

UNIVERSIDADE FEDERAL DO PARANÁ

CARLOS DANIEL RIVADENEIRA MONTENEGRO

ECOLOGICAL IMPLICATIONS IN THE SPECIATION OF MONTANE FROGS
WITH SKY ISLANDS DISTRIBUTION

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ECOLOGICAL IMPLICATIONS IN THE SPECIATION OF MONTANE FROGS
WITH SKY ISLANDS DISTRIBUTION

Dissertação apresentada ao Programa de Pós-Graduação em Zoologia do Departamento de Zoologia, Setor de Ciências Biológicas da Universidade Federal do Paraná como requisito parcial para a obtenção do título de Mestre em Zoologia.

Orientador: Prof. Dr. Marcio R. Pie
Co-orientador: Dr. Andreas L. S. Meyer

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RESUMO

As regiões montanhosas são hotspots que abrigam alta biodiversidade e endemismo. Essas regiões são caracterizadas por possuir heterogeneidade topográfica e características climáticas que interagem juntas para criar uma diversidade de spots ecológicos. Muitas espécies de montanhas estão restritas em pequenos parches de condições ambientais, sendo suscetíveis a oscilações climáticas abruptas durante períodos passados e presentes. Neste estudo, avaliamos as flutuações climáticas ao longo do tempo focadas nos ciclos glacial-interglaciais usando modelagem de nicho para avaliar se o clima afeta a especiação e diversificação de sapos microendêmicos do gênero *Brachycephalus* ao longo da serra do Mar, localizada na região sudeste e sul do Brasil na Mata Atlântica. Particularmente, focamos nas espécies do grupo *B. pernix* para prever sua distribuição potencial nos períodos contemporâneo e passado. Utilizamos modelos correlativos baseado na associação de registros de ocorrência e variáveis ambientais de forma a simular condições microclimáticas dessas espécies. Para isso, utilizamos 131 variáveis ambientais e avaliamos a importância dessas variáveis com base em sua classificação de importância para delimitar as faixas de distribuição das espécies. No geral, nossos resultados no período atual mostram faixas restritas nas cadeias de montanhas onde existem habitats adequados para o grupo *B. pernix*. Além disso, o desempenho de nossos modelos usando essa abordagem indica alta precisão. Nossos paleo-modelos destacam o papel central das montanhas como microrefúgios durante as mudanças climáticas no final do Plioceno e Pleitoceno. Esses resultados corroboram a ideia de que os *Brachycephalus* são espécies adaptadas ao frio, mantendo seu nicho semelhante ao ancestral, e que a especiação no grupo ocorreu por meio de processo vicariantes durante as flutuações climáticas ao longo desses sistemas de cadeias montanhosas.

Palavras-chave: microhabitat, Sky islands, conservadorismo de nicho, importância da permutação.

ABSTRACT

Montane regions are hotspots that harbor high biodiversity and endemism. These regions are characterized by having topographic heterogeneity and climatic features that interact together to create a diversity of ecological patches. Many montane species are restricted to small patches of environmental conditions being these species susceptible to abrupt climatic oscillations during past and present periods. In this study, we evaluate the climatic fluctuations over time focus on glacial-interglacial cycles using niche modelling to assess whether the climate affect the speciation and diversification of microendemic frogs of the genus *Brachycephalus* from montane system of the southeastern and southern Brazilian Highlands in Atlantic Forest. Particularly, we focus on the species of *B. pernix* group to predict their potential distribution in contemporary and past periods. We employ a correlative model based on association of occurrence records and environmental variables; to simulate the microclimate of these frogs we obtain 131 environmental variables and evaluate the ranking of these variables based on their importance in delimiting species' range boundaries. Overall, our results in present period show range-contracted in the mountain ranges where there are suitable habitats for *B. pernix* group; besides, the performance of our models using this approach indicate high accuracy. While our paleomodels highlight the central role of the mountains ranges as microrefugia during the climate changes in the late Pliocene and Pleistocene. These results support the idea that *Brachycephalus* are cold-adapted species tracking their ancestral niche and speciated via vicariance during climatic fluctuations in mountain ranges.

Key words: microhabitat, Sky islands, conservatism of niche, permutation importance.

