

Climate change will threaten endemic frogs in the Araucaria Forests of South America

Pedro de Oliveira Calixto (✉ pocalixto@gmail.com)

Universidade Federal do Paraná <https://orcid.org/0000-0003-2824-0025>

Fernanda Thiesen Brum

Universidade Federal do Parana

Lucas Batista Crivellari

Universidade Federal do Parana

Mauricio O Moura

Universidade Federal do Parana

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Abstract

Climate change threatens ecosystem dynamics and species with extinction. Endemic species with restricted geographic distribution are especially vulnerable to the impacts of climate change and land use. Using a geographic distribution modeling approach with two future projections in time (years 2050 and 2080), two scenarios (lowest and highest carbon emissions), and land use, we predicted the trends in changing climatic areas for the future geographic distributions of seven species of endemic frogs in the Araucaria Forest of southeastern Brazil. Our results indicate that all species will lose important fractions, from 35–100%, of their current climatically suitable areas over the next 50 years. The impact of land use, on average, was 76% on all climatically suitable areas. Refugia and climatically suitable areas for all species will tend to move south, towards the current southern and easternmost areas of Araucaria Forest. Only a small fraction (3–10%) of the remaining climatically suitable areas will be within conservation units. Thus, climate change will bring severe reduction in area, and the area will move further south, for these seven species of small, dispersal-limited, endemic frogs of the Atlantic Forest. Planning will be necessary to provide refugia in the near future to protect and save these species and their habitats.

Background

Climate change is a major ecological challenge and concern for the 21st century (IPCC 2019). Human population growth and the associated increased demand for energy resulted in greater greenhouse gas production leading to increasing average global temperatures (Cook et al. 2013; Belward et al. 2016). Climate change, both directly and indirectly, can influence population dynamics and patterns of biodiversity at species and ecosystem levels (Parmesan and Yohe 2003; Thomas et al. 2004; Lawler et al. 2009). Geographic distributions and patterns of abundance are changing, with some species moving to higher latitudes at an average rate of 6.1 km decade⁻¹ (Parmesan and Yohe 2003). Phenology is also changing and of 172 species evaluated, life cycles changed in 62% over time, including reproduction in amphibians and birds, migration timing changed in birds and butterflies, and timing of flowering and budding in trees (Parmesan and Yohe 2003).

Increasing loss of habitat may also occur with climate change, and habitat loss is the main cause of global diversity declines (Butchart et al. 2010; Keil et al. 2015). Climate change can influence how the landscape changes over time and consequently how species can track those changes which in turn will influence physiology, migration and reproduction (Becker et al. 2007; Gallant et al. 2007; Power and Jetz 2019; Borges and Loyola 2020). Direct effects are already becoming clear, while synergistic effects are more difficult to understand and predict for species and ecosystems. Changes in the structure of ecological networks and turnover of plant communities have already been reported (Prentice et al. 1992; Penuelas and Boada 2003; Scholze et al. 2006; Woodward et al. 2010; Abella et al. 2019).

Many endemic species also have relatively small geographical distributions and so are naturally more prone to extinction and thus threatened by any changes in their already restricted environments. Typically, they are locally adapted to particular conditions and so have narrower potential niche space than

widespread species (Sandel et al. 2011; Pie et al. 2013; Markle and Kozak 2018). Reactions to climate change are likely to depend on the taxonomic group of interest (Buckley et al. 2012). For example, the Lion Tamarin of the Atlantic Forest in Brazil is likely to have much smaller range of appropriate habitat in the future (Meyers et al., 2013). Similarly, at least 25% of Amazonian amphibian species studied (56 species) are likely to be affected under a hypothetical 3°C increase in temperature and that that interaction will depend on the body size of the species (Gouveia et al. 2014; Von May et al. 2019). Thus, small changes in temperature may have large, profound effects on future survival prospects of amphibians and smaller species are likely to be more vulnerable.

Climate change is likely to have different effects on different amphibian communities and clades as well (Loyola et al. 2014). Overall, basal clades (Gymnophiona, Hemiphractidae, and Pipidae) may be positively affected by climate change, while late divergent clades (e.g. "Ceratophryidae" [Frost, 2019], Craugastoridae, Cycloramphidae, Centrolenidae, Eleutherodactylidae, Hylodidae, Hylidae, Microhylidae, and Strabomantidae) may be negatively affected (Loyola et al. 2014). The increase in temperature in the southern Atlantic Forest is likely to be associated with the loss of some species and clades, in which the most specialized (either in habit or habitat) species are also the most likely to suffer (Loyola et al. 2014).

