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MAÍRA DALIA SAGNORI

DISTRIBUTION AND VULNERABILITY OF ATLANTIC FOREST AMPHIBIANS TO GLOBAL TEMPERATURE INCREASE

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Orientador: Prof. Mirco Solé Kinle
Co-orientador: Prof. Rafael Dias Loyola

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Mirco Solé Kinle – PhD
UESC
(Orientador)

Rafael Dias Loyola – PhD
UFG
(Co-orientador)

Miguel Tejedo Madueño – PhD
EBD-CSIC, Espanha

Priscila Lemes – PhD

UNESP

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DISTRIBUIÇÃO E VULNERABILIDADE DE ANFÍBIOS NA MATA ATLÂNTICA EM FUNÇÃO DO AQUECIMENTO GLOBAL

RESUMO: As mudanças climáticas atuais são uma ameaça real à biodiversidade. Essas mudanças surgem à medida que a população humana se expande e consome os recursos naturais do nosso planeta, logo as pressões antropogênicas são a causa principal destas mudanças. Mudanças climáticas podem estar levando espécies diretamente à extinção a medida que elas já respondem às novas condições através de mudanças e contrações em suas áreas de distribuição geográfica. Estudos que modelam o impacto potencial do aquecimento global na biodiversidade têm aumentado e contribuem para um melhor entendimento de quão ameaçadas a persistência e diversidade das espécies estão. No entanto, uma abordagem apenas correlativa do impacto dessas mudanças não incorporam correlações complexas das variáveis abióticas do nicho e respostas fisiológicas das espécies. Como uma tentativa de avaliar a causa dos padrões futuros de distribuição, modelos mecanísticos de nicho buscam ligar os dados espaciais aos traços funcionais dos organismos fornecendo uma melhor compreensão do nicho fundamental, e de quão vulnerável esses organismos estarão no futuro. Unir ambas as ferramentas é uma estratégia promissora para alcançar previsões mais realistas e adequadas de áreas prioritárias, de espécies ameaçadas e para evitar áreas pouco representativas em planejamentos para conservação.

Palavras-chave: Mudanças climáticas. Biodiversidade. Vulnerabilidade. Modelagem de distribuição de espécies. Abordagem mecanística. Conservação.

DISTRIBUTION AND VULNERABILITY OF ATLANTIC FOREST AMPHIBIANS TO GLOBAL TEMPERATURE INCREASE

ABSTRACT: Current climate change is a major threat to biodiversity. These changes arise as human population expands and consumes natural resources, thus anthropogenic pressures are the main causes of it. It can be a direct driver of extinction as species have already responded to novel climatic conditions by shifting or shrinking their geographic ranges. Studies modeling potential impacts of global warming on biodiversity are increasing and contributing to a more comprehensive knowledge of how threatened persistence and diversity of species are. However a correlative approach of the impacts alone does not incorporate complex correlation of abiotic variables and physiological responses. As an attempt to assess the cause of future distribution patters, mechanistic niche models intend to link spatial data to functional traits of organisms providing a better understanding of the fundamental niche, and how vulnerable species will be in the future. To aggregate both tools is a promising strategy to achieve more suitable and reliable predictions of priority sites, threatened species, and to avoid unrepresentative sites on conservation planning.

Keywords: Climate change. Biodiversity. Vulnerability. Modelling species distribution. Mechanistic approaches. Conservation.

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SUMÁRIO

Distribution and vulnerability of Atlantic forest amphibians to global temperature increase

1 OVERVIEW

Climate change is a determinant force of the geographic distribution of species, as species establish their populations upon their niche requirements - available resources and abiotic conditions. Currently, these changes are drastically affecting biodiversity by altering normal environmental conditions, forcing species to either move or adapt. However, commonly, many species are not able to move or adapt due to many specific reasons, as geographic barriers or physiological constrains. So, they may shrink their ranges, thereby increasing their vulnerability to changing environmental conditions, hence becoming at risk of extinction due to climate change. Throughout the history of Earth, climate has changed and species have coped and adapted to these changes, but currently it is understood as a major threat, and affecting geographical patterns is only one of the consequences.

This threat is highly associated with anthropogenic causes. The evidences of climate warming have been correlated with industrialization, urbanization, lands uses, deforestation, agriculture and livestock, and is rising rapidly compared with most past changes. These rapid changes and dynamic responses pose a new challenge to the scientific community: forecast what would be the future patterns of environmental conditions to prevent further extinctions. Predictions are specially challenging because nature is a dynamic and complex system in which every element is correlated with each other, such as climate, soil, vegetation and even organisms. Ecological niche models (ENMs) use spatial environmental data to make inferences on species' range limits and habitat suitability by mapping niche-abiotic components through space and time. Despite being important tools in ecology and conservation, a mechanistic view of the fundamental niche enables a more robust prediction and interpretation of range shifts in non-equilibrium contexts such as climate change.

Aiming to incorporate mechanistic links between physiological traits of organisms and their environments into modelling geographic distributions, we chose to test the physiological tolerance of temperature increase in tropical ectotherms and measure their vulnerability to future climate change. First we forecasted the most suitable ranges according to niche models. Then, we tested the critical thermal maxima of 17 tadpoles of species occurring in the Brazilian Atlantic Forest, and calculated a vulnerability index as their warming tolerance. To link both correlative and mechanistic approaches, we mapped inside those suitable areas, how the vulnerability pattern would vary spatially according to rising temperatures predictions.

With this work we hope to provide a functional interpretation of spatial predictions and enable further comparisons possibilities of both correlative and mechanistic approaches effectiveness in climate change predictions. Also, we believe that information on relative vulnerability of species to natural process are crucial for effective conservation planning besides capturing some complexity of species responses to climate change.

Climate change, ecological niche and species vulnerability: a review of concepts

2 LITERATURE REVIEW

2.1 Global climate change

2.1.1 Overheating: why, how and who

Earth’s surface temperature varies along time (Braconnot, et al. 2012). Since the pre-industrial era, new trends on temperature changes have been observed and recorded. However, it is now clear that there is a measurable difference between natural variability of climate and the one caused by external forces (i.e. human pressures) (IPCC 2015). Climate change is defined by the Intergovernmental Panel on Climate Change (IPCC) as a change in the state of the climate that can be identified by changes in the mean and/or the variability of its properties and that persists for an extended period, typically decades or longer (IPCC 2015).

Changes on temperature arise with elevations on greenhouse gases concentration in the atmosphere, especially carbon dioxide (CO_2), as well as methane (CH_4), and aerosols particles. Due to current atmosphere composition, the biosphere became a sink rather than a source of atmospheric CO_2 (IPCC 2015). In numbers, CO_2 and CH_4 atmospheric concentrations have increased in 31±4% and 151±52%, respectively from 1750 to 2000’s will cause an increase, of global mean temperature in the next century of about 0.3°Cper decade (IPCC 2015).

As human population expands worldwide followed by a continuous growth of human consumption of natural resources and development of infrastructure, the temperature increases globally at accelerated rates, placing humans as co-agents of global climate changes (Gardner et al. 2010; Rands et al. 2013; Macdougall et al. 2013). Combustion of fossil fuels, indiscriminate exploitation of natural resources, changes in land use (i.e. livestock, pasture), increase the deposition of anthropogenic nitrogen, urbanization, soil, water and air pollution, and deforestation among others are some examples of pressures that human populations enforce on the planet (Root & Schneider 1995; Chazal & Rounsevell 2009; Engler et al. 2011; Dasgupta & Ehrlich 2013)

2.1.2 Impacts and threats for biodiversity

Climate change is now posed as one of the major threats for biodiversity (Pereira *et al.*, 2010). It can be a direct driver of extinction – making habitat conditions unsuitable for species – or act synergistically with other threats – facilitating invasion of non-native species (Brook et al. 2008; Loyola et al. 2012). Extinction risk can increase by intensified climate change-induced threats such as sea level rises, water availability, and extreme events (IPCC 2013). Species have already responded to climatic shifts (i.e. precipitation regimes) across the globe and accurate predictions suggest an increase of the mean extinction probability of 10% across taxa and ecoregions by 2100 (Maclean & Wilson 2011).

According to the IPCC, most reported impacts of climate change are attributed to warming and/or to shifts in precipitation patterns. Those can be observed in many aspects of natural systems and ecological patterns as well as different scales. Garcia et al. (2014) proposed a framework to guide the selection of different climate-change metrics. They based this analysis on the various dimensions of climate change, each with distinct implications for biodiversity. For example, the contrasting pattern of forecasts between polar and tropical climates and the types of threats likely to be imposed on biodiversity at distinct levels. Nonrandom observed pattern of range shifts toward the poles averaged 6.1 km per decade for animals and plants of temperate regions (Parmesan & Yohe 2003; Thuiller 2011) are specially related to increased growing season length induced by global warming. Besides range shifts, at tropical regions many species are experiencing range contractions which means loss of their habitats, limited dispersal capability and even species interactions disturbs putting them at high risk of extinction (Brook et al. 2008; Engler et al. 2011; Hillerislambers et al. 2013).

Studies modeling potential impacts of global warming on biodiversity are increasing and contributing to a better understanding of how threatened persistence and diversity of species are. Eight out of ten models predict at least 20% loss of vertebrate species under lower emission scenarios at tropical and temperate regions of the western hemisphere due to loss of areas with suitable conditions (Laustein & Artlein 2009). Amphibians stand among other vertebrates as more susceptible with 95% of western hemisphere species projected to experience a net loss in range size under the lower emissions scenario (Lawler et al. 2009).

2.1.3 Implications for conservation

Conserving biodiversity under the current scenario of environmental changes comes out as a challenge for conservation scientists. For being a dynamic system, controlling all the variables and synergies related to changes on climate and its consequences seems to be an impossible task. If the rate of climate changes overtake the response potential of biological systems to adapt (i.e. migratory capacity), impacts on ecosystem functioning, community structure and species distributions can be irreversible. Therefore, enhanced conservation efforts will play a critical role to reduction of climate change impacts on the ecosystem.

How could ecologists and conservationists predict when, how and where those changes will happen (see Richardson & Whittaker 2010)? As an attempt to find these answers, modeling specie's responses to different possible scenarios of environmental conditions (see Araújo & Peterson 2012) has proved to be an effective tool (Beaumont *et al.*, 2007; Carnaval & Moritz, 2008; Diniz-Filho *et al.*, 2009; Austin & Niel, 2011). Trying to reach more reliable outcomes, scientist have implemented mechanistic approaches to forecasts by combining physiological and behavioral to spatial data as well as ecological processes (Kearney & Porter 2009; Elith et al. 2010; M. R. Kearney et al. 2010a; Franklin 2010). These predictions can make a significant contribution to decision and policy makers guiding their efforts to more effective management of biodiversity. However, uncertainties regarding the input data constrain the effectiveness of the models outcomes.

To improve conservation management, ecologists must quantify the risks of uncertainties and trade-offs associated with different climate scenarios by testing the sensitivity of different model results (Kujala et al. 2013). Moreover, strategies should be sensible for species adaptation, impact mitigation, and also should prioritize the protection and connectivity of climatically heterogeneous landscapes (Richardson & Whittaker 2010).

2.2 Ecological niche modeling

2.2.1 The niche concept

The niche concept relates a set of environmental conditions to the fitness of individuals and can be distinct in realized and fundamental niche. The niche can be interpreted as a property of the organism rather than the environment allowing one to explain the distribution and abundance of a given organism through its niche requirements (Kearney 2006). The fundamental niche describes the abiotic conditions in which a species is able to persist, whereas the realized niche describes the conditions in which a species persists given the presence of other species (e.g. competitors and predators) (Hutchinson 1957). The set of environmental conditions that characterize a specific niche is retained over evolutionary time at the population level is called niche conservatism and can be an explanation for the inability of species to simply adapt to changing abiotic conditions over a given timescale (Wiens & Graham 2005; Hirzel & Le Lay 2008).

2.2.2 Niche models

Among many applications, the interest in developing models to forecast species distributions exploded in recent years with the observations of dangerous or even lethal consequences of climate change, especially the overheating, jeopardizing the persistence of many species (Peterson & Soberón 2012; Diniz-Filho & Loyola 2012; Anderson 2013). Ecological niche models (ENMs) represent associations between the specie’s environments and its geographical distributions. Differently from species distribution models (SDMs), ENMs model the processes that shape the distributional area, focusing on a subset of environmental conditions (i.e. temperature variations) favoring a biological interpretation of the patterns, which necessarily involves niche-related theories and hypothesis (Peterson & Soberón 2012). Thus, facing the actual scenario of environmental changes, by predicting species range shifts, this tool has been used for solving conservation resource allocation problems for example (Kujala et al. 2013).

As a dynamic process, changes on climate impose unexpected risks on conservation planning, and decision making (Kujala et al. 2012). Uncertainties related to these changes can arise from different sources: i) differences in modeling methods and environmental models; ii) different levels of confidence between present and future distributions; and iii) range-shifts in species distributions. There are some strategies taken to reduce risks related to model uncertainties: i) ensemble forecast is one technique that emphasizes agreement of predictions, thus providing more robust and less variable forecasts (Araújo & New, 2007); (ii) coupling physiological and ecological knowledge with modeling outcomes to guide model evaluation (Elith et al. 2010); iii) mapping uncertainty distribution allows an investigation of the regions more affected by it (Diniz-Filho et al. 2009); and iv) accounting for dispersal estimation (Kujala et al. 2013).

