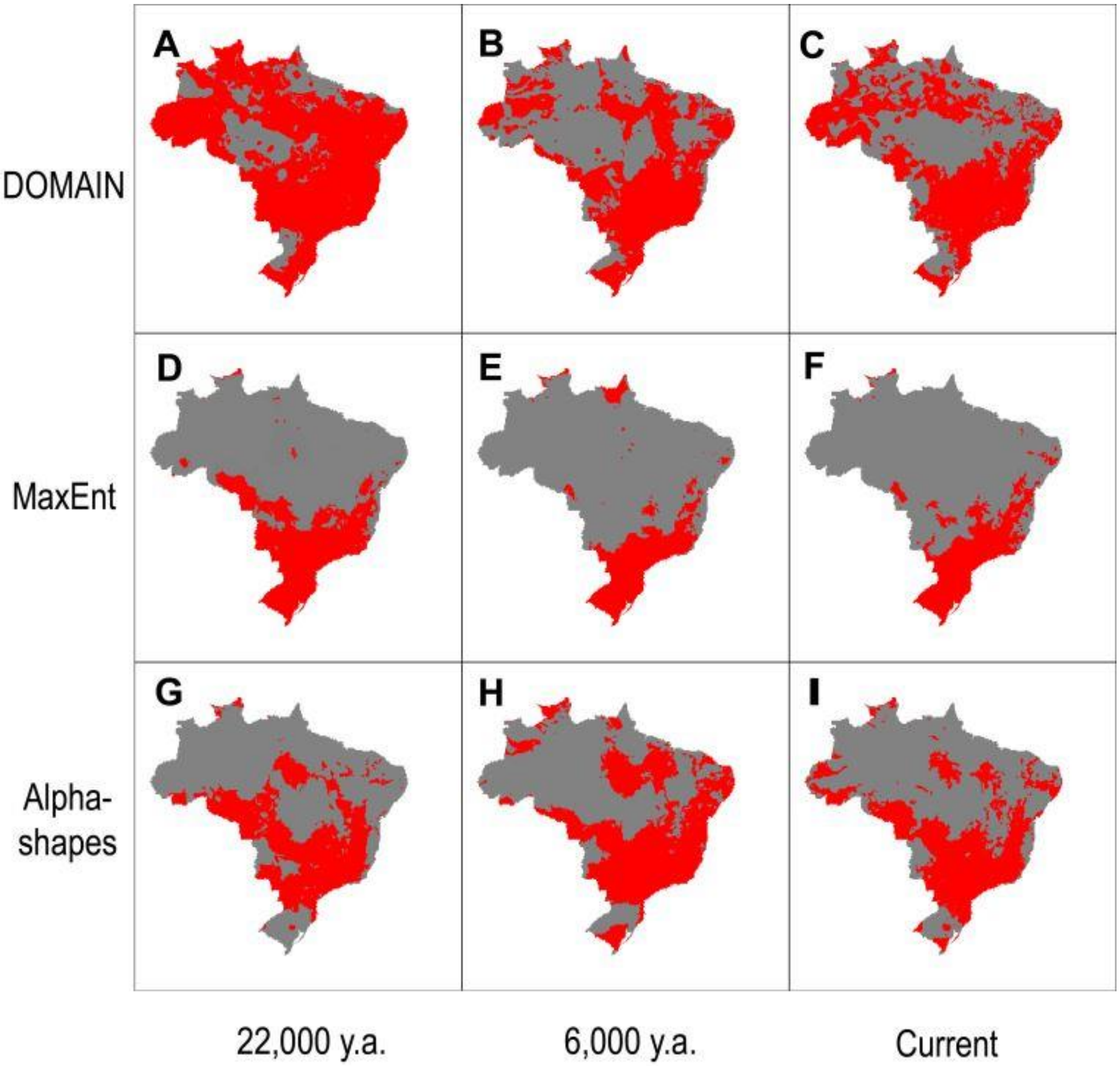
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