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1. INTRODUCTION

Fluctuations in global climatic conditions have influenced the distribution, migration, and speciation of organisms over space and time (Grinnell, 1917; Parmesan & Yohe, 2003; Parmesan, 2006; Moritz et al., 2008; Hua & Wiens, 2013). In particular, past climates underwent episodes of global warming and cooling (Zachos et al., 2001), which promoted divergence and demographic changes in many taxa (e.g., Carnaval & Moritz, 2008; Hoskin et al., 2011; Lorenzen et al., 2011; Jezkova et al., 2016; Leite et al., 2016; Younger et al., 2018). The climatic oscillations of the Quaternary glacial-interglacial cycles (Hewitt, 2000; Svenning et al., 2015) and the transitions in the climate system during the Plio-Pleistocene (Lisiecki & Raymo, 2007) have caused expansions and contractions of species ranges (e.g., Davis & Shaw, 2001; Silva et al., 2018; Hu et al., 2019). Montane species are particularly susceptible to rapid climatic fluctuations due to their narrow thermal tolerances and elevational distributions restricted (Janzen, 1967; La Sorte & Jetz, 2010; Gifford et al., 2012; Devitt et al., 2013). For instance, during past climatic oscillations in montane regions, warmer periods tend to shift species distributions upwards, producing fragmentation of populations and genetic divergence, whereas colder periods lead to range expansion to downslope, forcing secondary contact; montane regions are thus cradle of speciation and divergence for populations due to these climatic dynamics over time (McCormack et al., 2009; Rahbek et al., 2019a; e.g., Amaral et al., 2018).

In montane regions, the climatic features, topographic heterogeneity, erosion, and historical climatic oscillations interact together to create a diversity of microhabitats where species evolve and diversify (Kerr & Packer, 1997; Körner, 2004; Fjeldså et al., 2012; Chan et al., 2016; Antonelli et al., 2018; Rahbek et al., 2019a; 2019b). Montane species are restricted to a small range of environmental conditions where patches of suitable habitat could be isolated from another, despite of their geographical proximity (Janzen, 1967; Ghalambor et al., 2006; Rahbek et al., 2019a). For instance, slight differences in microclimate or microhabitats might constrain the ranges of high-elevation species (Gifford *et al.*, 2012). Therefore, montane forests are hotspots that harbor high endemism and biodiversity (Myers et al., 2000; Rahbek et al., 2019a; 2019b).

The Brazilian Highlands in Atlantic Forest (AF) are montane regions that comprise of peaks and plateaux, and have a strong influence in shifts in the climate (Safford, 1999a; 1999b; Behling, 2008). For example, the Serra do Mar, an Atlantic

mountain range, runs parallel to the Atlantic coast of Brazil (de Almeida & Carneiro, 1998) and has an influence on its climate because of the obstruction of moist winds from Atlantic all year round, making the southeastern littoral the wettest part of Brazil (Safford, 1999a; Grimm 2003; Behling, 2008). This constant source of precipitation could be responsible for the formation of montane and cloud forests throughout Serra do Mar (Behling, 2008). In the mountaintops, there are grassland formations (*campos de altitude*) in dry environments produced by the interaction of strong winds, cool-humid climate, thin soil layer and high levels of water run-off (Safford, 1999a; 1999b). The fossil pollen data also reveals complex environmental dynamics (from glacial to interglacial) during the last 130,000 kyr shifting the community composition of montane plant species (Behling 1997; Behling & Pillar 2007; Behling et al., 2007; Behling & Safford 2010). Additionally, Serra do Mar has suffered multiple episodes of uplift events during the upper Cretaceous, the Tertiary and the Quaternary (de Almeida & Carneiro, 1998; Cogné et al., 2012; Franco-Magalhaes et al., 2014) revealing to be a topographically complex region (Badgley et al., 2017). Hence, the topographic and dynamic climate could have contributed with the diversification (speciation, extinction and migration) of montane species (Badgley et al., 2010; e.g., Pie et al., 2013; Firkowski et al., 2016; Pulido-Santacruz et al., 2016; Amaral et al., 2018; Pie et al., 2018a) along microrefugia (Rull 2009; Mosblech et al., 2011; Hannah et al., 2014) and microclimates (Alves et al., 2010).