2.2.3 Mechanistic approach

Despite being a promising tool, reliable forecasts must include dynamic ecological factors as biotic and abiotic interactions, land-use changes, dispersal and adaptation ability, population trends, across both space and time. As an attempt to assess the cause of future distribution patters, mechanistic niche models intend to link spatial data to functional traits of organisms providing a better understanding of the fundamental niche, roles of range-limiting processes, and how vulnerable species are facing novel climate conditions (Kearney & Porter 2009; Elith et al. 2010; Huey et al. 2012; Buckley 2013). A mechanistic understanding of the fundamental niche, when combined with geographic data, enhances the robustness of extrapolated results as to novel circumstances such as climate change (Kearney & Porter 2004; Kearney et al. 2010a). Rather, it enhances the confidence and power of model predictions.

2.2.4 Applications in conservation science

Ecological niche modeling is an important tool for ecologists and conservation practitioners which can be used for, in addition to project future changes in species' geographic ranges (Loyola et al. 2014), examine reserve efficiency (Lemes et al. 2013), and estimate extinction risks (Bielby et al. 2010). Moreover, niche models finally guide conservation efforts helping to identify priority sites with high species complementarity in the present and in the future under climate change scenarios, and to avoid unrepresentative sites of biological diversity (Loyola et al. 2012b; Faleiro et al. 2013; Lemes & Loyola 2013).

Ignoring the uncertainties associated with future distribution modeling comes at the expense of irrelevant investments and also impairs decision-makings by over-estimating losses or gains of distributional area or the likelihood of a forecasted extinction under climate change for example. Porfirio et al. (2014) highlights the importance of directing variables choice according to characteristics of the organism modeled amenable to ecological interpretation, such as species with strong temperature dependencies that are strongly influenced by choice of emissions scenarios.

Schwartz (2012) created recommendations for scientist seeking to conduct management-relevant research using niche models to project future species distributions taking into account modeling uncertainties. Aiming to take successful conservation decisions a conservation scientist and a decision maker should: i) target research to questions relevant for management decisions; ii) identify how niche models balanced with uncertainties may inform conservation decisions; and iii) understand the differential risks associated with management errors before structuring an adaptive management decision.

2.3 Species vulnerability to climate change

2.3.1 What is it about

According to the IPCC, “vulnerability is a predisposition to be adversely affected”. This propensity or predisposition could be linked to sensitivity or susceptibility to harm and lack of capacity to cope and adapt to novel conditions. Although there is no currently scientific consensus regarding the definition of this term, it is generally agreed that there is not a single cause for vulnerability (IPCC 2014). Rather it is a function of intrinsic and extrinsic factors, depicting a product of specie’s exposure and sensitivity to environmental changes, its resilience to perturbations and its potential to adapt to novel changes (Williams et al. 2008a; Huey et al. 2012; Foden et al. 2013). While exposure is determined by extrinsic factor relevant to each species group as rainfall or fire regime, sensitivity, resilience, and adaptive capacity are determined by intrinsic factors such as species abundance, dispersal ability, and the ability to adjust in response to disturbances, respectively (Williams et al. 2008b).

The information carried with vulnerability measurements is about what aspects of the ecology, evolutionary biology, physiology, and the environment a species is adapted determine its vulnerability to present changing conditions (i.e. thermal tolerances under climate change), and thus evaluate what are the best management options to minimize the impacts of these changes (Foden et al. 2013).

2.3.2 Application of species vulnerability measures

In a comprehensive review on the subject, Pacifici et al. (2015) described different approaches and metrics to assess the vulnerability of a species concerning on data availability, and objectives. Approaches can be correlative, mechanistic, trait-based or a combination of them. Metrics can be changes in distribution and population indicating limited dispersal ability or adaptability (Ameca y Juárez et al. 2013), extinction probability calculated with species life-history characteristics (Fordham et al. 2009), or scoring systems as indices – quantitative indicators of the relative vulnerability of species – which are often easier for scientists and practitioners to interpret and to identify species at risk (Lee et al. 2015).

Vulnerability frameworks vary depending on the available data and what aspect of vulnerability one aims to study. Vulnerability indices are mostly used to express a general measure of the potential impairs of climate change to a species or ecosystem, and because they are built on detailed information about the elements leading to vulnerability, despite being summarized in a single number, they can also be unfold to spatial and taxonomic variation in the fundamental causes of vulnerability due to climate change (see Williams et al. 2008b). Crossman et al. (2012) created a spatial index to identify areas of increased vulnerability based on dispersal ability (proxy of resilience) and spatial distribution (proxy of exposure) weighted by the likely change in species distribution (proxy of sensitivity) of each species. Summers et al. (2012) applied on their work a complementarity-based index to assess spatial conservation priorities, thereby ensuring that each unique element of vulnerability had a minimum level of representation, which proved to be an effective framework to identify spatial conservation priorities. On the other hand, different aspects of climate change vulnerability may be important in different biological systems, which may cause low spatial congruence between species distribution and vulnerability aspects (Gardali et al. 2012; Foden et al. 2013).

2.3.3 A promising tool for conservation planning

Vulnerability assessments coupled with niche modeling offers a more rigorous method to point at species which are currently not threatened, but are likely to become so under future scenarios, ensuring better resource allocation and helping to guide decisions regarding the most appropriate adaptation strategies (Cabrelli et al. 2014). Because of taxonomic and geographic variations in drivers of climate change vulnerability, this coupled method can assist to address on-ground spatial prioritization for climate adaptation actions for threatened species (Lee et al. 2015). It also can be useful to route conservation managers who need to allocate limited resources among a large number of taxa to maximize conservation gains (Maggini et al. 2014).

Trait-based vulnerability assessments (TVAs) can be notably important for species whose distributions are not reliably predicted by climate alone which in turn is traditionally done in modeling exercises grounded on niche conservatism (Chessman 2013). As scientists strive to get to more feasible extinction risk assessments in an attempt to warrant conservation costs, including intrinsic traits (i.e. clutch size, body size, thermal tolerances, habitat specialization) integrated with spatial patterns of key threats would improve conservationist’s ability to detect species bioclimatic envelope, and manage endangered species in the future, particularly where data deficiency is a problem (Murray et al. 2011; Pacifici et al. 2015).

2.4 Physiological limits

2.4.1 Thermal tolerances

To characterize the thermal sensitivity of a system we need three measures: optimal temperature – under which the organism performs better; and minimum and maximum critical thermal limits that limit a performance breadth – under which the organism performs well (Huey & Stevenson 1979). The curve associated with these values (TPC - Thermal Performance Curve) allows predicting performance (y-axis) at any given body temperature (x-axis) proving its potential utility in helping to predict the responses of species to climate change (Deutsch et al. 2008). Under the optimal thermal conditions the organism performs activities that make significant contribution to fitness as higher growth and reproductive rates, predation success and avoidance, maximum acceleration and velocity (Angilletta et al. 2002; Schulte et al. 2011). Thereby, TPC is a useful tool for mechanistic approaches of species distribution and vulnerability under climate change (Kearney et al. 2008; Kearney & Porter 2009). Furthermore, the study of physiological tolerances at large scales, its temporal and spatial variability, and the ecological implications has been of great importance to the macrophysiology field, analysis of thermal ranges and its plasticity under changing climate conditions (Gaston & Blackburn 2000; Addo-Bediako et al. 2000; Chown & Gaston 2008).

Physiological performance is conditioned by abiotic factors, such as temperature and humidity (Cossins & Bowler, 1987), and therefore is important to define the fundamental niche of species. The influence of temperature on biochemical processes of organisms is a determinant factor on the survival, and therefore on the species distribution, abundance, interactions, and its fitness (Titon et al. 2010; Prates et al. 2013). Thus, the study of thermal tolerances is important to describe the range of temperatures under which organisms can persist and evolve, and also describe the geographic region suitable for the animal’s occurrence (Kearney 2006; Kearney et al. 2010b).

The nature and relative importance of certain niche properties will vary from organism to organism. Important axes of any organism’s fundamental niche will include those environmental variables that permit the metabolism to function efficiently and avoid high amplitude of body temperature (Kearney & Porter 2004). All organisms require an optimal and somehow steady thermodynamic interaction with their environment. It means that organisms are not able to rapidly adjust to abiotic fluctuations, as temperature and precipitation regimes (Richter-Boix et al. 2011). However, some animals can persist through short and rapid periods of extreme climatic conditions, which in this case can be a driver of species distribution adaptation (Overgaard et al. 2014).

2.4.2 Critical thermal limits

There are two experimental methods used to estimate critical thermal limits (CTmax or CTmin), a static and a dynamic (Rezende et al. 2011). In the static method the animal is placed immediately at a stressful temperature until it reaches a physical incapacitation. In the dynamic method or ramping method the animal is exposed to a constant heating/cooling rate until an end-point (upper or lower critical limit) in which it will become motionless and will fail to respond to any external stimuli (Huey & Stevenson 1979; Lutterschimidt & Hutchinson 1997a,b; Gutiérrez-Pesquera et al. 2016).

Animals submitted to extreme thermal conditions, close to the safety margin, in the long-term might adapt by evolving phenotypic characters (plasticity), while in the short-term might shift to new habitats, but it depends on the heating speeding rates (Schulte et al. 2011; Rezende et al. 2011). Whereas the critical limit refers to an intrinsic physiological trait, the heating and cooling rates of thermal change can be explored to render ecologically realistic values. Consequently, it is ecologically appealing to use this measures in addition to mechanistic models considering the interest in calculating the impact of predicted rises of temperatures on species persistence or distribution, or else they will be able to adapt without the need to disperse (Carvalho et al. 2010; Tejedo et al. 2012; Overgaard et al. 2014). It is an important endeavor to get closer to a reliable assessment of species’ extinction risk to global warming.

2.5 Tropical habitats and ectotherms

2.5.1 The Brazilian Atlantic Forest: an imperiled biome

Vegetation and climate are deeply related in a way that biomes can be classified and described by its climate characteristics (Tabarelli et al. 2012). Climate change has affected global distribution of vegetation from the past, and has become a threat as important as deforestation, and logging (Corlett 2012). Notwithstanding, it will likely be affected even more in the future due to continuous expansion of metropolitan and agricultural areas (Tabarelli 2010).

The Atlantic forest is a tropical biome. It has been affected by human-induced degradation from centuries and nowadays only *ca.* 12.5% of native forest remains

(Ribeiro et al. 2009; SOS Mata Atlântica Foundation and INPE 2015; Martins et al. 2015). Since this biome hosts an outstanding number of endemic plant species, of which a large proportion is threatened with extinction due to alarming rates of habitat loss, it has been recognized as a global Biodiversity Hotspot (Myers et al. 2000; Tabarelli et al. 2010).

Tropical biomes face large-scale environmental changes. Rising temperatures facilitate the invasion of exotic plant species causing a biotic reassembly of plant species, and so changes in habitat composition with drastic consequences to the fauna (Tabarelli et al. 2012). Threats imposed by elevated temperatures are expected to be heightened by heat waves and adiabatic declines (Laurance et al. 2011). As tropical climate commonly presents low variability during the year, tropical species evolved thermal and elevational specialization and accordingly, have reduced physiological tolerances and limited acclimation capacities (Janzen 1967; Tewksbury et al. 2008, Gutiérrez-Pesquera et al. 2016).

2.5.2 An imperiled taxonomic group

The gap between thermal physiology and ecology that characterizes sensitivity to temperature changes has been elucidated specially in studies with ectotherms whose body temperatures often track environmental temperature closely, hence experience environmental constraints distinct from endotherms (Cossins & Bowler 1987; Huey & Stevenson 1979; Angilletta et al. 2002; Huey et al. 2009). Amphibians are a representative of this group and feature stringent water requirements, besides the temperature dependence, closely related to energetic costs and performance, and to the magnitude of richness and distribution within and among regions (Buckley & Jetz 2007).

According to the International Union for the Conservation of Nature (IUCN 2015) approximately 41% of the amphibians are threatened worldwide. According to the “National List of Species Threatened with Extinction” (MMA 2015), Brazil is the first world country in amphibian species richness. It guards 973 amphibian species, of these 41 are in categories of threat (endangered, vulnerable, and critically endangered). Given the direct influence of temperature on ectotherms survival, studies are increasingly demonstrating shifts in distributions and vulnerability related to rising global temperature (Thomas et al. 2004; Pounds et al. 2006; Sodhi et al. 2008; Lawler et al. 2009; Blaustein et al. 2010; Stuart et al. 2004; Duarte et al. 2012; Loyola et al. 2013; Pimm et al. 2014; Nori et al. 2015). Discoveries that extrinsic forces increase the susceptibility of high-risk species holds the inquiry that global warming and the increased climatic variability this entails, spell a compounded future for amphibians (Sodhi et al. 2008). To reinforce this hypothesis, recent work contrasted predicted extinction risk with and without climate change, and the result suggests that climate change will cause a pronounced increase in extinction risk for these taxonomic groups over the coming century (Pearson et al. 2014).

Species unable to adapt or move will face local or global extinction and this is more likely to happen to species with narrow climatic and habitat requirements and limited dispersal abilities, such as amphibians and reptiles (Carvalho et al. 2010). Modeling studies revealed that up to 85% of amphibian species of the Atlantic Forest are expected to experience range contraction while 12% are expected to be regionally extinct by 2080 due to climate change (Loyola et al. 2014). One worrying conclusion that emerges from recent work is that tropical species are currently closer to their upper thermal limits (Tewksbury et al. 2008; Huey et al. 2009; Duarte et al. 2012; Pacifici et al. 2015). Taking this into account, obtaining realistic estimates of upper critical thermal limits is a relevant effort to provide a feasible evaluation of species' extinction risk to global warming.