The Araucaria Forest is within the Atlantic Forest domain and a hotspot for biodiversity (Myers et al. 2000). The Paraná pine (*Araucaria angustifolia* (Bertol.) Kuntze) is the dominant feature of this forest and belongs to an old Gondwanan genus (Forest et al. 2018). During the twentieth century commercial interests led to very rapid deforestation and loss of area of Araucaria forests (Thomé 1995; Koch and Corrêa 2002; Ribeiro et al. 2009). Currently, Araucaria forests occupy a mere 13% of their original area (~250,000 km²) in southern Brazil and adjacent Argentina (Ribeiro et al. 2009). At higher elevations, Araucaria forests can have patches of grassland where endemic diversity is very high (Overbeck et al. 2007; Boldrini 2009; Crivellari et al. 2014). For example, 109 species of frogs are found in Araucaria forests, of which about a quarter (28 species) are endemic (Rossa-Feres et al. 2017). Studies involving climate niche modeling showed that Araucaria Forest will lose large portions of climatically suitable areas over the next 50 years and that coldspots will be concentrated in the south-southeast regions of the current distribution (Wrege et al. 2016; Bergamin et al. 2019; Wilson et al. 2019).

As the Araucaria Forest is impacted by climate change, endemic species will also be affected. However, to what degree climate change will influence climatically suitable areas (size, shape and distribution) and, as a consequence, how those changes will affect each species remains uncertain. Here, using climate modeling, we predict how climate change will influence the geographic distribution of endemic frogs in Araucaria forests by its influence on climatically suitable areas that are also limited by human land use patterns. Specifically, we 1) delineate future climatically suitable areas based on different scenarios of climate change and land use patterns, and 2) predict the local geographic distributions of possible climate refugia, and examine their congruence with the spatial distribution of protected areas. Together, we predict probable future distribution trends for a variety of species, many of which are likely to become endangered or extinct.

Materials And Methods

Frog species and their distributions

Our study system comprises frog species that are endemic to the Araucaria Forest (Rossa-Feres et al. (2017), for which we compiled where they occurred from several sources, including GBIF, SpeciesLink, museum records and literature (Vancine et al. 2017; Supplementary Table S1). Only species encountered in seven or more sites (to avoid model overfitting from small samples) were included: *Melanophryniscus cambarensis* Braun and Braun, 1979, *M. simplex* Caramaschi and Cruz, 2002, *Rhinella henseli* (Lutz, 1934), *Boana leptolineata* (Braun and Braun, 1977), *Pseudis cardosoi* Kwet, 2000, *Sphaenorhynchus surdus* (Cochran, 1953), and *Proceratophrys brauni* Kwet and Faivovich, 2001. These species are in important frog families in the Neotropics (first three Bufonidae, next three Hylidae and the last Odontophrynidae).

Climate, present and future

We began describing current climate using the 19 bioclimatic variables, with 30 second resolution, available from WordClim database (Hijmans et al. 2005), within the region of interest (Fig. 1). With that set of data, we avoided multicollinearity by correlation analysis and separated eight variables with $|r_{\text{Pearson}}| < 0.70$ (Dormann et al. 2007; Brun et al. 2020) for use in our models: mean annual temperature (bio1), mean diurnal range (bio2), max temperature of warmest month (bio5), temperature annual range (bio7), annual precipitation (bio12), precipitation seasonality (bio15), precipitation of warmest quarter and (bio18), precipitation of coldest quarter (bio19). Biologically, these eight variables should be important for ectothermic frogs whose lives are strongly influenced by temperature and rainfall (Buckley and Jetz 2007; Wells 2010).

Building current environmental suitability models

We modeled current environmental suitability areas for frogs using the package *dismo* in R (R Core Team 2013) and using maximum entropy algorithms in the program MaxEnt (Phillips et al. 2006). We used MaxEnt because it is known to perform well when data include only presences, often with few occurrence records, and is conservative when using extrapolation (van Proosdij et al. 2015; Shabani et al. 2016). We selected the adjacent region surrounding the Araucaria Forest as the background for our models simply because dispersal (if it occurred) must pass these other formations (e.g., *cerrado* – Brazilian savanna, pampas, dense rain forest, Fig. 1, Olson et al. 2001).