A valuable model system to study the diversification in Brazilian Highlands is the genus *Brachycephalus* Fitzinger 1826 (Amphibia: Anura: Brachycephalidae) where the most of its species have a distribution in sky islands in AF from the states of Bahia in northeastern Brazil to Santa Catarina in southern Brazil (Pie et al., 2013; Ribeiro et al., 2015; Bornschein et al., 2016a; Pie et al., 2018a). These toadlets are characterized by having: cryptic and aposematic coloration patterns (Ribeiro et al., 2015), direct development (Pombal, 1999), and an extreme level of miniaturization (Hanken & Wake, 1993; Yeh, 2002). Overall, *Brachycephalus* inhabits leaf litter on the forest floor (Pombal et al., 1994; Fontoura et al., 2011; Ribeiro et al., 2015), and their small size could determine the microclimate where it can access over smaller spatial scales (e.g., Potter et al., 2013). They are thus exposed to microclimate variables (i.e., air humidity, surface temperature, precipitation, radiation, and wind speed) that circulate on the ground surface through local topography, where the microclimatic variables interact together to maintain temperature and mesic conditions for the organism, and affect in the population density (Hanna et al., 2014; e.g., Oliveira et al., 2013). Besides, the topography (i.e., elevation,

slope and aspect) could have profound consequences in the persistence of species under warming scenarios providing relict climates (Dobrowski, 2011; García et al., 2020). All these factors could explain the high level of microendemism and small geographical ranges of *Brachycephalus* in montane regions (Pie et al., 2013; Ribeiro et al., 2015; Bornschein et al., 2016a).

Brachycephalus has been divided into three phenetic groups: *ephippium*, *didactylus* and *pernix* groups (*sensu* Clemente-Carvalho et al., 2011; Ribeiro et al., 2015), where *Brachycephalus ephippium* and *pernix* groups are montane with few records at lowlands, whereas *B. didactylus* group has a wide elevational distribution from lowlands to highlands (Bornschein et al., 2016a; 2019a). Recent phylogenomic analysis of *Brachycephalus pernix* group show a robust support for its monophyly (Pie et al., 2018; 2019). These species are cold-adapted organisms in Serra do Mar in southern of the state of São Paulo and in Paraná and Santa Catarina states (Pie et al., 2013). Pie et al. (2018a) indicate that the diversification of lineages of *B. pernix* group occurred abruptly in late-Miocene, and during the Pliocene and Pleistocene (Condez et al., 2020). The mechanism of diversification for this group could be a combination of climatic niche conservatism and a climatic shift towards warmer climates, which might have isolated populations on sky islands (Firkowski et al., 2016; Pie et al., 2018a). Climate gradients work as barriers to dispersal (i.e., physiological constraint), limiting dispersion to new environments found in lowlands and thus promoting allopatric divergence (Wiens, 2004; Kozak & Wiens, 2006; Hua & Wiens, 2013; Pyron et al., 2015). Particularly, the past climatic oscillations have a role in species range shifts in Serra do Mar, but with the persistence of certain small pockets as microrefugia that might influence in the speciation of *Brachycephalus* (*sensu* Pie et al., 2018a). Under this scenario, the mountains in periods of climate change during past and present-day might be buffers of suitable habitat; however, the suitable climate could not remain stable in the geographical space over time (Ashcroft, 2010; see Carnaval et al., 2014).

We expect that the complex topography, and past and modern climates have an important role to define geographical areas with suitable environmental conditions where the populations of *Brachycephalus pernix* group can persist and evolve. To address the potential geographic distribution and range boundaries of these taxa over time, we focus on Grinnellian niche (Grinnell, 1917), which includes abiotic conditions in coarse-scale with occurrence data where the organism can persist (Soberón, 2007; Peterson et al., 2011). The ecological distribution models (Ecological niche models, hereafter) with

microclimate dataset are unavailable for *Brachycephalus* where solar radiation, infra-red radiation, air (or water) temperature, surface temperature, wind speed and relative humidity are key for suitable microclimate model (Kearney & Porter, 2009). Nevertheless, Pie et al. (2013) obtained a reasonable estimation of distribution of *Brachycephalus* using a correlative model with coarse-resolution ($\sim 1 \text{ km}^2$). They employed a multivariate approach to discriminate groups of occurrence records based on their climatic similarity, and model-selection procedures to choose model variables based on the size-corrected Akaike Information Criterion. Hence, they modeled climatic suitability with bioclimatic variables associated with occurrence records to find potential habitats for *Brachycephalus*. Paleoclimatic models are also absent to test ancestral climatic tolerances of *Brachycephalus* during dynamic climate.

In this study, we (i) model the environmental niche of species of the *Brachycephalus pernix* group to project their suitable habitat at finer scales with an approach retrieving present-day environmental variables based on topography information, and thus infer more certainty their microclimate, and (ii) project suitable climatic conditions to past time with different global circulation models to infer whether their diversification was associated with potential refugia in the mountain ranges.