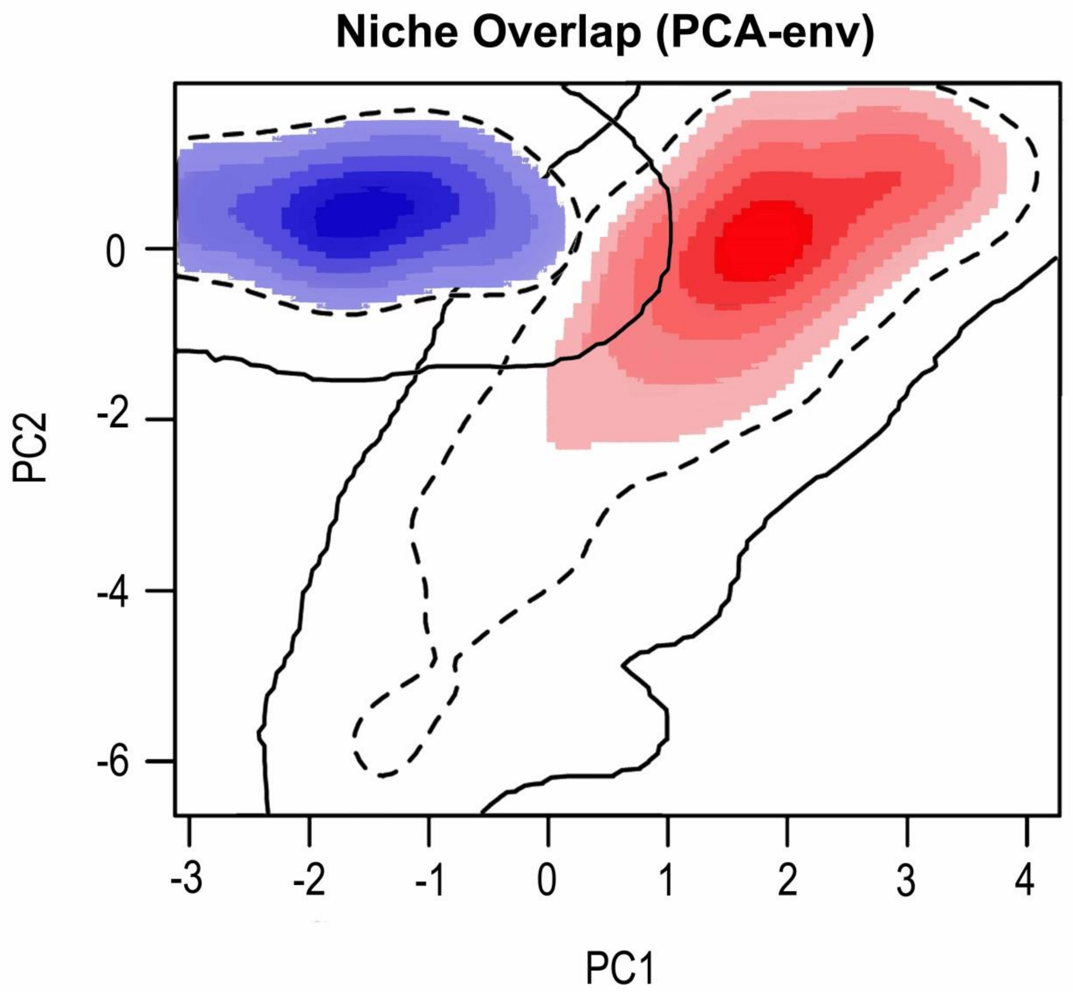
Fig 4