2.1 What we aim to

Although previous studies have identified ecological and life history attributes that characterize endangered species (Franklin 2010; Engler et al. 2011; Schwartz 2012; Chessman 2013; Gerick et al. 2014), few studies have performed a quantitative analysis of intrinsic species attributes that are potentially related to vulnerability specifically due to global warming (see Pearson et al. 2014). Furthermore, vulnerability assessments have been focused on birds, followed by mammals and plants, mainly in temperate and developed regions of the globe (Pacifici et al. 2015).

Facing the deficiency of studies with amphibians in tropical regions concerning to physiological aspects of vulnerability added to niche modeling, we aim to find i) how increases on mean temperatures will affect the geographic ranges of species; ii) how temperatures and warming tolerance will determine vulnerability inside species geographic ranges; and iii) if there are physiological and/or ecological attributes that can explain vulnerability patterns. We focused our studies on 17 anuran species of the Atlantic Forest collected in the south of the state of Bahia, in Brazil. This region is part of the Central Atlantic Forest and it was the greatest refuge for amphibians during the Quaternary due to its climatic stability (Carnaval & Moritz 2008). Today, the southern of Bahia is amongst the richest spots when it comes to diversity of trees and vertebrates, and yet there is still a lack of information about the occurrence of amphibians in the state (Pardini et al. 2009; Dias et al. 2014). A comprehensive analysis on the likely impacts of climate change on native species vulnerability and spatial distribution is therefore crucial to conservation managers and planners to proactively respond to climate stresses and address investments in appropriate sites to safeguard the known and maybe the unknown diversity that this biome has.

Ecological niche models and physiological tolerance limits: assessing the drivers of amphibian vulnerability to climate change in the Atlantic forest

ABSTRACT: The effects of climate change and its interactions with anthropogenic disturbances are being observed on many aspects of biodiversity. Climate change is predicted to be a major cause of extinctions for the next years. Predicting the impacts of these changes, especially of global warming on imperiled groups of species aiming to achieve the most feasible prediction has been a challenging task for conservationist scientists. By applying a vulnerability assessment with physiological data and ecological niche modeling techniques, here, we evaluate how climate change affects the geographic distribution of amphibians and their vulnerability patterns in the Atlantic Forest Hotspot, Brazil, and tested some ecological traits as indicators of vulnerability. Surprisingly, we found that most species will expand their ranges. An elevation of temperature across species' ranges is expected, however vulnerability patterns will vary geographically and are species specific. In case of lacking physiological data, ecological attributes are not adequate to predict species vulnerability. A deep analysis of temperature increase on species thermal limits, and its relation with species' traits might improve the predictions of species extinction risks, and foster the discussion on how the impacts could be prevented, avoiding unforeseen consequences on biodiversity.

Keywords: Climate change. Biodiversity. Vulnerability. Thermal tolerances. Atlantic Forest. Amphibians.

3 INTRODUCTION

The concept of vulnerability – the predisposition of a system to be adversely affected - is increasingly important for the study of natural hazards and global environmental changes and can be applied in many different systems (Turner et al. 2003; Janssen & Ostrom 2006; IPCC 2014; Turner 2016). More recently, vulnerability assessments are being developed to quantify the impact of global climate changes on biodiversity as a function of exposure, sensitivity, resilience, and adaptive capacity (Dawson et al. 2011; Huey et al. 2012; Maggini et al. 2014; Pacifici et al. 2015). Facing climate change as an ongoing threat to biodiversity, vulnerability analysis could reinforce a useful framework for assessing the likely impacts of climate change on the spatial distribution of species and ecosystems, extinction risks, as well as improve foundations for selecting priority areas and actions for conservation (Wilson et al. 2005; Glick et al. 2011; Forrest et al. 2012; Crossman et al. 2012).

Projections of climate change reveal negative effects on species persistence across the globe forcing them to either move or adapt. In this sense, ecological niche modeling (ENM) has proven to be a promising tool to forecast areas where species could find their abiotic niche requirements (Peterson 2011; Warren 2012; Diniz-Filho & Loyola 2012). Correlative ENMs relating occurrence data to spatial environmental data does not incorporate physiological processes that strongly influence species dispersal capacity and thus range distribution pattern (Kearney et al. 2010a). When they are used to make predictions, one assumes that all of these hidden processes are preserved in the new suitable area, when in fact functional traits and physiological constrains, as lethal thermal tolerances, limit dispersal and range distribution as novel climatic conditions can arise with continuous environmental changes (Estrada et al. 2015). Integrating ENM results and mechanistic analysis of how different environmental factors in an organism’s habitat interact with the organism itself, can help us to understand how such factors define species’ potential niche and affect its survival, besides helping us to get more accurate predictions (Kearney et al. 2009; Monahan 2009; Kearney et al. 2010a).

Impacts of anthropogenic climate change on tropical forests are already apparent, as vegetation coverage reduction, exotic species invasion, changes in native plant species composition and distribution (Oyama et al. 2007; Colwell 2008; Corlett 2012; Scarano & Ceotto 2015). As worrisome as tropical biomes modification, is the threat that climate change imposes on amphibian species diversity, which is already amongst the most vulnerable species of the world as they apparently have narrow thermal limits, limited capacity to acclimate – as a characteristic of ectotherms (see Overgaard et al. 2011) – and high rates of water loss (Laurance et al. 2011; Foden et al. 2013; Gerick et al. 2014). However many potential biological consequences of these changes are still unknown due to lack of empirical information.

Here, we modeled future suitable areas for 17 amphibian species in the Atlantic Forest, and estimated where they would be more vulnerable inside their predicted geographic distribution. We focused our analyses on the Atlantic Forest Biodiversity Hotspot, which holds 18% of all South American amphibian species, many of them endemics (Carnaval et al. 2009). In addition, its intense fragmented status makes it highly vulnerable to climate change (Scarano & Ceotto 2015). More specifically we addressed the following questions: i) How increases on mean temperatures will affect the geographic ranges of species? ii) How temperatures and warming tolerance will determine species' vulnerability within their geographic ranges? iii) Are there physiological and/or ecological traits that can explain vulnerability patterns across species?

4 MATERIAL AND METHODS

4.1 Climatic data

We used current and future climatic data developed by the CMPI5 (http://cmip-pcmdi.llnl.gov) projected to the Neotropics, from four coupled atmosphere-ocean global climate models (AOGCMs): CCSM, GISS, MIROC, and MRI, simulated for 2080-2100 at high emissions scenario (RCP8.5 – see Taylor et al. 2012): annual mean temperature, maximum temperature of the warmest month, annual precipitation, and precipitation seasonality. These variable are usually used on studies of amphibian projected distribution, owing to interaction of temperature and moisture availability as determinants of amphibian occurrence (Buckley & Jetz 2007; Buckley 2013). The data was downloaded at the ecoClimate database (Lima-Ribeiro et al. 2015; http://ecoclimate.org), at a 0.5° x 0.5° resolution. We downscaled data to 0.1° x 0.1° using interpolation to match the spatial resolution of the grid cells comprising the Atlantic Forest biome. Although CMPI5 climatic variables correspond to atmospheric measurements, recent studies have shown that air temperature variations correspond well with temperature of streams and lakes, being credible predictors in studies with aquatic organisms such as amphibian larvae (Chessman 2013; Gerick et al. 2014).

4.2 Ecological niche modeling

To model the ecological niche of species we used point location as the occurrence data, obtained from two different databases: the speciesLink Network – http://splink.org.br; and the Global Biodiversity Information Facility – http://gbif.org. We excluded from the analysis species with less than five occurrence records, otherwise models would over-predict the potential distribution of individuals with a very small number of records. We generated a presence matrix using the R package Maptools.

We modeled the species' ecological niche using five presence-only methods: BIOCLIM, MaxEnt, Mahalanobis Distance, Ecological Niche Factor Analysis (ENFA), and General Algorithm for Rule Prediction (GARP), using the platform BioEnsembles (see Diniz-Filho et al., 2009), as a function of four climatic variables obtained from the AOGCMs as cited above. Presence-only methods were built to model species-niche variables relationship using large-scale environmental data and simple occurrence data, as points of occurrence. The methods were applied independently for each species, not generating an ensemble forecast as the output, so we could evaluate the most appropriate model for each species. We compared the predictive performance of each model generated through the TSS (True Skill Statistics) and chose one, among 20 models, with the highest TSS value (>0.5) to represent the future distribution of each species. Considering that predicted species distribution are not always in equilibrium with the modeled envelope (see Rahbek et al. 2012), we established a threshold of suitability to assess the area where species will most likely occur. This threshold is a criterion of model evaluation (Sensitivity + Specificity) and gives the highest probability of avoiding false positive and false negative errors (Franklin 2009), and is specific for each species. Thus, we considered a species as present in a grid cell if the suitability value of the regarding cell was equal or higher than the threshold value. Finally, we assessed the range expansion or contraction as the percent of change on species' geographic range. This estimate was obtained by subtracting the number of cells in the future from the number of cells in the present, divided by the number of cells in the present, where number of cells is a proxy of range size (Loyola et al. 2012c).

4.3 Estimates of thermal tolerance

Species and thermal data used were provided by Gutiérrez-Pesquera et al. (2016). Tadpoles between 25 and 38 Gosner stages of development (Gosner 1960), were collected in the state of Bahia, between 13^{o}-15^{o} S of latitude from November-December 2011. The number of individuals collected varied due to availability of samples. The studied species inhabit different habitats in the Atlantic Forest biome, such as ponds, streams, and coastal moist forest (Table S1 in Supporting Information).

The thermal microenvironments were monitored with data loggers (HOBO pendant) placed at the specific tadpole location, and programed to record the local temperature every 15 minutes during 45 to 374 days, depending on the location. Thermal tolerance experiments were developed in laboratory. The individuals were acclimated during 2-3 days at a constant room temperature of 20°C. The critical thermal maximum (CTmax) was determined by the Hutchinson's dynamic method, in which the individuals were exposed to a heating rate of 25°C per minute until it reached the upper limit tolerance, considering the water temperature similar to the body temperature (Tejedo *et al.*, 2012).

4.4 Vulnerability estimates

Following the protocol of Gutiérrez-Pesquera et al. (2016), our vulnerability index represents the mean warming tolerance of each species in the future (WT'), which means how many degrees Celsius the environment "could" heat until the species collapses. The current warming tolerance (WT) was calculated by the difference between CTmax and the higher value of the maximum daily temperature (Tmax) obtained from data loggers' records (Table S1 in Supporting Information).

To calculate the future warming tolerance, we overlaid occurrence data previously obtained with niche modeling, and climate data onto our grid and extracted the annual mean temperature values of each cell comprising the current distributional area of each species, in the current and future times. Third, we calculated the mean projected temperature range through the difference between current and future projections inside each species' range (ΔT). Finally, we considered WT' as the difference between WT and ΔT. Therefore, every cell had a value of WT', and so we were able to calculate a mean future warming tolerance per species (see Table S1 in Supporting Information).

Differences between current and future temperatures were projected onto the grid according to each species' range to evaluate changes on species' climatic niches. Further, we combined maps of future warming tolerance with future predicted temperature for each species to show how vulnerability patterns vary according to rising temperatures. This combination generated a bivariate map that portrays two different phenomena in one map (Dunn 1989). It has potential to reveal relationships between variables more effectively than a side-by-side comparison of the corresponding univariate maps (Leonowicz 2006). By analyzing this combination of maps we will be able to assess geographic areas inside species' range that characterizes conditions of more or less vulnerability for those species.

4.5 Multivariate analysis of mixed data

Multivariate analyses refer to descriptive statistical methods applied to data with more than two variables. Ordination methods is one kind, it can be used to visualize a standard variation among objects explained by their descriptors in an Euclidian space (Gower 1966). In this sense, mixed data are characterized by a mixture of numerical and categorical variables describing a set of objects (Chavent et al. 2014). To develop this analysis we used the package "PCAmixdata" on R software (Chavent et al. 2014). It works by engaging a two steps procedure, using Principal Component analysis (PCA) to handle with numerical variables and Multiple correspondence analysis (MCA) to handle with categorical variables. The PCA is used to explore a data set, for example by finding a pattern on the variation of the data; MCA is used to quantify the relationships among rows and columns. Both are ordination and robust method that preserves the geometric distances among objects in a reduced space as well as possible (see Legendre & Legendre 1998). These methods calculate a series of eigenvalues that represent how much of the data variance is represented in each eigenvector. Eigenvectors are therefore images of the original data and can express the difference among species based on different ecological traits, and can therefore be used to evaluate the influence of these traits on the warming tolerance variation (i.e. Diniz-Filho et al. 2011).

In order to find if there are certain traits that can be attributed to vulnerability to warming climate, and thus facilitate vulnerability predictions in case thermal limits information is not available, we performed the PCA of mixed values analysis. As our variables we selected ecological attributes (qualitative) from the Guide to the amphibians of the Atlantic Forest: diversity and distribution (Haddad et al. 2013), body size measures and distributional data (quantitative) from the literature (see Table S1 in Supporting Information). The quantitative variables were $\log_{10}$ transformed. We separated species into quartiles based on the vulnerability index (future warming tolerance), so we could visualize similarities within and between groups. Thereby, species in the first quartile presented smaller warming tolerance and so would be more vulnerable to climate change than the species in the following quartiles (see Table S1 in Supporting Information). Grouping species by vulnerability index could help identify adaptation strategies or attributes that impair the resilience to climate changes, as migratory ability or reproduction strategy (Pacifici et al. 2015).