2. MATERIALS AND METHODS

The potential distribution of species of the *Brachycephalus pernix* group was visualized at different time periods using ecological niche models across the range of distribution of these species in the states of São Paulo, Paraná and Santa Catarina (Pie et al., 2013; Bornschein et al., 2016a; 2019a). We used a correlative model for the niche modelling (Beerling et al., 1995; Robertson et al., 2003; Elith et al., 2010) based on association of occurrence records and a broad set of candidate environmental variables.

2.2 LOCALITY RECORDS

Building upon previous compilations (Pie et al., 2013, Bornschein et al., 2016a; 2019a), we added all new occurrence records from the literature since their publication, as well as new records based on our field work between November of 2018 and April of 2019 in Serra Dona Francisca, state of Santa Catarina, as well as additional unpublished records (Table 1; Fig. 1). The *Brachycephalus pernix* group contains 19 species: *B.*

acteus, *B. albolineatus*, *B. auroguttatus*, *B. boticario*, *B. brunneus*, *B. coloratus*, *B. curupira*, *B. ferruginus*, *B. fuscolineatus*, *B. izecksohni*, *B. leopardus*, *B. mariaeterezae*, *B. mirissimus*, *B. olivaceus*, *B. pernix*, *B. pombali*, *B. quiririensis*, *B. tridactylus*, and *B. verrucosus*. Many of these species are microendemics with a narrow distribution of suitable habitat (Pie et al., 2013; Ribeiro et al., 2015; Bornschein et al., 2016a), but with some exceptions as *B. acteus* (Monteiro et al., 2018a), *B. brunneus* (Bornschein et al., 2019a) and *B. olivaceus* (Bornschein et al., 2019a) with more of two localities. Due to their microendemism, there is not a sufficiently small grid cell size with environmental data at finer scales from global circulation models to do species-level analyses (Potter et al., 2013). Therefore, our niche modelling was carried out at the species-group level (e.g., Ferrier & Guisan, 2006); all species occurrences of *B. pernix* group were represented as a single species occurrence records *sensu* Pie *et al.* (2013). In total, 50 unique occurrences records were included for 19 species.

2.3 ENVIRONMENTAL VARIABLES COLLECTION

The species of *Brachycephalus pernix* group are montane and leaf litter frogs; therefore, to build a simulation of suitable climate of these species under topographic and environmental predictors, we compiled 131 environmental variables to account for environmental heterogeneity across the range of their distribution (Table S1): Nineteen bioclimatic variables, and a monthly dataset of minimum temperature, maximum temperature, average temperature, precipitation, wind speed, vapor pressure, and solar radiation were included from WorldClim v. 2 database (Fick & Hijmans, 2017; www.worldclim.org/version2). Fifteen macro-environmental variables were extracted from the Consortium for Spatial Information (<http://www.cgiar-csi.org>): Annual actual evapotranspiration, annual aridity index, annual potential evapotranspiration, and Priestley-Taylor alpha coefficient (P-T alpha) (Trabucco & Zomer, 2019). P-T alpha is the ratio of annual actual evapotranspiration over annual potential evapotranspiration (Trabucco & Zomer, 2019). Thirteen metrics of habitat heterogeneity based on the textural features of Enhanced Vegetation Index were derived from EarthEnv (<https://www.earthenv.org/texture>): Coefficient of variation, Evenness, Range, Shannon, Simpson, Standard deviation, Contrast, Correlation, Dissimilarity, Homogeneity, Maximum, Uniformity, and Variance (Tuanmu & Jetz, 2015). Five land cover classes were taken from EarthEnv (<https://www.earthenv.org/landcover>): Evergreen Broadleaf

Tree, Deciduous Broadleaf Trees, Mixed/Other Trees, Shrubs, and Herbaceous Vegetation (Tuanmu & Jetz, 2014). Two layers of soil properties and classes were obtained from SoilGrids v. 0.5.3 (SoilGrids, 2018; <https://soilgrids.org>), and net primary productivity (for the month of November 2016) from NASA Earth Observations (NEO) dataset (<https://neo.sci.gsfc.nasa.gov>). Finally, we obtained four topographic variables of: (1) elevation with a resolution of 3 arc-second (~30 m) SRTM data from Consortium for Spatial Information (CGIAR-CSI) database (Jarvis *et al.*, 2008; <http://srtm.csi.cgiar.org/srtmdata>); (2) roughness and (3) slope from EarthEnv using median value (Amatulli *et al.*, 2018; <https://www.earthenv.org/topography>); and (4) aspect, which was computed using the function *terrain* from our elevation layer with the RASTER package (Hijmans *et al.*, 2019) in R v. 3.6.0 (R Core Team, 2019). All variables were at a spatial resolution of 30 arc-seconds (~1 km²).