MaxEnt requires presence data and a background (that may be random background, target-group background, or pseudo-absences), and so we wrote a script to randomly select 10 target-group background points from a list of all points where any one of our study species was found for each of the points in which any species was found. Thus, the number of background points was 10 times the number of observed presences. We then repeated that a total of 100 times, and for each, we used 75% of the data for model training (calibration) and the remaining 25% for model testing (validation). Thus, 100 models

were used, and 100 maps generated, per species. Model accuracy was determined using the threshold-dependent True Skill Statistic (TSS), which can vary from -1 to 1 (similar to correlation coefficients), where 0 is random, -1 is worse than random fit, and 1 is a perfect fit (Loyola et al. 2014). We selected models with averaged TSS scores > 0.7 to be used in subsequent GIS analysis. While criticized in some situations, TSS can evaluate model performance because it is based on sensitivity and specificity, including commission errors. After modeling species distributions (with 100 maps per species), we conservatively mapped the potential distribution using all points (pixels of 30" resolution) on the map that were shared between 80 or more maps.

Future distributions under changing climate and land use patterns

We used two scenarios to model future frog distributions: future projections of 2050 (2041-2060) and 2070 (2061-2080). These scenarios were derived from three atmosphere-ocean global circulation models (AOGCMS): CCSM4, HadGEM2-AO, and MIROC-ESM, using the average of the three models. We used these three AOGC models because climatic information for all projections into the future were available and because they use different approaches and scenarios for climate change (Belda et al. 2015). By averaging these three AOGCMS we generate a conservative forecast of future climate. We used the same bioclimate variables as for the current model, with the scenarios from the averaged AOGCMS). We used two representative concentration pathways (RCPs) to predict future distributions (RCP 2.6 – optimist scenario with low emissions, RCP 8.5 – pessimist scenario with high emissions) because they are two extreme, but realistic, scenarios for the future. We name our predictions as RCP combined with the scenario, and thus RCP 2.6 for year 2050 is 2650, for year 2070 is 2670 (and so on, generating a total of eight future models). We retain 80% of the converging areas of the models in the construction of the binary models for the future scenarios, as in the current model. Also, we calculated the proportional loss of climatically suitable areas for each species and for different scenarios and RCP. In addition, we identify the climatic refugia areas for the future considering the sum of all scenarios (current, 2050 and 2080) and RCPs (2.6 and 8.5). The climatic refugia areas were those with 80% congruence with the predicted areas of all models, by species.

Finally, we refine the predicted species distribution areas using human land use maps overlaying the climatically suitable areas to subtract out the area no longer suitable due to humans. Using the MapBiomas Project 4.1 (<http://mapbiomas.org>) map for the year 2018, we removed areas classified as anthropic for any reason (e.g., agriculture, urban, mining, and related activities) from the natural areas that may be habitat (e.g., forest, grassland, and other non-forest natural formation, river and lake). The resultant maps were more realistic representations of suitable habitats and used these maps with the models as described above, appending the letter b (e.g., current.b, 2650.b).

Protected areas

We map formally protected natural areas that may overlap the climate refugia allowing us to evaluate how protected areas might be important in the future. We calculated the proportion of the refugia that was within a protected area to examine whether the protected areas are effective. Here, we define protected

area to be areas that in Brazil are called integral conservation areas (ISA, 2018) and in which human activities are very limited and, therefore, have well-preserved natural remnants (MMA 2020).

Results

We acquired data for and used in modelling the following (number of records in parentheses): *Melanophryniscus cambarensis* (11), *M. simplex* (7), *Rhinella henselli* (34), *Boana leptolineata* (73), *Pseudis cardosoi* (44), *Sphaenorhynchus surdus* (82), and *Proceratophrys brauni* (25, Supplementary Table S1). The average TSS of our models was ~ 0.97 (SD = 0.02) and so they fit the data very well (Supplementary Table S2). In the 100 replicates for each species, all models predict that climatically suitable habitat will be lost for all species, two of which will lose 100% of their habitat at most threshold values (Supplementary Table S3, S4, and Figures S1-7). Of the two species with the smallest distributions, *Melanophryniscus* spp., one will lose all available habitat due to climate change under all thresholds, and the other will lose all habitat under all but the most optimistic threshold (Figure 2, Supplementary Table S3 and Fig. S2-3).