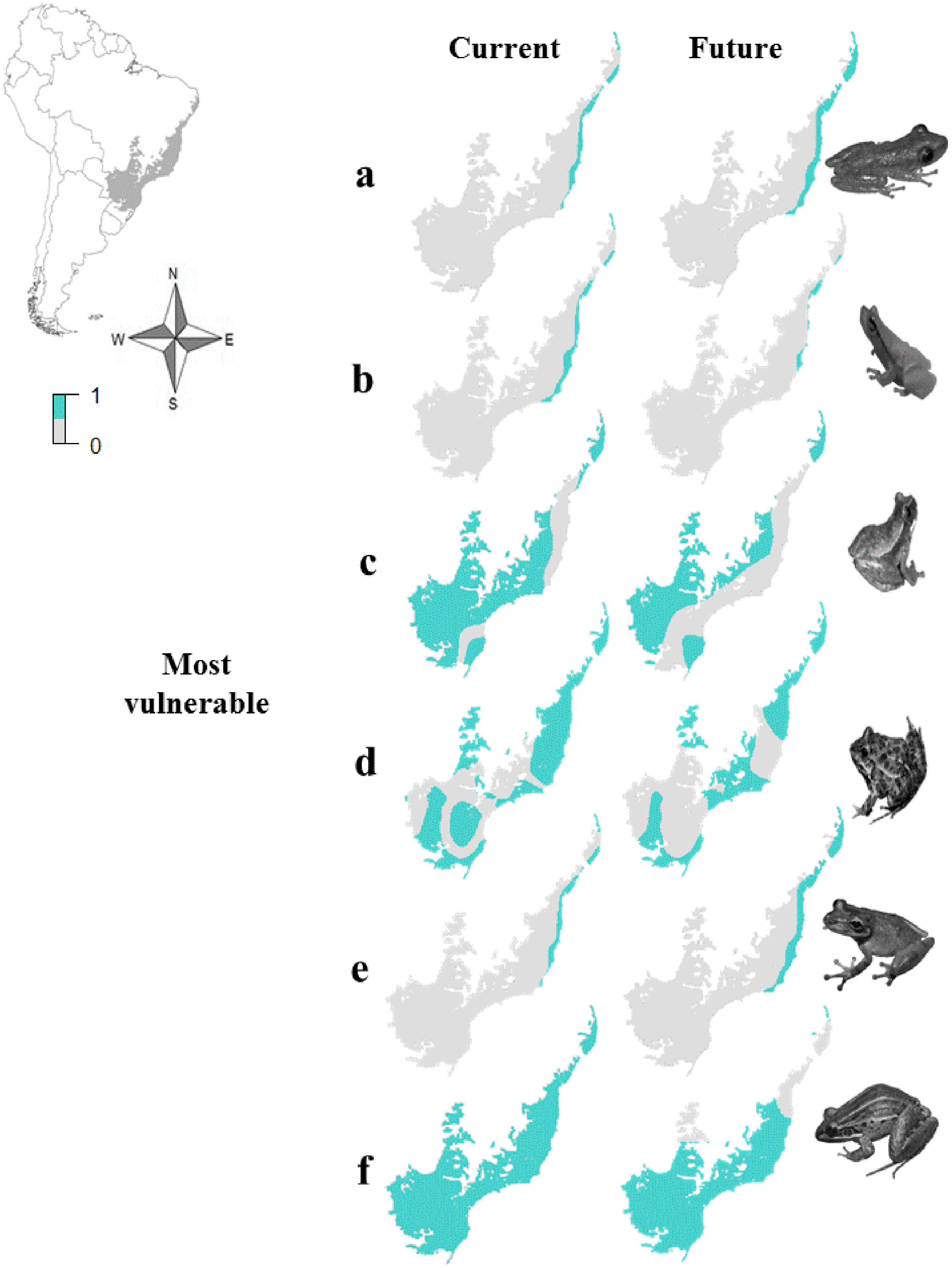
5 RESULTS

The highest TSS values used to choose the best model as well as the threshold of suitability are specified in Table 1 (see Table S2 in Supporting Information). Projections of current and future distributions of species are shown in Figure 1.

Species	**Best model**	**Best AOGCM**	**TSS**	**Sensitivity**	**Specificity**	**Threshold (Sensitivity + Specificity)**
Dendropsophus branneri	ENFA	giss	0.7552	0.2111	0.1778	0.3889
Phyllodytes luteolus	MaxEnt	ccsm	0.8977	0.4	0.4613	0.8613
Scinax agilis	MaxEnt	ccsm	0.9715	0.5	0.4732	0.9732
Scinax eurydice	MaxEnt	ccsm	0.9715	0.5	0.4732	0.9732
Leptodactylus fuscus	ENFA	giss	0.6717	0.2017	0.2175	0.4192
Leptodactylus latrans	GARP	giss	0.9356	0.3026	0.2458	0.5484
Rhinella hoogmoedi	MaxEnt	ccsm	0.9453	0.4125	0.3944	0.8069
Rhinella jimi	MaxEnt	giss	0.8236	0.5	0.4606	0.9606
Ceratophrys aurita	ENFA	miroc	0.6558	0.2125	0.3038	0.5163
Hypsiboas albomarginatus	ENFA	ccsm	0.5636	0.2114	0.2026	0.414
Trachycephalus mesophaeus	ENFA	giss	0.7035	0.1688	0.1481	0.3169
Pipa carvalhoi	GARP	giss	0.933	0.5	0.1274	0.6274
Rhinella crucifer	ENFA	giss	0.7896	0.1553	0.191	0.3463
Dendropsophus elegans	ENFA	miroc	0.5674	0.0969	0.206	0.3029
Dendropsophus haddadi	MaxEnt	ccsm	0.8199	0.5	0.4352	0.9352
Hypsiboas faber	MaxEnt	giss	0.7309	0.3321	0.3579	0.69
Phyllomedusa rohdei	MaxEnt	mri	0.6492	0.475	0.3915	0.8665

Table 1. Species modelling methods chosen by the best TSS values, and the respective model evaluation criterion (threshold).

From the 17 species, on average, eight have lost 21.30% (± 14.46%) of their range while nine have gained 35.56% (± 34.06%) (Figure 2 and Table 2). Both representatives of the genera *Scinax* almost doubled their distributional area (Figure 2 and Table 2), while *Phyllomedusa rhodei*, classified as less vulnerable has lost the larger distributional area among species, approximately 45% of its range (Figure 2 and Table 2). Species geographic distributions overlap mainly in the coastal region, which is consequently, the richest region (Figure 3). Considering our vulnerability index, species classified in the first quartile have WT’ ≤ -1.7°C. The negative sign means that if the maximum temperatures in the tropics increase as projected, it will overtake their physiological limits, thus the environment will be unbearable for their survival, making these the most vulnerable species. Species classified in the third quartile could tolerate an increase of 12°C in the maximum temperature (WT’ ≥ 11.9°C).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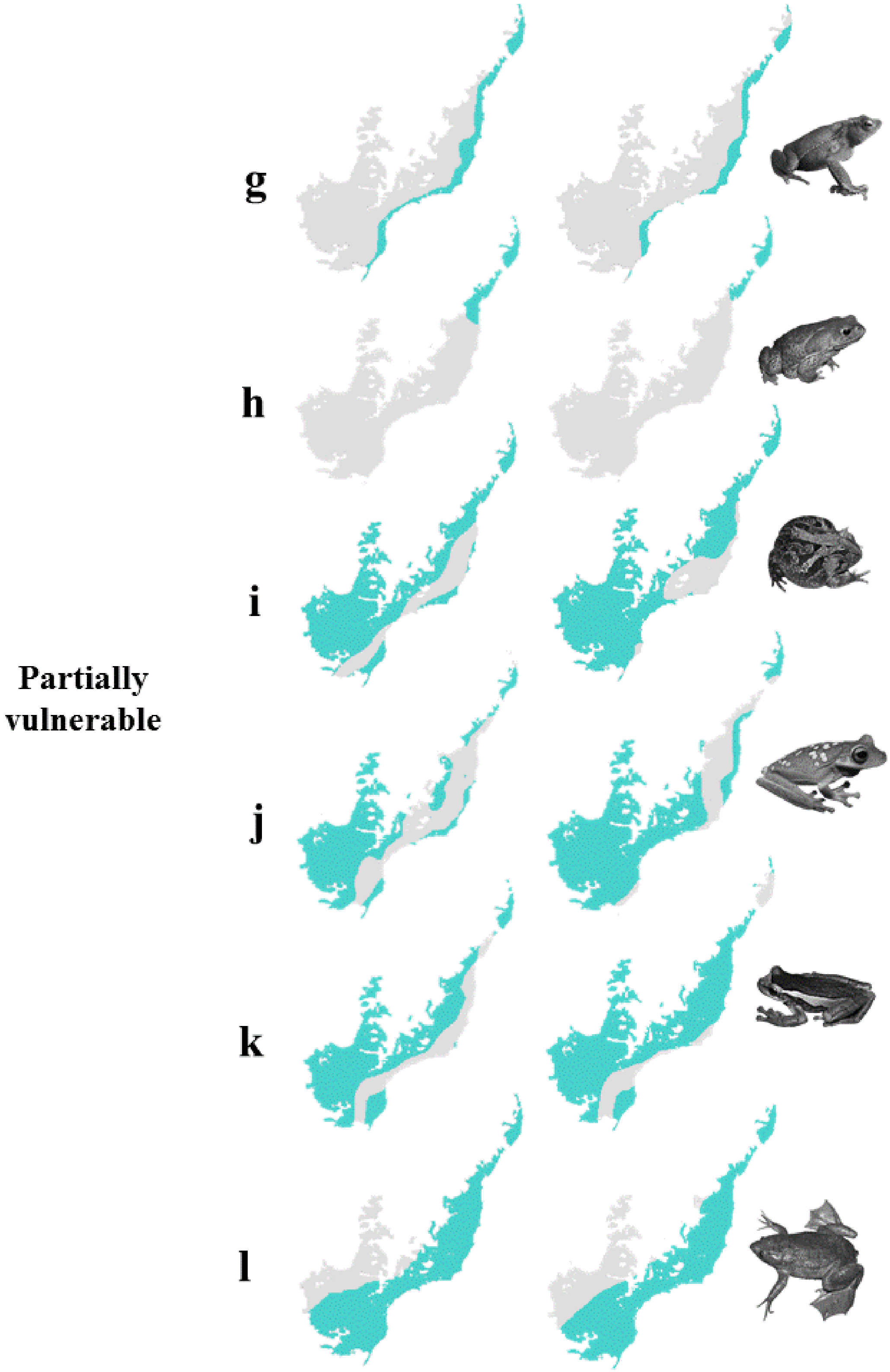
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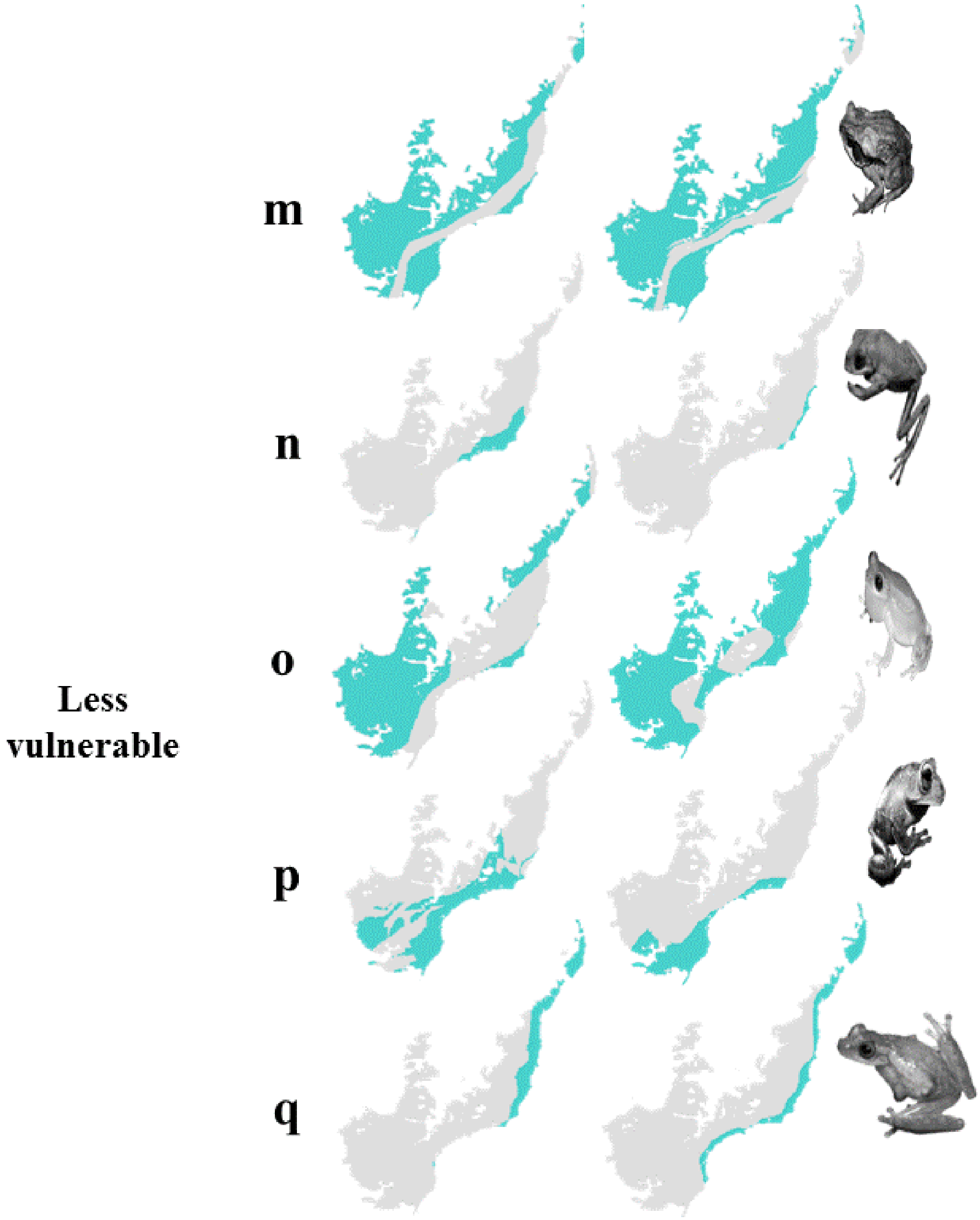