To project suitable climatic conditions in different time periods, present-day models were initially developed from the global climate database WorldClim v. 2 (Fick & Hijmans, 2017; www.worldclim.org/version2). We project past climate data from the Late-Holocene (~4.2–0.3 kyr; Fordham *et al.*, 2017), Mid-Holocene (~6 kyr) Early-Holocene (~11.7–8.326 kyr; Fordham *et al.*, 2017), last glacial maximum (LGM; ~20 kyr), the last interglacial (LIG; ~130 kyr; Otto-Bliesner *et al.*, 2006), the mid-Pliocene Warm Period (mPWP; ~3.264–3.025 Myr; Hill, 2015), and the Marine Isotope Stage M2 (M2), a glacial interval in the Late Pliocene (~3.3 Myr; Dolan *et al.*, 2015). The paleoclimate simulations were based on snapshot paleoclimatic simulations using the Hadley Centre Coupled Model Version 3 (HadCM3; Singarayer & Valdes, 2010), and the Community Climate System Model (CCSM; Otto-Bliesner *et al.*, 2006) general circulation model for mPWP and M2, and Late-Holocene, Early-Holocene, LGM and LIG, respectively. LGM was also estimated from Model for Interdisciplinary Research on Climate (MIROC; Sugiyama *et al.*, 2010) and from Climatologies at High-Resolution for the Earth's Land Surface Areas (CHELSA; Karger *et al.*, 2017) dataset. The bioclimatic variables of Late-Holocene, Early-Holocene, LGM (CHELSA), LIG, mPWP and M2 were extracted from PaleoClim (Brown *et al.*, 2018; <http://www.paleoclim.org>), and LGM (CCSM and MIROC) from WorldClim v. 1.4 (Hijmans *et al.*, 2005, www.worldclim.org). Mid-Holocene was predicted using CCSM downloaded from PaleoClim and WorldClim databases. Moreover, we used Oscillayers to reconstruct the historic climates: LGM, LIG, mPWP and M2. Oscillayers are global-scale and region-specific bioclimatic dataset, over Plio-Pleistocene time scales in 10 kyr time periods

(Gamisch 2019). To project paleo-layers of Pliocene, the bioclimatic variables from WorldClim database: Mean Diurnal Range (Mean of monthly (max temp - min temp)) (BIO 2), Isothermality (BIO2/BIO7) (BIO 3), Max Temperature of Warmest Month (BIO 5), Min Temperature of Coldest Month (BIO 6), and Temperature Annual Range (BIO5-BIO6) (BIO 7) were not used in order to have the same variables as in mPWP and M2 (Brown et al., 2018; <http://www.paleoclim.org>). All models were downscaled to the spatial resolution of 2.5 minutes.

2.4 BUILDING AND TUNING ENVIRONMENTAL NICHE MODELLING

To build niche models of the potential distribution of *Brachycephalus pernix* group over time, we employed the maximum entropy algorithm in Maxent v. 3.4.1 (Phillips *et al.*, 2006; Phillips *et al.*, 2017) using ENMEVAL (Muscarella *et al.*, 2014) and DISMO (Hijmans *et al.*, 2017) packages in R v. 3.6.0 (R Core Team, 2019). Maxent works with presence-background data to estimate relative probability distribution indicating the environmental suitability of the species (Phillips *et al.*, 2006; Phillips & Dudík, 2008). We used 10,000 background points randomly within a polygon of presence localities with a buffer of 2 degrees in all directions.

Models were evaluated using the method k-fold cross-validation, which partitions the dataset in training and testing points randomly into bins (k=5) (Peterson *et al.*, 2011; Muscarella *et al.*, 2014). To find the best fitting model, we tuned models with two settings: features classes, which determines the shape of the response curve between occurrence records and environmental variables; and regularization multipliers (rm), reduce the overfitting of the models (Phillips *et al.*, 2006; Merow *et al.*, 2013; Shcheglovitova & Anderson, 2013; Muscarella *et al.*, 2014). We used six combinations of feature classes as follow: (1) Linear; (2) Linear and Quadratic; (3) Hinge; (4) Linear, Quadratic and Hinge; (5) Linear, Quadratic, Hinge and Product; and (6) Linear, Quadratic, Hinge, Product, and Threshold. For regularization multipliers, we tested values between 0.5 to 5 with 0.5 increments.