Supplementary material

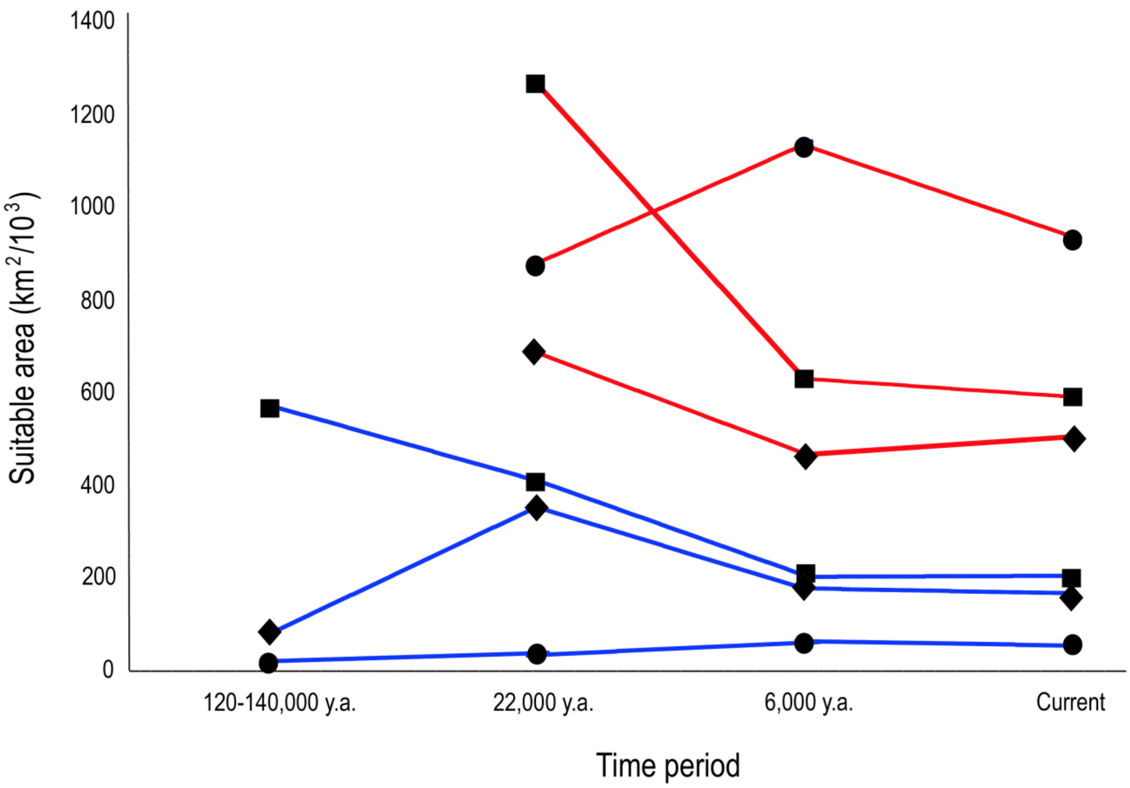


Fig S1 – Comparison of suggested range extension (km^2) of habitat suitability for *Bd*-Brazil (blue lines) and *Bd*-GPL (red lines) lineages from the three modeling algorithms used. Squares represents variation of range extension in DOMAIN, diamonds is the variation calculated in MaxEnt, and circles in alpha-shapes.

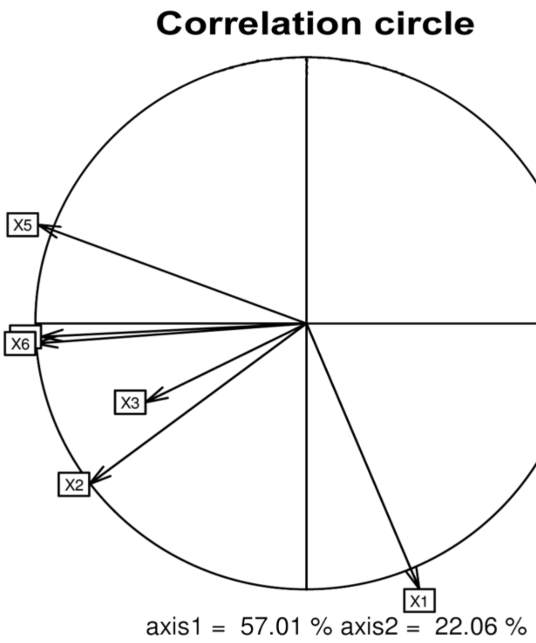


Fig S2 – Correlation circle represents the contribution of the climatic variables on the two axes of the PCA, where X1 is annual mean temperature, X2 is maximum temperature of the warmest month, X3 is minimum temperature of the coldest month, X4 is annual precipitation, X5 is precipitation of the wettest month, and X6 is precipitation of the driest month.