Figure 1. Distribution of species showing the most suitable areas at current and future times according to the maximum criterion of model evaluation. Most vulnerable species (1st quartile): *Scinas agilis* (a), *Phyllodytes luteolus* (b), *Dendropsophus branneri* (c), *Leptodactylus fuscus* (d), *Scinax eurydice* (e), *Leptodactylus latrans* (f); partially vulnerable species (2nd quartile): *Rhinella hoogmoedi* (g), *Rhinella jimi* (h), *Ceratophrys aurita* (i), *Hypsiboas albomarginatus* (j), *Trachycephalus mesophaeus* (k), *Pipa carvalhoi* (l); less vulnerable species (3rd quartile): *Rhinella crucifer* (m), *Phyllomedusa rhodei* (n), *Dendropsophus ellegans* (o), *Hypsiboas faber* (p), *Dendropsophus haddadi* (q).

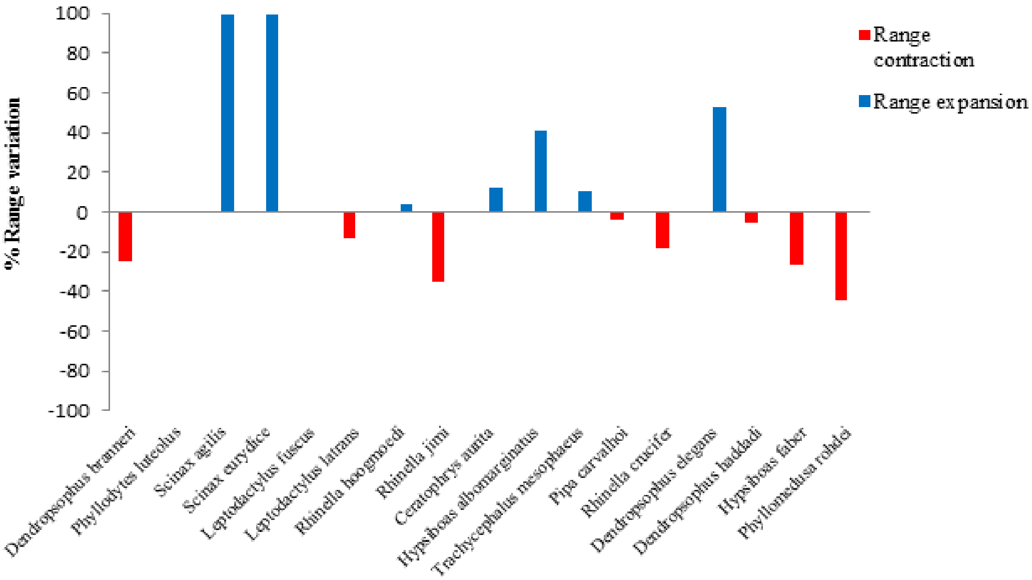

Figure 2. Percentage of range contraction and expansion for each species in the future. The zero mark refers to the current range.

	Species	Current range(km²)	Future range(km²)
Most vulnerable	*Dendropsophus branneri*	102,960	77,583
	Phyllodytes luteolus	7,678	7,700
	Scinax agilis	6,809	13,596
	Scinax eurydice	6,809	13,596
	Leptodactylus fuscus	80,124	80,146
	Leptodactylus latrans	126,038	109,802
Partially vulnerable	*Rhinella hoogmoedi*	22,165	23,023
	Rhinella jimi	10,010	6,479
	Ceratophrys aurita	97,471	109,846
	Hypsiboas albomarginatus	79,079	111,573
	Trachycephalus mesophaeus	96,316	106,260
	Pipa carvalhoi	93,973	90,673
Less vulnerable	*Rhinella crucifer*	99,110	80,960
	Dendropsophus elegans	78,309	119,350
	Dendropsophus haddadi	16,434	15,598
	Hypsiboas faber	37,862	27,940
	Phyllomedusa rohdei	8,503	4,719

Table 2. Species projected geographic ranges for current and future times.

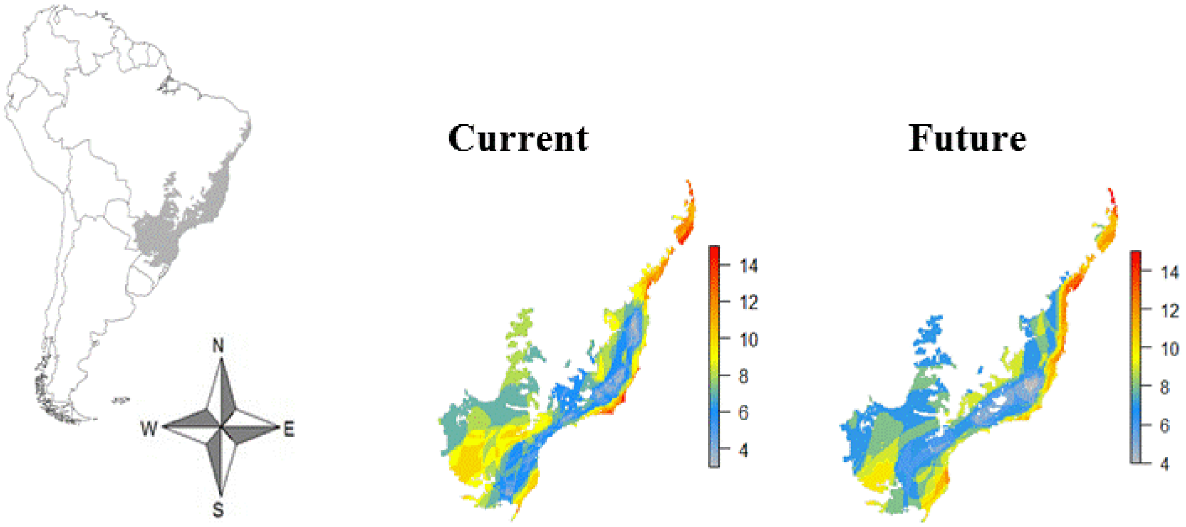

Figure 3. Current and future species richness pattern.

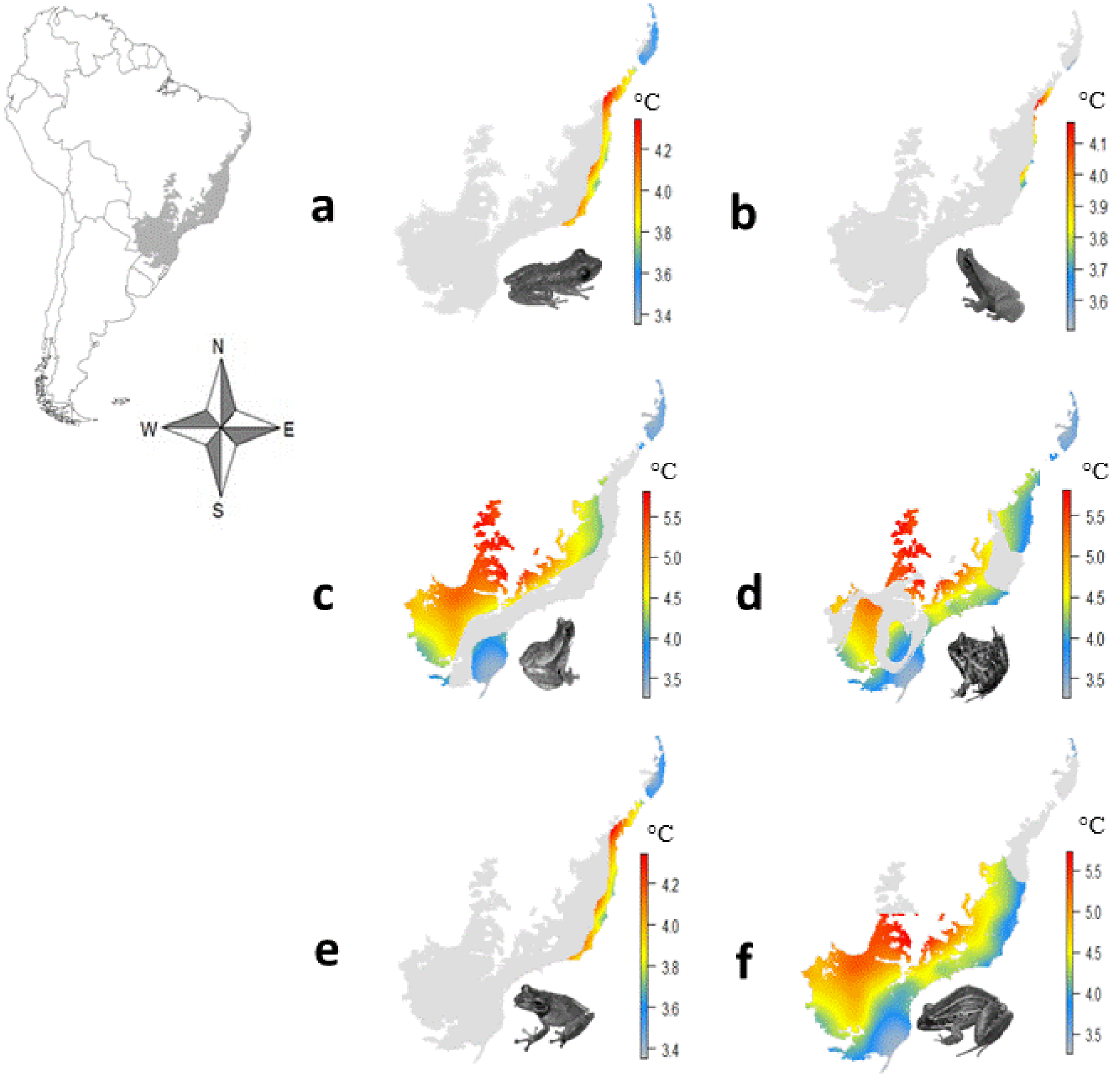

Figure 4. Maps showing the difference between current and future temperature projections (°C) along most vulnerable species’ geographic ranges. Red areas represent higher elevations of future temperature,

while blue areas indicate lower elevations. *Scinas agilis* (a), *Phyllodytes luteolus* (b), *Dendropsophus branneri* (c), *Leptodactylus fuscus* (d*), Scinax eurydice* (e), *Leptodactylus latrans* (f).

Giving attention to the most vulnerable species, we mapped the projected temperature variation (difference between future and current temperatures) within their future ranges (Figure 4 and Fig. S1 in Supporting Information for more species). Projections indicate increase of future temperature across all geographic ranges, going from 3.4°C to 5.5°C of increase. Overall, higher increase will occur on the interior portion of the ranges.

The geographic pattern of vulnerability is represented as bivariate maps (Figure 5 and Fig. S2 in Supporting Information for more species). Areas in orange are a combination of increased temperature and low warming tolerance, characterizing the worst condition for species persistence. Interestingly, yellow areas represent a low vulnerability condition, where species will experience a drastic increase in environmental temperature although it will not become a threat due to species high warming tolerance. In this case, species will be potential persisters if the environmental conditions change following the predictions. As opposed to that, black areas represent high vulnerability meaning that on those areas species will not tolerate temperature elevations. The best scenario is found on the blue area, where species with high warming tolerance will face lower temperature elevations.