2.5 MODEL SELECTION AND EVALUATION OF MODEL PERFORMANCE

To select the best-fit models, we used the size-corrected Akaike Information Criterion (AICc; Akaike, 1974). AICc exhibits a superior performance over other

generally applied criteria, such as AUC_{TRAIN} and AUC_{TEST} (Warren & Seifert, 2011). Moreover, $AICc$ is calculated for small samples size (e.g., Ciach & Peęksa, 2018; Freitas et al., 2019) based on Warren & Seifert (2011), i.e. 50 samples in our study [51 samples in Warren & Seifert (2011)]. We generated models from an overall model with 131 environmental variables (overall model, hereafter) and other with only 19 bioclimatic variables (bioclimatic model) plus occurrence records for each one, to compare with which model we will obtain a finer resolution of suitable habitat for microendemic species. In addition, to obtain more accurate of environmental niche boundaries for these microendemic frogs, we inspected the permutation importance of each variable of each full model; this approach of permutation importance has been supported by an empirical study of Searcy and Shaffer (2016). The permutation importance is determined by randomly permuting the values of variables among the training presence and background points, and measuring which model depends on more the variables (Phillips, 2006; Searcy & Shaffer, 2016). We simplified the full models by successively omitting the variables with the lowest permutation importance, and the model selected was the one with the lowest $AICc$ (e.g., Pie et al., 2013; Meyer et al., 2014). All variables with zero values in permutation importance were discarded after the first run; thus, in the second run, the overall model with 131 variables started with 20 variables, and the bioclimatic model with 19 bioclimatic variables started with 11 variables. Additionally, to evaluate the performance of the best-fitting models, we calculated the area under the curve (AUC) of the receiver operating characteristics (ROC) curves, which is the probability that a randomly chosen presence site will be ranked above a randomly chosen background site (Phillips & Dudík, 2008; Merrow et al., 2013). Models with AUC scores > 0.75 are considered informative (Phillips & Dudík, 2008) and scores of > 0.9 indicate high accuracy (Manel et al., 2002). The AUC was based on predicted values for the test localities, averaged over k ($k=5$) iterations (AUC_{TEST}), and we also examined the degree of model overfitting using AUC_{DIFF} (difference between the AUC of training and the testing data) and the 10% training omission rate (OR_{10}). For AUC_{DIFF} , high value of AUC_{DIFF} indicates overfit models (Warren & Seifert, 2011; Muscarella et al., 2014), whereas OR_{10} indicates the value that excludes the 10 percent of the localities having the lowest predicted values (Radosavljevic & Anderson, 2014), omission rates greater than the expectation of 10% typically indicate model overfitting (Muscarella et al., 2014). Moreover, to compare the logistic output among general circulation models from the past, we used Schoener's D (Rödder & Engler, 2011), a measure of niche overlap well suited

to compare resulting predictions in geographic space (Galante et al., 2018). Values of D range from 0 to 1, where 1 indicates complete overlap (identical distribution models) and 0 indicates no overlap (Rödger & Engler, 2011). This analysis was carried out using DISMO package (Hijmans et al., 2017) in R v.3.6.0 (R Core Team, 2019).

The threshold to distinguish suitable and unsuitable areas was the maximum-training-sensitivity-and-specificity logistic. This threshold was chosen because it has a high performance due to accurate estimate between the observed and predicted values (Liu et al., 2005; Cao et al., 2013), and minimize the probability of commission errors that can lead to an inaccurate identification of actual suitable areas (Loiselle et al., 2003; e.g., Pie et al., 2013; Meyer et al., 2014). Besides, we also used the threshold 10th percentile training presence to convert the continuous to binary predictions. This uses the suitability threshold associated with the presence record that occurs at the 10th percentile.

2.6 CORRELATION AMONG VARIABLES

Maxent is a robust predictor of collinearity among variables in model training (Elith et al., 2011; Feng et al., 2019). Nevertheless, to assess the effect of correlation of 131 environmental variables of our full model, we removed collinearity using the VIRTUALSPECIES package (Leroy et al., 2016) in R v. 3.6.0 (R Core Team, 2019). We used Pearson's correlation to select non-correlated variables with a threshold less than $|0.7|$ (Dormann et al., 2013) with 10,000 sample points within our polygon of presence localities (see the building and tuning environmental niche modelling section; Leroy *et al.*, 2016). This method reduced to 28 variables, and we simplified the models examining the permutation importance (see the model selection and evaluation of model performance section). The model without collinearity was called as uncorrelated model.