Models predict that the remaining species will lose between 35% (*B. leptolineata*) to 99% (*S. surdus*) of climatically suitable areas in the future, depending on the scenario and thresholds used (Supplementary Table S3). With a threshold of 0.8 (overlap of 80% with the prediction maps), the loss of climatically suitable area varied from 39 - 94% (Fig. 2; Supplementary Table S4). The species *Rhinella henselli* lost less of its distribution than did the other species, and will lose from 38% - 84% (from optimistic to pessimistic thresholds). At a threshold of 0.8, the species will lost suitable areas that vary from 46 - 77% (Fig. 2, Supplementary Table S4 and Figure S3). *Boana leptolineata* is predicted to lose 35 - 98% of its current range, and at a threshold of 0.8, *B. leptolineata* will lose 39 - 84% of its current range (Fig. 2, Supplementary Table S3, S4, and Figure S4). After *Melanophryniscus* spp., *Pseudis cardosoi* was the most threatened species and will lose from 52 - 98% of its current range. At a threshold of 0.8, the models predict it will lose 66 - 94% of its current range (Fig. 2; Supplementary Table S3, S4, and Figure S5). With all scenarios and RCPs, *S. surdus* will lose 47 - 99% of climatically suitable areas, and with a threshold of 0.8, will lose 58 - 91% (Fig. 2; Supplementary Table S3, S4, and Figure S6). Finally, *P. brauni* will lose 47 - 99% of climatically suitable areas, and at a threshold of 0.8, from optimistic to pessimistic, will lose 59 - 89% (Fig 2; Supplementary Table S3, S4, and Figure S7).

When we improve our predictions with land use we have even more pessimistic scenarios. Thus, the reduction in area will vary from 56 - 95% over all species, thresholds, and models (not including the 100% loss for the two *Melanophryniscus* species, Fig. 2; Supplementary Table S4 and Figure S1-7). *Pseudis cardosoi* at the extreme, will lose from 72 - 95% of climatically suitable area. *Proceratophrys brauni* will lose 73 - 91% of its area, *S. surdus* will lose 71 - 93%, and *B. leptolineata* will lose 57 - 86%. The most optimistic scenario is with *R. henselli*, which will still lose 64 - 82% of appropriate habitat.

Climatically suitable areas in all these models tend to move south (except for *Melanophryniscus* spp.) and will be available mostly in the southernmost extreme of the Araucaria Forest in our area of interest

(Supplementary Figure S3-7). As a consequence, only 3% – 10% of the resulting refugia will be found within Protected Areas, and that will be mostly in smaller pieces (Fig. 3; Table 1). For example, for *P. cardosoi*, only 10% refugia area, 4% for *B. Leptolineata*, *P. brauni*, and *S. surdus* and 3% for *R. henseli* will be included in some protected area (Table 1). Finally, a loss of 11% of all refugia areas after maintaining only the climatically suitable areas plus natural remnants, and the species with the smallest climatic refuge with natural remnants was *R. henseli* (76% in protected areas), while *P. cardosoi* had only a 10% reduction in relation to its refugia area (Fig. 3; Table 1).

Discussion

Seven species of endemic frogs in the threatened Araucaria Forest of the Atlantic Forest formation of Brazil are likely to suffer the potential losses of climatically suitable areas of 35 to 100% due to climate change over the next 50 years. All of our models predict that two species, *Melanophryniscus cambarensis* and *M. simplex*, are very likely to become extinct due to complete loss of the appropriate climate habitat. Our models also show that climate change will cause the Araucaria forest to lose its northernmost and inland areas as its geographic range moves south. Whether climate change will happen faster than species can adapt is a major concern for the future of biodiversity in many regions (Jezkova and Wiens 2016; Diniz-Filho et al. 2019). Species may have two options, either to adapt locally to changing climate (changing niche), or move along with the biome as it follows changing climate. For instance, rates of evolution for niche change are likely to be much slower than rates of climate change (Jezkova and Wiens 2016). Will species persist is a very important question.

Whether there will be sufficient time for species to adapt facing climate change is a major concern about the impact of climate change on biodiversity (Jezkova and Wiens 2016; Diniz-Filho et al. 2019). For instance, from a macroecological and evolutionary approach to different groups (*e.g.*, amphibians, reptiles, birds and plants), evolution rates of for a changing climatic niche would be much lower than evolution rates for future conditions (mean difference > 200,000-fold for temperature variables). Thus, whether species will persist, adapt, or go extinct due to changing conditions is important for conservation (Jezkova and Wiens 2016).