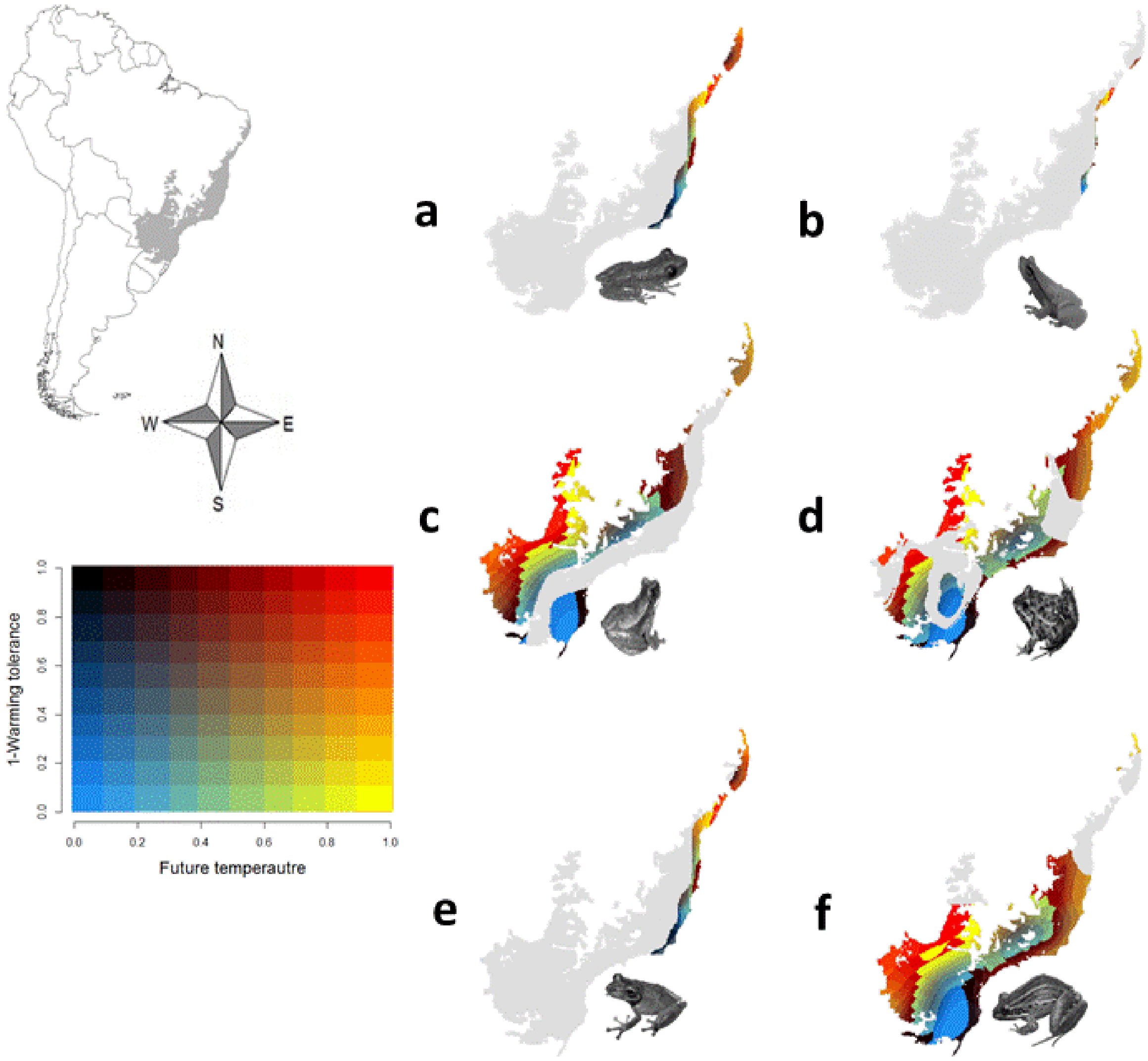

Figure 5. Bivariate maps showing spatial pattern of vulnerability as a function of “future temperature” and “1-warming tolerance” for most vulnerable species (1st quartile) with WT’≤-1.7°C. Noteworthy, as values of “1-warming tolerance” increase, warming tolerance decreases. *Scinas agilis* (a), *Phyllodytes luteolus* (b), *Dendropsophus branneri* (c), *Leptodactylus fuscus* (d), *Scinax eurydice* (e), *Leptodactylus latrans* (f).

Principal component analysis generated 14 eigenvectors. The first principal component accounted for 24.12% of the correlation amongst species whereas the second one reported 17.88% (Figure 6). Observing the individual component map (Figure 6a), there is no distinct pattern of aggregation between species, meaning that vulnerability is not directly related to the ecological and morphological traits used in this study. The second plot (Figure 6b) shows the squared loadings that measure the link between variables and principal components.

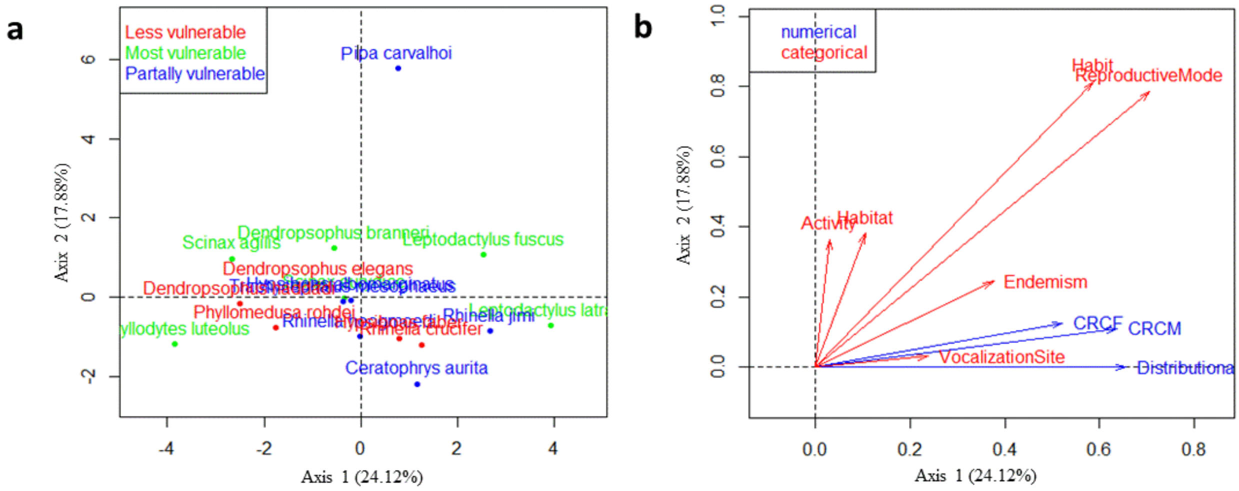

Figure 6. Graphical output of PCA of mixed values. Individual components map with species coordinates colored according to the respective vulnerability pattern (a). Plot of squared loading of all variables (b).

Habit and reproductive mode were the most significant traits, followed by body size. Distributional area was only related to the first axis, thus it does not provide good quality projection of the variables. Vocalization site was the less significant trait. Following the link between both plots, species on the right side of the first axis are, overall, bigger than species on the left side, and species clustered in the center (*Dendropsophus elegans*, *Trachycephalus mesophaeus*, *Scinax eurydice*) share the same reproductive mode (m1) and habitat (arboreal). *Pipa carvalhoi* stands out from the other species because it has a particular habitat (acquatic) and reproductive mode (m15) (see Table S1 in Supporting Information).

6 DISCUSSION

We forecasted expansion and contraction in species’ ranges under future climatic conditions for most of the amphibians studied here. On the one hand, more species would gain distributional area, about 3%, most part being classified as partially or less vulnerable. On the other hand, only two vulnerable species would lose distributional area. Although, proportionally it would be more area than the other groups together, approximately 8%, enhancing the concern with this group. It is unknown how much of a species’ fundamental niche, exclusively determined by the species’ requirements and/or tolerances is represented by its currently realized niche, so this expansion could be determined also by biotic interactions, geographic and historical factors rather than seasonality, and water availability (Walther et al. 2002; Sodhi et al. 2008; Whitton et al. 2012).

Scinax agilis and *S. eurydice* classified as most vulnerable, surprisingly almost doubled their range, while *Phyllomedusa rhodei*, less vulnerable, contracted its range almost in half. In the Atlantic Forest, the family Hylidae shows one of the greatest number of reproductive modes which is positively related to adaptive capacity, and could explain the distributional expansion of some species of this family (Haddad & Prado 2005, Foden et al. 2013). It means that species-specific response to climate change could be largely different (Loyola et al. 2014), and suggests that some species could enhance their spatial representativeness under elevated temperatures but not exceeding their tolerance limits. Mismatches between species classified with the same vulnerability pattern can occur when species differ in ecophysiological responses to temperature change, or when they do not share the same evolutionary history and, for instance, it can be reflected on future distribution projections (Berg et al. 2010). This result contradicts the overall pattern of range contraction predicted for amphibian species of the Atlantic Forest (Kujala et al. 2013; Loyola et al. 2013; Nori et al. 2015, but see Loyola et al. 2014).

Recent biogeographic description of biodiversity and range size patterns of amphibians, found that the Atlantic Forest currently harbors a high number of species with restricted ranges which are poorly represented by the protected area system, especially in the north-eastern portion of the biome (Whitton et al. 2012; Villalobos et al. 2013). Coupling this pattern with our range expansion predictions, the scenario of biodiversity richness and distribution could be brighter in the future. However, it is known that species rich spots that are located near to urban centers which tend to develop even more, thus if amphibian assemblages remain not incorporated into protected areas, the discontinuity between adequate habitats will not permit species migration, hence increasing the list of species threatened with extinction (Becker et al. 2010; Nori et al. 2015).

All species will experience temperature increases across all ranges, especially in the inland portions, which could explain patterns of highest richness on the coast (Villalobos et al. 2013). By adding physiological information to temperature variation we achieve a mechanistic approach of the fundamental niche, which in turn provides a better approximation of the bioclimatic space in which an organism can exist, including areas that have, or may, become newly suitable, besides providing explicit consideration of important biological factors such as evolutionary changes and physiological responses (Kearney & Porter 2009; Pearson et al. 2014; Rougier et al. 2015). We applied the same reasoning to better understand vulnerability patterns. Although it is expected that vulnerability increases with temperature, it varies spatially in terms of different variables as thermal tolerances, water loss, and dispersal abilities (Maggini et al. 2014; Estrada et al. 2015; Lee et al. 2015; Pacifici et al. 2015). Deeming that temperature varies along the range and that it interacts with species' thermal limits assessed here, we observed a range of possible vulnerability conditions on which species would be susceptible to. This result could assist decision makers to focus funding for management actions on those particular areas (Crossman et al. 2012; Summers et al. 2012). Shoo et al. (2011) suggested daring but interesting management ideas, embedding several disciplines, which could minimize the harms that climate change imposes on vulnerable species worldwide, as installation of microclimate and microhabitat refuges and manipulation of hydroperiod or water levels at breeding sites. Moreover, using mechanistic approaches can be advantageous because it is theoretically more defensible than correlative models for predicting species' responses to climate change.

Exposure, as one of the key aspects of vulnerability, can be more easily assessed by distributional data and potential distributions. However, aspects such as biotic interactions, adaptive responses, dispersal abilities and habitat requirements represent the sensitivity and resilience of a system and play a more determinant role on this inquiry (Williams et al. 2008; Foden et al. 2013; Pacifici et al. 2015). Theoretically, for those species whose range decreases or shifts geographically are attributed higher sensitivity than those species that increases geographic range or remains unchanged even facing environmental constrains (Crossman et al. 2012). Aiming to facilitate vulnerability assessments when physiological data is not available, we tested the correlation among functional and ecological traits, potentially related to sensitivity and resilience, with vulnerability. Following the IUCN Red List (2015), the major determinants of both threat and decline risk are range and body size. According to our ordination analysis, range and body size did not play a significant role in determining species' vulnerability. In this case, Bergmann's and Rapport's rule are not supported by our results (Olalla-Tárraga & Rodríguez 2007; Whitton et al. 2012), which means small bodied species with restricted distributions could be equally vulnerable or at risk as large bodied and highly distributed species. As opposed to those traits, habit and reproductive mode were the most significant ones. Another contradictory result compared to Sodhi et al. (2008) study which has demonstrated that life history habit and reproductive cycle terms have a weak relationship with threat risk.

Ectotherms show a relatively rapid and strong thermal adjustment response of life-history traits to climate change, although there is little evidence for changes in the absolute climate tolerance of species, meaning that resilience could be more related to phenotypic plasticity in thermal responses than to genetic adaptation (Berg et al. 2010). Besides being important traits, no relationship with vulnerability patterns was found. Species habitat requirements for reproduction, and foraging are not the only factors determinant of system's susceptibility to adverse effects of climate change (Füssel & Klein 2006; Füssel 2007; Glick et al. 2011). The predictive power of trait analysis might be enhanced by ensuring that relationships between species' attributes and their responses to climate are intrinsically and simultaneously related (Chessman 2013). For example, families negatively associated with climate change generally have more specialized reproductive modes and narrow habitat requirements, which make them more vulnerable to elevation of temperatures and likely prone to range contractions (Haddad & Prado 2005). It was not the case of our selected species, which shared mostly the same and most generalized reproductive mode (m1). Yet, there is a knowledge gap between physiological performance and ecology compounding the record of trustworthy information about species' physiological limits (Huey et al. 2012).

The ability to adapt to range changes in response to shifting climates varies both spatially and between species (Crossman et al. 2012). Our results show that actions to address climate adaptation will need to be spatially appropriate, and that in some regions a complex suite of factors driving climate change vulnerability will need to be addressed. Indeed, conservation is most important in those areas that become more bioclimatically suitable for the most vulnerable species (Araújo et al. 2011). Targeting conservation actions in those areas with predicted range expansion that can be more easily colonized by vulnerable species, and that will less likely present threatening processes, enhance the chances of adaptation and resilience, and so increase their chances of persistence as climate changes (Wilson et al. 2005). Information on threatening processes and the relative vulnerability of areas and natural features to these processes is therefore crucial for effective conservation planning. However, it has to be considered that amphibians are frequently characterized as having limited dispersal ability, strong site fidelity, and spatially disjunct breeding habitat. As such, a conservation strategy based on more realistic approaches like metapopulation theory, effects of fragments and estimation of dispersal distance could be a powerful choice (Smith & Green 2005).