Overall, we modeled three different models: (1) overall with full variables; (2) bioclimatic with only 19 bioclimatic variables; and (3) uncorrelated removing collinearity.

3. RESULTS

3.1 ECOLOGICAL NICHE MODELLING

Niche models showed that the high environmental suitability predicted for *Brachycephalus pernix* group is distinctly concentrated on the mountain ranges with a scattered distribution throughout Serra do Mar in the states of São Paulo, Paraná and Santa Catarina, Serra Geral (i.e. Morro da Igreja), northeastern foothills of the Serra Geral (i.e. Serra da Boa Vista) and Serra do Tabuleiro in the state of Santa Catarina, and Serra dos Itatins in the southeast coast of the state São Paulo (Fig. 2A-F; Appendix 1). Nevertheless, the logistic probability maps of the uncorrelated model showed more suitable areas in the mountain ranges of the state of Santa Catarina than bioclimatic and overall models (Fig. 2E). For instance, there are suitable habitats with higher suitability values in mountain chains of the coast of Santa Catarina (“Serras Litorâneas”), i.e. Serra do Itajaí, Serra do Tijucas and Serra do Pinheiral, and in the sedimentary plateaus of the Serra Geral in the upper valley from Itajaí, i.e. Serra do Mirador and Serra dos Faxinais (Fig. 2E, F).

The best-fit model of our three models: overall, bioclimatic, and uncorrelated were using eight, six and ten environmental variables, respectively with model-selection procedures, these niche models had the lowest AICc (Table 2). The three models had a high performance with AUC_{TEST} (Table 2), and the overall model was slightly better than other models for indicating no overfitting (AUC_{DIFF}; Table 2); however, the threshold OR₁₀ for three models was slightly above the theoretically expected 10% (Table 2). The overall and bioclimatic models were built with linear and quadratic feature classes, and regularization multipliers of 1.5 (for overall model) and 0.5 (for bioclimatic model); the settings for uncorrelated model were linear, quadratic, hinge and product features with regularization multipliers value of 5.

The niche modelling inspecting the permutation importance identified the most important environmental variables that seem determine the distribution of *Brachycephalus pernix* group for each model in the mountain chains (Table 2; Fig. 2A-F). The net primary productivity and topographic-related variables were present in the overall and uncorrelated models which were inferred with the same dataset (131 variables; see Table S1). Moreover, the most important variables with more than 50% of permutation importance that explain the distribution of *B. pernix* group for each model were P-T alpha (for overall model), Precipitation seasonality (BIO 15), Precipitation of wettest month (BIO 13) and Mean diurnal range (BIO 2) (for bioclimatic model), and Precipitation of warmest quarter (BIO 18), Solar radiation of September and Vapor pressure of January (for uncorrelated model; Table 2).

3.2 PALEOCLIMATE

The potential distributions into past conditions estimated different spatial patterns in highlands and lowlands with high and low suitability values depending on the each paleoclimatic model (Fig. 3A-E). Additionally, the comparisons of projected paleoclimatic distributions using different global circulation models resulted in different predictions (Table 3). For Pleistocene and Holocene scenarios, the best-fit model of the current climate model had the lowest AICc (635.82) with high performance ($AUC_{TEST} = 0.9794$) and without indication of overfitting ($AUC_{DIFF} = 0.00725$; $OR_{10} = 0.14$). The most important environmental variables were the precipitation of wettest month (33.05%; BIO 13), precipitation of coldest quarter (25.38%; BIO 19), precipitation seasonality (23.28%; BIO 15), precipitation of driest quarter (8.51%; BIO 17), mean diurnal range (Mean of monthly (max temp - min temp)) (5.82%; BIO 2), and max temperature of warmest month (3.96%; BIO 5). The logistic probability map showed suitable climate in mountain ranges (Appendix 2A).