SÍNTESE

Vimos nos primeiros capítulos que as mudanças climáticas e alguns fenômenos associados, como a elevação oceânica, possuem potencial para gerar diversos impactos sobre organismos terrestres. Assim, investir em estudos para antecipar consequências pode promover uma conservação mais efetiva da biodiversidade.

Nesse contexto, identificamos nos capítulo 1 e 2 os potenciais problemas que podem ser causados pelas mudanças climáticas em um futuro próximo como a diminuição da oferta de hábitat para algumas espécies, o aumento para outras ou mesmo a inexistência de hábitat potencialmente adequado, evidenciando uma vez mais as mudanças climáticas como um desafio para a conservação de espécies. Também identificamos a Australasia como região biogeográfica potencialmente mais suscetível aos efeitos da elevação oceânica sobre sua anurofauna. Além disso, também identificamos prováveis efeitos negativos que podem ser causados pela elevação oceânica, como o decréscimo (em termos de área) de hábitat adequado por alagamento, a possibilidade de intrusões marinhas em áreas climaticamente adequadas ou ainda a fragmentação dessas áreas, com potencial para isolamento de populações.

Na escala da Mata Atlântica abordada no capítulo 2, de modo geral tanto as mudanças climáticas quanto a elevação oceânica aparentemente não possuem potencial para causar efeitos alarmantes sobre as espécies estudadas, com exceção de alguns casos. Entretanto, algumas espécies parecem suscetíveis por possuírem distribuição potencial próxima a áreas passíveis de alagamento e merecem maior atenção no sentido de antecipar efeitos negativos e promover sua proteção.

Tendo em vista o grande número de espécies insuficientes em dados com os quais nos deparamos no decorrer desses estudos, no capítulo 3 desenvolvemos um índice de classificação para espécies com dados insuficientes (DD). Nossa expectativa é de fomentar a busca de informações para esses táxons, permitindo assim sua apropriada classificação dentro das categorias de ameaça existentes. O índice é simples e agrega diversos fatores biológicos, de distribuição, raridade e tempo de descrição entre outros, de modo que pode ser utilizado para outros grupos em situação semelhante. O resultado do índice parece consistente e esperamos que seja utilizado para sanar as lacunas envolvendo espécies DD.

No quarto capítulo constatamos a possibilidade de existência de clima adequado passado tanto para a ocorrência do *Bd*-Brazil como para o *Bd*-GPL. Com relação ao *Bd*-Brazil, nossos resultados demonstram que a hipótese do patógeno endêmico é plausível, sendo possível o surgimento dessa linhagem no Brasil ou na América do Sul. Para o *Bd*-GPL, como o local de sua origem ainda é incerto, de acordo com nossos resultados não se pode descartar uma origem também na América do Sul. Além disso, constatamos a baixa sobreposição de nicho climático entre as linhagens, o que deixa aberta a discussão sobre uma possível competição entre elas. Se confirmada, essa hipótese pode ajudar a explicar a raridade da linhagem *Bd*-Brazil.

Sendo assim, analisamos nessa tese diversos fatores que podem afetar a conservação dos anfíbios no Brasil e no mundo. Nossos resultados nos permitem afirmar que as mudanças climáticas constituem um grande desafio a ser superado. Potenciais efeitos relacionados à elevação oceânica em conjunto com populações estritamente costeiras devem ser monitorados a fim de antecipar e prevenir efeitos negativos. Além disso, esperamos que nossos resultados fomentem a busca de informações para espécies pouco conhecidas e que tenhamos contribuído para a compreensão da ecologia do fungo quitrídio.