The seven species we examine here comprise large neotropical frog families and the species are very different in their ecologies, including their climate regimes. For instance, in the case of *Melanophryniscus* spp. (family Bufonidae), our projections may underestimate the gravity of their position. These two species are small (2.8 – 3.5 mm in length, Haddad et al. 2013) and size is a major limit for dispersal of any particular distance. Thus, changing climate may quickly create inhospitable conditions between areas that are hospitable, making it impossible for the frogs to disperse to new areas. On the other hand, *Rhinella* (also Bufonidae) is a genus known for adaptability and the variety of habitats in which any particular species may be found (Urban et al. 2008; Mittan and Zamudio 2018), and so *R. henseli* is predicted to suffer less under changing climate. Even so, this species is likely to lose 64 – 82% of its habitat, and if it is unable to either persist and disperse towards the south (Parmesan and Yohe 2003), whether it adapts or goes extinct remains to be seen.

Scenarios are similar for the Hylidae, but their different ecologies suggest that they will be threatened by different factors. Predicted loss of 35 – 99% of their suitable habitat, while species varied, all are likely to lose more than half of their current areas. Climate change, in synergy with other human-caused threats, will act in different ways on different species (Botkin et al. 2007). For example, *B. leptolineata* is found in meadows (“*campos de altitude*”) associated with Araucaria Forest (Conte and Rossa-Feres 2007; Crivellari et al. 2016; Rossa-Feres et al. 2017), and which are highly sought after by agricultural interests for pasture. Livestock, in synergy with climate, will change the landscape and the bodies of water they use for breeding, by some combination of walking in the water, opening up the vegetation, and increased water temperatures that result, and so their persistence is questionable (Hiert and Moura, 2010). The situation is even worse for *P. cardosoi*, which, due to being exclusively aquatic (Haddad et al. 2013), is predicted to be more affected by changing land use in conjunction with climate change.

Finally, associated with and restricted to leaf-litter within forests (Haddad et al. 2013), *P. brauni* is likely to suffer even more than predicted. The extremely fragmented, current extent of the Araucaria Forest is 12% of the original forest (Ribeiro et al. 2009) and 90% of these fragments are small (< 100 ha) and isolated from one another (often separated by more than 5km, Ribeiro et al. 2009). Thus, the future fragmented populations of *P. brauni* are likely to become reproductively isolated, exacerbated by its small size and limited dispersal ability (3.9 mm in length, Haddad et al. 2013). Therefore, these effects will be occurring alongside the effects of climate change that will influence physiology and reproduction, which requires flowing water where their exotrophic tadpoles develop (Prado and Haddad 2005; Haddad et al. 2013; Loyola et al. 2014).

While all predictive studies should be viewed carefully, we feel that the consistency and similarity with other studies, along with the changing environment, our results are likely to encompass the true consequences for these frogs of changing climate in the next 50 years. Also, our results are similar to those found in other studies with different approaches and algorithms to identify climatically suitable areas in the future, including the Araucaria Forest species and for different species of frogs elsewhere in the Atlantic Forest (Warren and Seifert 2011; Loyola et al. 2014; Rezende et al. 2015). Thus, we believe that our findings reinforce the concerns associated with climate change and loss of biodiversity. Our predictions are based on correlative rather than mechanistic models. Mechanistic models use physiological characteristics of the species of interest, such as tolerance limits (temperature, pH, etc.), to attempt to understand species distribution limits (Kearney and Porter 2009; Kearney et al. 2010). While mechanistic models may explain limits to some degree, correlative models simply assume that physiological limits are associated with the climatic limits of the species (Buckley et al. 2010; Pacifici et al. 2015). A combined analysis, using the models we describe here, in concert with predicted land use patterns, geographical analysis of forest fragmentation (to better understand dispersal limitation), and so on, may provide better predictions for the future of these frogs, but those predictions are likely to be even more pessimistic (Soberón 2007; Thuiller et al. 2013; Pacifici et al. 2015). That is so, because in our study, we assumed that current large-scale conditions (land use patterns, climate) will continue in the future, but in fact, growing human populations are likely to reduce available habitat, prevent dispersal due to fragmentation, and so on, and so available habitat will be reduced even more than simply due to climate

change. Thus, we suggest that our results are all optimistic predictions of future consequences of climate change, and indeed, the dire situation we describe underestimates the true likelihood of habitat loss for these seven species of frogs.