As predicting species response to different climate scenarios is complex, so is the evaluation of different vulnerability status. The study of potential distribution coupled with vulnerability directs attention to such questions as: Who is vulnerable to multiple climate change scenarios? What are the impacts of these changes on vulnerability pattern? Where these changes will heighten the vulnerability status? How are these changes attenuated or avoided? What can be done to reduce vulnerability to these changes? A comprehensive assessment of vulnerability would consider all of these questions and the possible threats affecting the species and the area, including the dynamic responses of interacting factors related to species exposure, sensitivity and resilience to climate changes.

7 CONCLUSIONS

To sum up, our study demonstrate that, inside its geographic distribution, a species will find different climatic conditions that, despite being adequate from the niche point of view, can represent a risk from the physiological one. Thus, a species could be more or less exposed to climatic changes along its range. The linkage between distributional models and mechanistic approaches works as a filter of physiologically adequate areas to species persistence in a long-term. The usage of multiple approaches not only permits one to know whether a species is a thermal specialist of generalist but also predict its vulnerability to future environmental conditions. It is also a good strategy to identify areas in the landscape for targeting specific conservation actions to reduce vulnerability to climate change, because it captures the complex nature of species' multiple responses at a spatial scale. Modelling and mechanistic studies as this can untangle the complex network of projected impacts of climate change on biodiversity, and demonstrate that the integration of other specific aspects is necessary in assessing species vulnerability to climate change.

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9 SUPPORTING INFORMATION

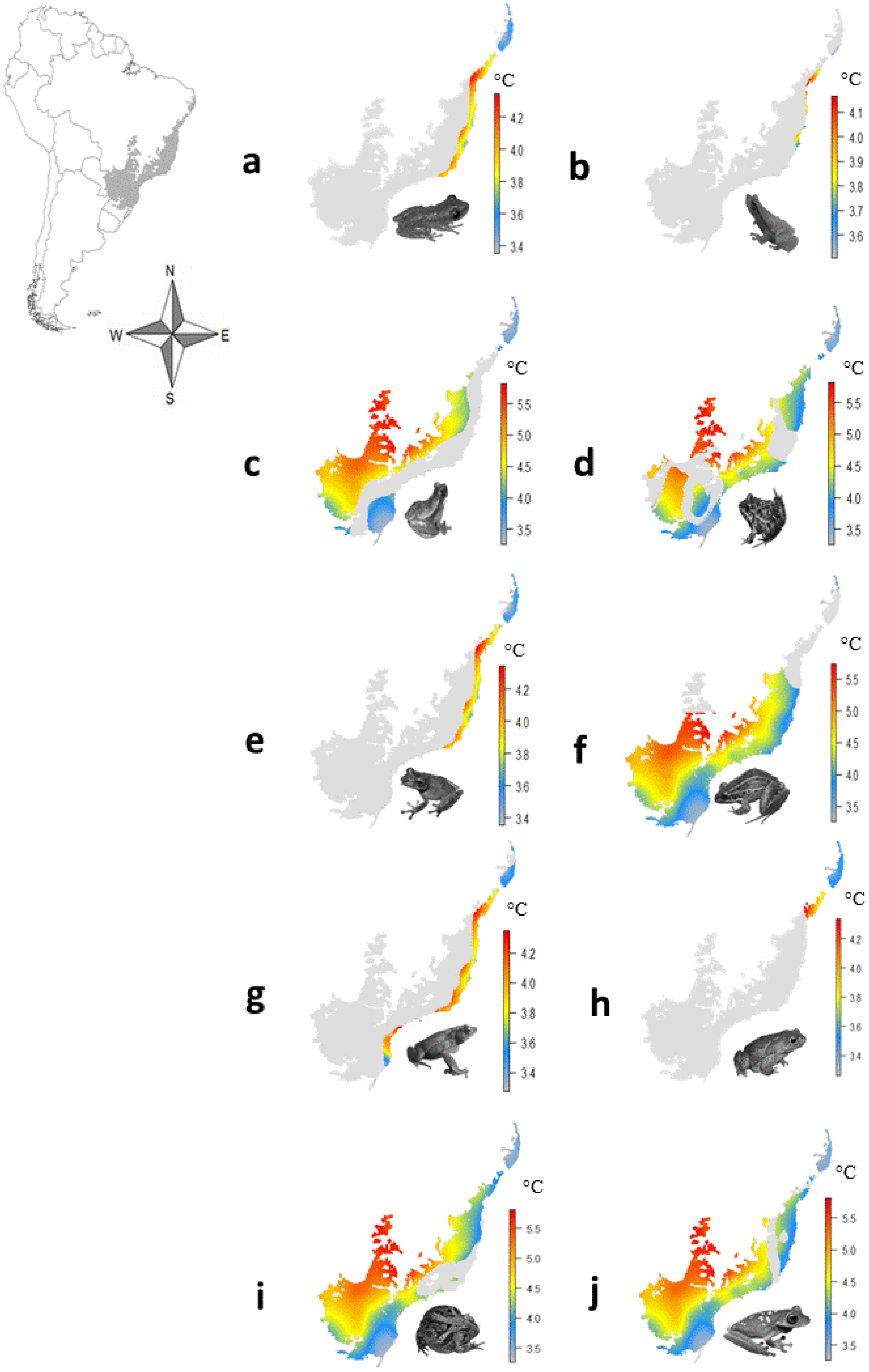
		Traits								Mean annual temperature (°C)			Thermal limits (°C)		
Quartile	**Species**	**Habitat**	**Activity time**	**Reproductive mode***	**Habit**	**Vocalization site**	**Female body size in mm (CRCF)**	**Male body size in mm (CRCM)**	**Distributional area in km²**	**Projected present**	**Projected future (2080-2100)**	**Mean variation**	**Upper critical limit**	**Current warming tolerance**	**Future warming tolerance**
1°	*Dendropsophus branneri*	open	night	m1	arboreal	pond	17.7	23.4	10109.55	22.25	26.16	3.91	41.8	0.46	-3.45
	Phyllodytes luteolus	forested	night	m6	arboreal	bromeliad	29.9	24.4	1212.53	23.07	26.78	3.71	40.9	0.99	-2.72
	Scinax agilis	both	full	m1	arboreal	pond	16	18	185.68	23.23	26.55	3.31	42.5	1.16	-2.15
	Scinax eurydice	open	night	m1	arboreal	pond	48.2	52.5	4031.06	22.2	26.05	3.85	42.4	1.06	-2.79
	Leptodactylus fuscus	open	night	m30	terrestrial	pond	44.2	44.2	106763.36	21.74	25.55	3.81	43.6	2.26	-1.55
	Leptodactylus latrans	both	night	m11	terrestrial	pond	92	96	101900.59	21.73	25.54	3.81	41.7	0.36	-3.45
2°	*Rhinella hoogmoedi*	foreted	night	m1	terrestrial	pond	55.5	41.6	2354.99	22.42	26.11	3.69	39.4	12.23	8.54
	Rhinella jimi	both	night	m1	terrestrial	pond	144.8	133.2	5815.7	22.54	26.42	3.88	42.6	8.01	4.13
	Ceratophrys aurita	forested	night	m1	criptozoic	pond	149	101.1	5653.01	21.03	24.67	3.64	41	6.1	2.46
	Hypsiboas albomarginatus	open	night	m1	arboreal	pond	58.3	51.4	4865.41	21.44	25.25	3.81	41.4	5.86	2.05
	Trachycephalus mesophaeus	forested	full	m1	arboreal	pond	68.5	65.5	7674.81	21.25	25.07	3.83	41	13.83	10
	Pipa carvalhoi	open	full	m15	acquatic	pond	54.5	44.5	4116.53	22.77	26.64	3.86	40.8	12.44	8.58
3°	*Rhinella crucifer*	both	night	m1	terrestrial	pond	96.2	81.6	3337.51	23.04	26.84	3.8	41.8	17.16	13.36
	Dendropsophus elegans	open	night	m1	arboreal	pond	32.4	28.7	5966.62	21.54	25.44	3.9	40.8	16.45	12.55
	Dendropsophus haddadi	both	night	m24	arboreal	pond	22.6	20.9	379.17	23.24	26.68	3.44	39.6	15.25	11.81
	Hypsiboas faber	both	night	m1	arboreal	pond	89.4	87.7	14567.63	21.39	25.17	3.78	41.6	16.96	13.18
	Phyllomedusa rohdei	forested	night	m24	arboreal	pond	44.4	38.4	1406.13	21.03	24.8	3.77	41.1	16.75	12.98

*m1, m6, m11, m15 = acquatic eggs; m24, m30 = terrestrial or arboreal eggs.

Table S1. Species' ecological, morphological, and physiological attributes and projected mean temperatures for the range of each species according to the climate models used. This data was compiled to the vulnerability index, temperature variation measurements, ordination analysis.

	CCSM					GISS					MIROC					MRI				
Species	**BioClim**	**MaxEnt**	**Mahalanobis Distance**	**ENFA**	**GARP**	**BioClim**	**MaxEnt**	**Mahalanobis Distance**	**ENFA**	**GARP**	**BioClim**	**MaxEnt**	**Mahalanobis Distance**	**ENFA**	**GARP**	**BioClim**	**MaxEnt**	**Mahalanobis Distance**	**ENFA**	**GARP**
Dendropsophus branneri	0.5	0.5	0.5	0.5947	0.5	0.5	0.5346	0.5524	0.7552	0.5	0.4466	0.5361	0.5484	0.7256	0.386	0.5	0.6801	0.5158	0.5502	0.5
Phyllodytes luteolus	0.5	0.8977	0.5	0.5004	0.48	0.5	0.5	0.6061	0.5	0.5	0.5	0.4606	0.5812	0.4955	0.4706	0.5	0.8749	0.5	0.5023	0.4879
Scinax agilis	0.5	0.9715	0.5	0.4587	0.4516	0.5	0.5	0.4973	0.4981	0.5	0.4992	0.6475	0.4713	0.5361	0.4065	0.5	0.7464	0.5077	0.5026	0.6441
Scinax eurydice	0.5	0.9715	0.5	0.4587	0.4535	0.5	0.5	0.4973	0.4981	0.5552	0.4992	0.6475	0.4713	0.5361	0.5828	0.5	0.7464	0.5077	0.5026	0.4554
Leptodactylus fuscus	0.5112	0.6025	0.5279	0.5452	0	0.5	0.6198	0.566	0.6717	0	0.4457	0.4823	0.4736	0.5179	0.5	0.4979	0.4049	0.5	0.4396	0
Leptodactylus latrans	0.4958	0.6644	0.494	0.4503	0.535	0.5	0.6024	0.5	0.5423	0.9356	0.4294	0.5017	0.4969	0.5962	0.6504	0.4939	0.5308	0.5	0.548	0.5212
Rhinella hoogmoedi	0.5	0.9453	0.4958	0.5	0.5	0.5	0.5	0.5	0.4935	0.5	0.5	0.6238	0.4805	0.4908	0.496	0.5	0.6933	0.5	0.5	0
Rhinella jimi	0.5	0.618	0.4787	0.401	0.4066	0.5	0.8236	0.6384	0.6034	0.5	0.5	0.6748	0.4587	0.4887	0.376	0.5	0.7372	0.5	0.4982	0.4767
Ceratophrys aurita	0.5	0.6126	0.5	0.5261	0.5061	0.5	0.5	0.5	0.5007	0.5	0.5	0.5014	0.5	0.6558	0.4859	0.5	0.5004	0.5	0.5	0.5
Hypsiboas albomarginatus	0.4962	0.5614	0.5419	0.5636	0.5076	0.5	0.5	0.5	0.5443	0	0.4875	0.4521	0.5	0.5614	0.5	0.5	0.5	0.5	0.4992	0.5
Trachycephalus mesophaeus	0.5	0.5268	0.5	0.522	0.5	0.5248	0.5495	0.558	0.7035	0.5	0.5	0.5	0.5	0.4977	0.5	0.5	0.5741	0.5	0.4999	0.5
Pipa carvalhoi	0.5	0.8189	0.4906	0.2662	0.5	0.5	0.5	0.7132	0.5436	0.933	0.4887	0.5119	0.5695	0.5558	0.5	0.5	0.7522	0.5978	0.5327	0.492
Rhinella crucifer	0.4961	0.46	0.4834	0.4156	0.542	0.5	0.5	0.5	0.7896	0.5	0.5	0.5033	0.4976	0.5206	0.4196	0.5	0.6124	0.5	0.5753	0.5
Dendropsophus elegans	0.5	0.5	0.5	0.5388	0.5	0.5	0.5	0.5012	0.5511	0.5	0.5	0.4911	0.5	0.5674	0.5	0.5	0.5509	0.5279	0.5369	0.5
Dendropsophus haddadi	0.5	0.8199	0.4782	0.3445	0.5	0.5	0.5	0.5	0.4797	0.5	0.4983	0.8013	0.4967	0.5888	0.4969	0.5	0.6867	0.5059	0.5419	0.4987
Hypsiboas faber	0.5	0.5089	0.5178	0.4129	0.5	0.5	0.7309	0.553	0.6968	0.5	0.5	0.4778	0.5	0.447	0	0.5	0.4998	0.5	0.5	0.5
Phyllomedusa rohdei	0.5	0.6324	0.5	0.5459	0.5	0.5	0.5	0.5	0.4999	0.5	0.5	0.5	0.5	0.542	0.497	0.5	0.6492	0.5	0.5017	0.5

Table S2. Values represent the TSS of each combination of modelling method and AOGCM for each species. The values in red are the highest ones among all models possibilities, and represents the chosen ecological niche model.