APÊNDICE

A elevação oceânica e o futuro da conservação da biodiversidade na região costeira de terras baixas no Brasil

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As mudanças climáticas (*climate change*, CC) produzirão modificações no planeta, impactando a diversidade biológica e o modo de vida humano. O *Intergovernmental Panel on Climate Change* (IPCC) define CC como "mudança no estado climático identificada por alterações nas médias e/ou na variação de suas propriedades que persistem por períodos (de tempo) extensos" (IPCC 2007). De magnitude global, as CC são assunto importante e recorrente na agenda de líderes mundiais e organizações multinacionais. Embora a menção das CC invoquem seus efeitos primários como as alterações na temperatura e chuvas, esse fenômeno acarreta diversos outros efeitos agregados, como atrasos/antecipações das estações do ano, derretimento de geleiras, decréscimo dos recursos hídricos em zonas semiáridas e elevação oceânica (IPCC 2007).

Dentre os citados, a elevação oceânica (*sea level rise*, SLR) é um fenômeno que desperta interesse por seu potencial de transformações. Mudanças no nível do mar já ocorreram em diversas ocasiões na história da Terra. Por exemplo, há 20 mil anos o nível do mar era 120 m mais baixo, pois a água estava aprisionada em imensas geleiras continentais nesse período de glaciação; ou no Plioceno, quando o nível do mar esteve entre 25 e 35 m mais alto que o atual com temperaturas de 2 a 3° C mais elevadas (Rahmstorf 2012).

Mudanças no nível do mar afetam áreas imediatamente suscetíveis com alagamentos e erosão (IPCC 2007). Dessa forma, áreas protegidas como Unidades de Conservação (UCs) que possuem porções costeiras estão sujeitas a tais efeitos. Todavia, embora a SLR seja uma consequência esperada das CC (Nicholls & Cazenave 2010), despertando preocupação, há poucos estudos relacionando a SLR e a diversidade biológica (Bellard *et al.* 2014).

Entendendo o problema

A comunidade acadêmica tem concentrado seus esforços em compreender e prever a SLR de duas formas: com modelos físicos e semi-empíricos (Rahmstorf 2012). Modelos físicos descrevem quantitativamente os diferentes processos físicos que geram a SLR, i.e., expansão térmica (aumento de volume por acréscimo de temperatura), aporte hídrico (água que chega ao mar pelo derretimento de gelo continental) e por mudanças de profundidade em bacias oceânicas por movimentos da crosta terrestre. Entretanto, modelos físicos esbarram em incertezas derivadas do conhecimento limitado sobre dinâmica de geleiras (Church *et al*. 2013b) e para sanar esse déficit seria necessário conhecer a dinâmica de cada uma das 130 mil geleiras existentes no planeta (WGMS & NSIDC 1989). Diante desse cenário, os modelos semi-empíricos são aplicados, associando estimativas de SLR com as mudanças de temperatura observadas ao longo da história. Assim, utilizam dados pretéritos para projetar o futuro, seguindo a lógica de que quanto mais quente, mais rápido o nível do mar subirá. O AR5 (relatório climático) do IPCC (Church *et al.* 2013a) levou em conta ambas as métricas de modelagem para calcular os cenários de SLR futuros, concluindo que a SLR será maior do que previamente imaginado para 2100, com SLR de até um metro.

Diante dessa complexidade, inúmeros estudos sobre SLR são encontrados na literatura. Alguns preveem poucos centímetros de SLR (e.g., AR4 do IPCC 2007), mas a maioria apresentam cenários potencialmente catastróficos, com modelos de SLR de 2 m (Grinsted *et al.* 2009) ou até 6 m (Overpeck *et al.* 2006). Contudo, é importante observar que as magnitudes de elevação modeladas constituem valores médios de elevação global e não contemplam efeitos locais. A SLR será diferente através das zonas costeiras mundiais devido à dinâmica dos oceanos, ventos, movimentos do assoalho marinho e mudanças na gravidade terrestre pela redistribuição da massa de água (Rahmstorf 2012; Church *et al.*

2013a). Assim, modelos preditivos de SLR em escalas locais também envolvem incertezas, sendo de construção complexa (Rahmstorf 2012), principalmente no que diz respeito ao potencial avanço horizontal da SLR (e.g. Wetzel *et al*. 2012).