Establishment of protected areas is among the best, most effective, strategies for the conservation of biodiversity (Margules and Pressey 2000; Le Saout et al. 2013). But the choice of areas to protect is not simple because resources are limited, socioeconomic and political interests are often at odds, and so using science and biological principles to establish protected areas is often not possible (Margules and Pressey 2000; Brooks et al. 2006; Loucks et al. 2008; Moore et al. 2016). Despite the difficulties, we must begin with sound biological principles and understanding of the nature of the problem for each species, such as in this study, where we better understand climate limitations for these species in a threatened landscape in southern Brazil. We also demonstrate that current protected areas are not congruent with what will be needed to help conserve these species and their habitats within the Araucaria Forest. Indeed, our results suggest that the establishment of protected areas should always be accompanied by the analysis of future climates for those areas to attempt to predict the effectiveness of those areas for conservation.

Conclusion

Here we demonstrate that the geographic distributions of seven species of frogs that are endemic to the Araucaria Forest will be often drastically reduced due to climate change. As a consequence of climate change, the current locations of conservation units in the Araucaria Forest will not be effectively located with respect to future climate for conservation of these species in the future. Predicting future climate, and making appropriate conservation decisions, will require understanding of changing climates and land-use patterns, especially in already threatened areas that are hotspots for endemism, such as the Atlantic Forest of southern Brazil.

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Conflicts of interest/Competing interests

there is no conflicts of interest

Authors' contributions:

POC idealized, analyzed the data and wrote the article; FTB analyzed the data and revised the article; FTB, LBC and MOM revised and gives theoretical contributions the article.

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Table 1

Table 1 Total areas of refuges in integral protected areas and those with natural remnants in the Araucaria Forest.

Species	Useful Area, km ²		
	Climatic refugia	Protected (%)	Climatic refugia + Land use (%)
<i>Rhinella henseli</i>	68,886	1,794 (3)	52,522 (76)
<i>Boana leptolineata</i>	30,324	1,249 (4)	25,472 (84)
<i>Pseudis cardosoi</i>	7,508	740 (10)	6,801 (91)
<i>Sphaenorhynchus surdus</i>	41,585	1,731 (4)	33,774 (81)
<i>Proceratophrys brauni</i>	34,506	1,461 (4)	27,931 (80.9)
All refugies' species	16,062	953 (6)	14,346 (89)

Melanophryniscus cambarensis and *M. simplex* are not within refuges or protected areas.

Figures

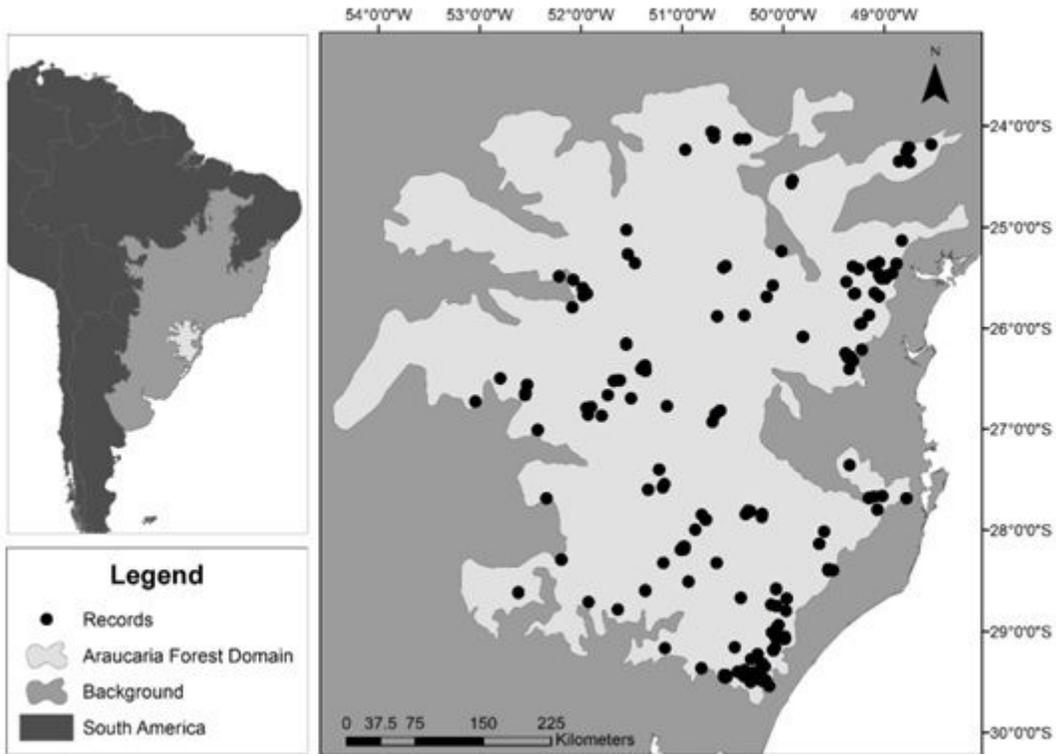


Figure 1

Study area and location records for the seven species of frog in the Araucaria Forest.