N
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E
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a
°C
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c
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5.5
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°C
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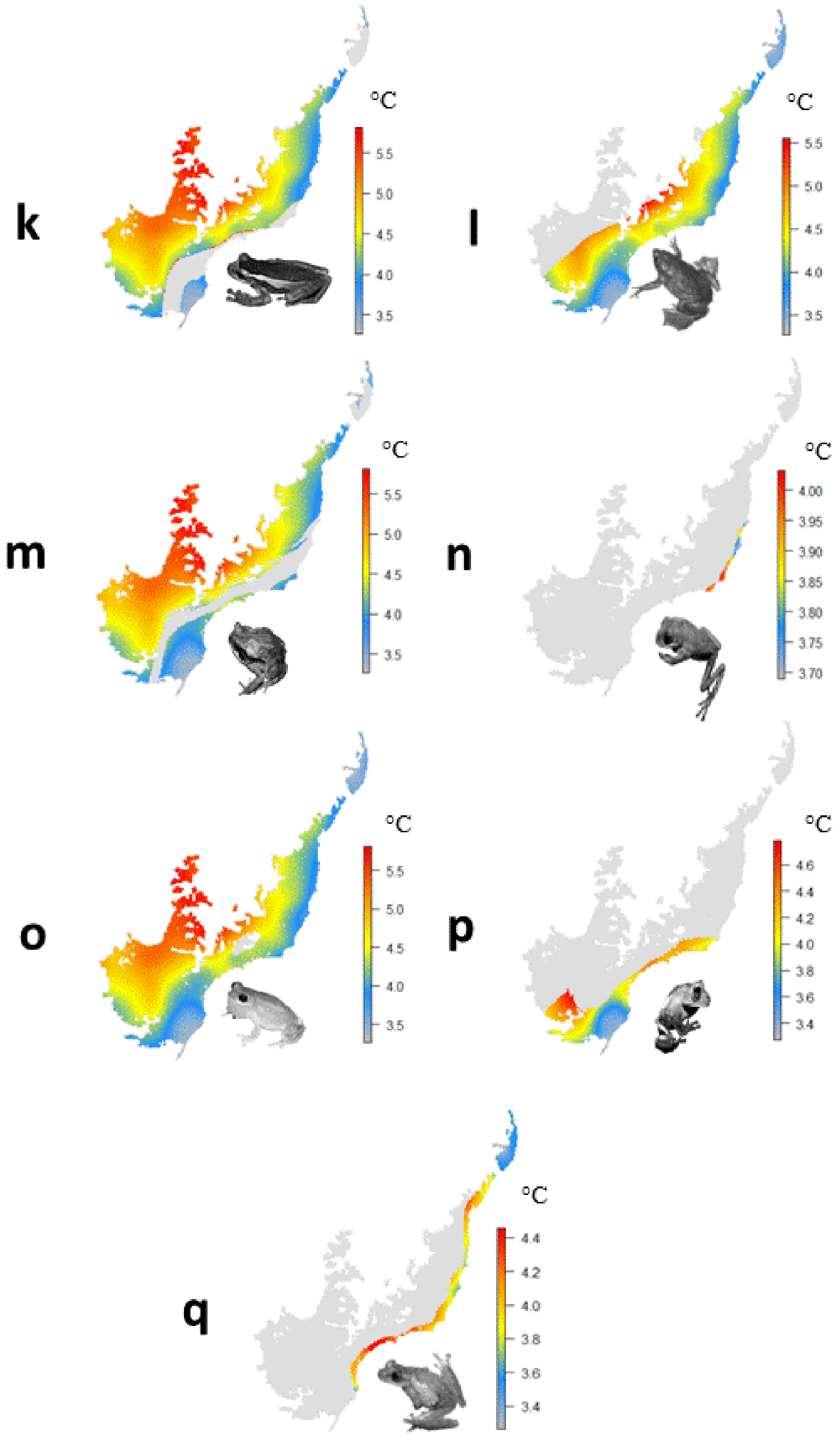
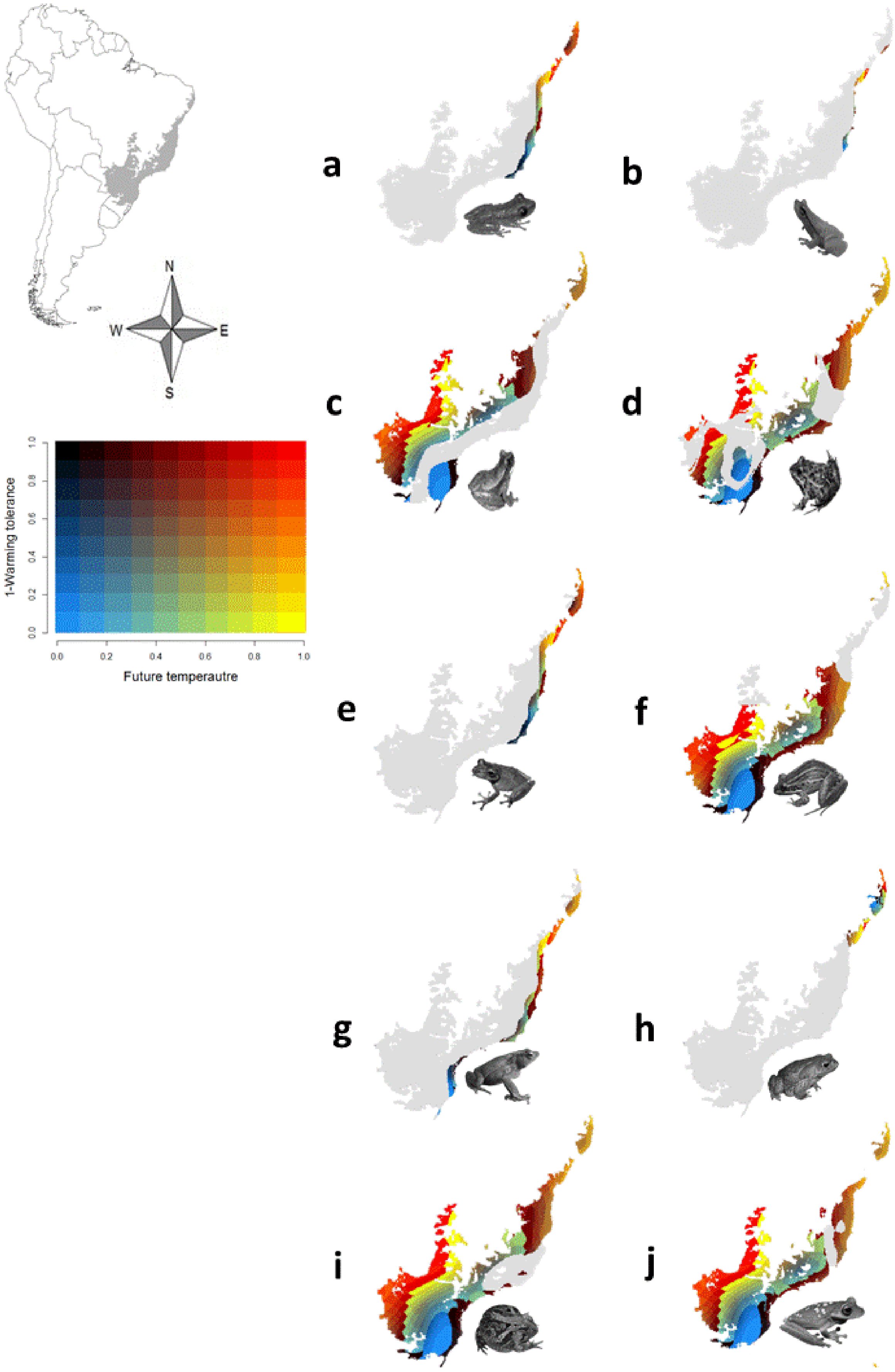


Figure S1. Maps showing the difference of temperature (°C) between current and future projections along most vulnerable species' geographic ranges. Red areas represent higher elevations on future temperature, while blue areas indicate lower elevations. Most vulnerable species (1st quarile): *Scinas agilis* (a), *Phyllodytes luteolus* (b), *Dendropsophus branneri* (c), *Leptodactylus fuscus* (d), *Scinax eurydice* (e), *Leptodactylus latrans* (f); partially vulnerable species (2nd quartile): *Rhinella hoogmoedi* (g), *Rhinella jimi* (h), *Ceratophrys aurita* (i), *Hypsiboas albomarginatus* (j), *Trachycephalus mesophaeus* (k), *Pipa carvalhoi* (l); less vulnerable species (3rd quartile): *Rhinella crucifer* (m), *Phyllomedusa rhodei* (n), *Dendropsophus ellegans* (o), *Hypsiboas faber* (p), *Dendropsophus hadaddi* (q).


N
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1-Warming tolerance
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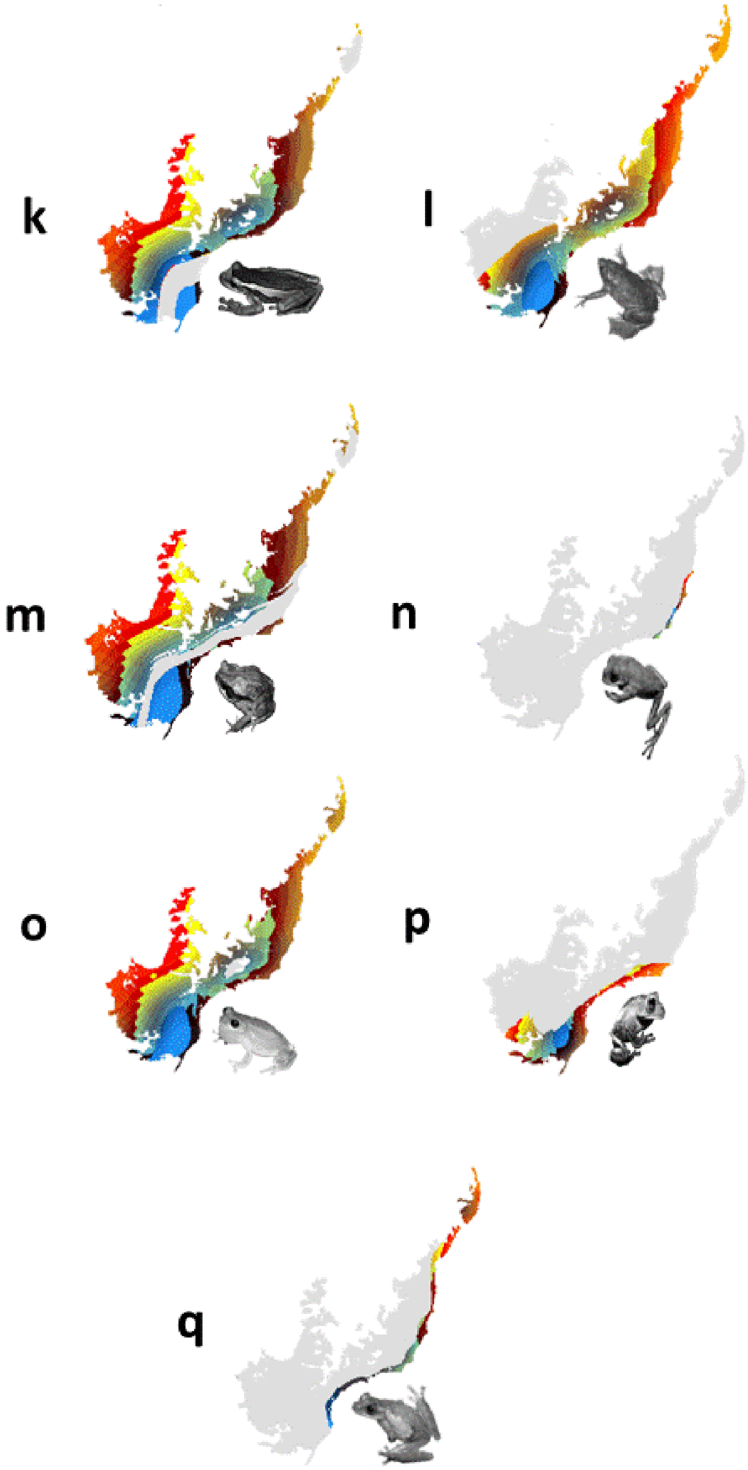

Figure S2. Bivariate maps showing spatial pattern of vulnerability as a function of “future temperature” and “1-warming tolerance” for most vulnerable species (1st quartile) with WT’≤-1.7°C. Noteworthy, as values of “1-warming tolerance” increase, warming tolerance decreases. Most vulnerable species (1st quarile): *Scinas agilis* (a), *Phyllodytes luteolus* (b), *Dendropsophus branneri* (c), *Leptodactylus fuscus* (d), *Scinax eurydice* (e), *Leptodactylus latrans* (f); partially vulnerable species (2nd quartile): *Rhinella hoogmoedi* (g), *Rhinella jimi* (h), *Ceratophrys aurita* (i), *Hypsiboas albomarginatus* (j), *Trachycephalus mesophaeus* (k), *Pipa carvalhoi* (l); less vulnerable species (3rd quartile): *Rhinella crucifer* (m), *Phyllomedusa rhodei* (n), *Dendropsophus ellegans* (o), *Hypsiboas faber* (p), *Dendropsophus hadaddi* (q).