Impactos potenciais da SLR

Efeitos imediatos da SLR envolvem erosão com consequente perda de terreno por alagamento (Rahmstorf 2012) e intrusões marinhas também podem se tornar frequentes com tempestades (Scavia *et al.* 2002; Rahmstorf 2012). Bellard *et al.* (2014) identificaram *hotspots* de biodiversidade insulares altamente suscetíveis à SLR e Menon *et al.* (2010) avaliaram regiões continentais igualmente propensas. Além disso, intrusões de água salgada podem representar uma barreira intransponível para organismos pouco tolerantes à salinidade como observado por Ríos-Lopez (2008) que registrou efeitos negativos sobre abundância, crescimento e metamorfose de anuros em poças que sofreram intrusões marinhas na Costa Rica. Assim, sistemas costeiros como manguezais, estuários, restingas e sua diversidade associada podem estar ameaçados pela SLR.

Além do século 21

A dinâmica oceânica não estará estável até o fim do século (Church *et al*. 2013a) e os pesquisadores tentam agora desenvolver modelos para além de 2100. Um elemento chave que limita o poder de previsão desses modelos é o colapso ou não do gelo na Antártica, maior reservatório de água do planeta (Rahmstorf 2012; Church *et al*. 2013a). Seu eventual derretimento poderia acarretar em uma SLR de vários metros (Gomez *et al*. 2010; Church *et al.* 2013a), apesar desse cenário ainda ser pouco provável (Church *et al*. 2013b), pois não há derretimento significativo na Antártica (Shepherd *et al*. 2012) até o momento. Contudo, se o derretimento for desencadeado, é esperado um redesenho completo das costas em escala global.

SLR e a conservação da biodiversidade brasileira em áreas potencialmente afetadas

Apesar dos importantes avanços no estudo dos efeitos das CC no Brasil (e.g. Loyola *et al*., 2013) pesquisas sobre eventuais impactos da SLR sobre a biodiversidade ainda são incipientes. Por exemplo, embora o Brasil possua diversas UCs em áreas costeiras (e.g. Estação Ecológica Jureia-Itatins, Arquipélago de Marajó, Refúgio da Vida Silvestre de Una, entre outras), é provável que essas unidades percam áreas de terra firme devido à SLR (Menon *et al*. 2010). Entretanto, ainda é incerto qual a magnitude desses impactos e quais grupos podem ser afetados.

A maior parte da costa brasileira é constituída pela Mata Atlântica (MA), a qual abriga grande diversidade e endemismos (Myers *et al*. 2000). Considerando que no futuro áreas climaticamente adequadas para alguns grupos animais podem se concentrar em montanhas (Loyola *et al*. 2013), essas áreas poderiam agir como um refúgio, minimizando eventuais efeitos da SLR em terras baixas costeiras. Entretanto, migrar pode ser um fator limitante para espécies com baixa vagilidade e capacidade restrita de dispersão. Por outro lado, mudanças nos padrões de distribuição altitudinal podem causar "atrito biótico", i.e., perda de diversidade quando o número de espécies que emigram de uma área excede o número de imigrantes para essa área, gerando lacunas de ocupação e baixa diversidade, principalmente em terras baixas (Colwell *et al*. 2008). Contudo, efeitos severos potencialmente causados pela SLR aparentemente podem ocorrer na costa norte brasileira, sobretudo no delta do Amazonas (Menon *et al.* 2010), com perdas prováveis de grandes extensões de terra firme.

Esta é uma região que carece de estudos taxonômicos, sendo presumível que lá ocorram espécies animais e vegetais ainda não descritas, mas já potencialmente ameaçadas.

Diante desse panorama, fica claro que a SLR trará impactos sobre a diversidade de áreas costeiras de terras baixas. Assim, ressaltamos a necessidade de maiores investimentos no estudo e compreensão do fenômeno pela comunidade acadêmica e órgãos ambientais para antecipar e prevenir a perda de diversidade biológica. Desenvolver estudos locais com espécies, populações e comunidades na costa, elaborar modelos locais para a SLR e incluir potenciais efeitos em planos de conservação pode minimizar perdas futuras e auxiliar na implantação de futuras UCs, garantindo sua funcionalidade e potencializando a capacidade de conservação.

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