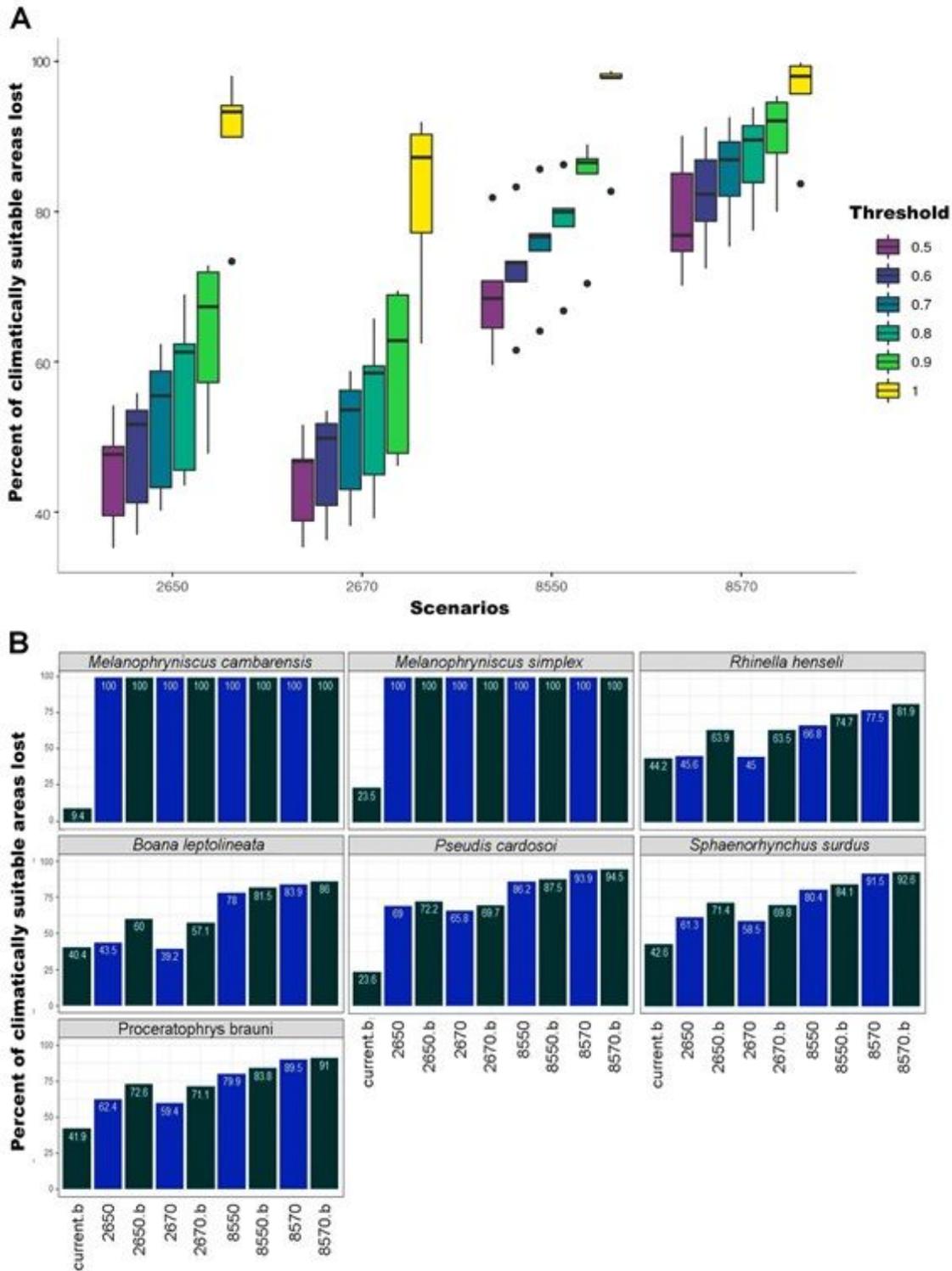


Figure 2

A) Comparisons of climatically suitable areas (%) that are likely to be lost under different scenarios and thresholds for seven endemic frog species in the Araucaria Forest of Brazil. B) Percent loss of climatically suitable using a congruence threshold of 80% of the models, in which black bars indicate the average loss of climatically suitable area as a total, while the blue bars indicate climatically suitable areas subtracting land use patterns.

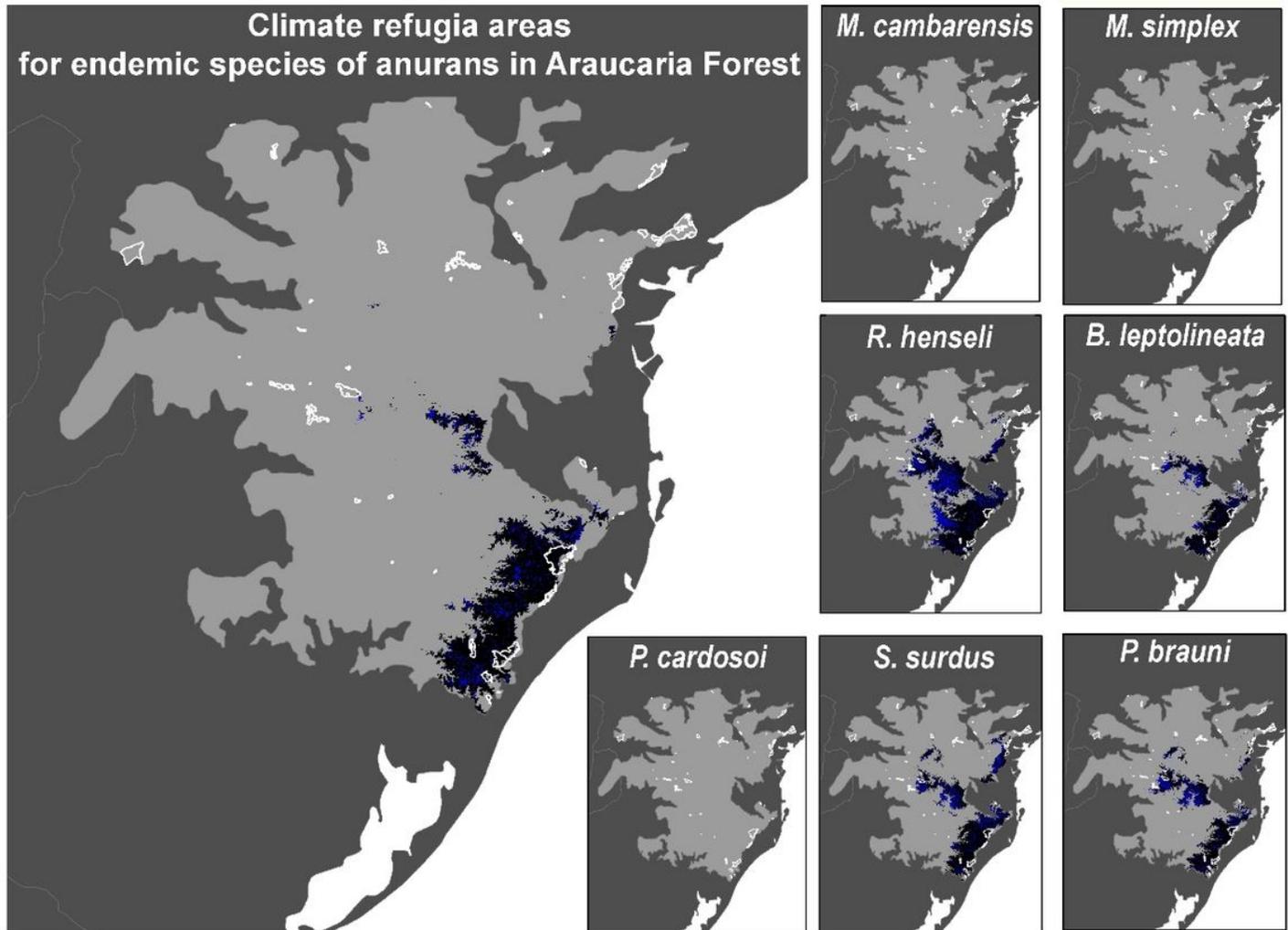


Figure 3

The larger map shows the sum of all climate refugia for seven endemic frog species in the Araucaria Forest with 80% of overlap. Smaller maps are the areas of climatic refugia for each species. Protected areas are outlined in white. Black areas indicate regions with correct climates together with natural remnants; blue areas indicate only climatically suitable areas without natural remnants.

Supplementary Files

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