During the Pleistocene, the paleomodels predicted slightly stability of suitable climatic conditions with fragmented distribution in the geographical space (Fig 3B, C; LIG: Oscillayers model and LGM: Oscillayers, CCSM and MIROC models). Paleomodels for the Holocene showed suitable environment with higher suitability values in Serra do Juqueriquerê (state of São Paulo; WorldClim: CCSM and MIROC), the islands of São Paulo northern coast (WorldClim: CCSM, PaleoClim: CCSM and MIROC), and in plateaus and lowlands of the states of São Paulo, Paraná and Santa Catarina (Fig. 3A, Appendix 3A, B; WorldClim: CCSM, PaleoClim: CCSM and MIROC). The CCSM projection for Early-Holocene predicted suitable areas onto continental shelf in front of Santa Catarina northern coast (Appendix 3B; see Suguio et al., 2005). For the LGM, Oscillayers, CCSM and MIROC paleomodels showed suitable habitat in the Serras Litorâneas in the state of Santa Catarina, whereas CHELSA projection predicted suitable conditions in Serra das Furnas, São Jerônimo da Serra and Mauá da Serra in the state of Paraná (Fig. 3B). The predictions for LIG was different for each model, Oscillayers projection showed few scattered suitable areas in the Serras Litorâneas in Santa Catarina, whereas CCSM projection predicted suitable conditions in Serra Paranapiacaba in the São Paulo southern (Fig. 3C).

Present-day model projected to Pliocene scenarios had the lowest AICc (661.95), an excellent fit to the data ($AUC_{TEST} = 0.9727$) and no indication of overfitting ($AUC_{DIFF} = 0.00789$; $OR_{10} = 0.14$). The most important environmental variables were precipitation of warmest quarter (permutation importance = 23.34%; BIO 18), precipitation of driest quarter (21.84%; BIO 17), precipitation of wettest month (16.49%; BIO 13), precipitation of coldest quarter (16.27%; BIO 19), precipitation seasonality (12.61%; BIO 15), precipitation of wettest quarter (3.57%; BIO 16), mean temperature of coldest quarter (2.84%; BIO 11), annual precipitation (2.56%; BIO 12), and temperature seasonality (0.48%; BIO 4). The annual mean temperature (BIO 1) variable is part of this present-model, but it had a value of zero for their importance. The climatic model showed suitable habitats concentrate in the mountains (Appendix 2B).

The past climatic conditions in the Pliocene during mPWP (~3.264–3.025 Myr) and M2, a glacial interval in the Late Pliocene (~3.3 Myr), showed a displacement of suitable habitats in the north of mountains of state of Paraná (during M2) toward the south of mountains in state of Santa Catarina (during mPWP) (Fig. 3D, E). For the mPWP (~3.264–3.025 Myr), Oscillayers projection predicted suitable climatic conditions in the state of Santa Catarina northern coast (i.e., Serra da Tiririca), São Paulo southern coast and Paraná coast, and in Serra do Mar in the region northeastern of São Paulo (Fig. 3D), whereas HadCM3 projection showed a fragmented distribution of suitable areas with higher suitability values in mountain ranges of the state of Santa Catarina such as Serra do Mar, Serra Geral, Serras Litorâneas, Serra do Tabuleiro and sedimentary plateaus of the Serra Geral, slightly similar to the current climate (Figs. 2, 3D). Besides, this paleomodel also predicted suitability areas in Serra do Mar in the Ribeira valley in state of Paraná. The M2, a glacial interval in the Late Pliocene (~3.3 Myr) for HadCM3 and Oscillayers model projections, indicated an expansion of suitable climatic conditions onto the emerged continental shelf, particularly facing the São Paulo subtropical gap (Fig. 3E). HadCM3 projection predicted fragmentation of few suitable habitats in Serra do Mar of state of Paraná and Serra Paranapiacaba in the states of Paraná and southern São Paulo, whereas Oscillayers projection showed suitable areas in the state of Santa Catarina northern coast (Fig. 3E).

4. DISCUSSION

Our niche projections highlight the central role of the mountain ranges as suitable habitats or microrefugia for species of *Brachycephalus pernix* group during climatic oscillations. The present-day niche modelling showed that mountain ranges are climatically suitable for these species supporting a Sky Island distribution (Pie et al., 2018a), and cold adaptation (Pie et al., 2013). Hence, the range-contracted of these cold-adapted species in mountains is constrained by contemporary environmental (interglacial conditions) (Carnaval et al., 2014). Additionally, our model-selection procedures with a broad set of environmental variables including bioclimatic variables can build suitable habitats more accurate for modelling microendemic species. Moreover, our results of the paleomodels indicated climatic fluctuations during Pliocene through mountain chains, which supports that mountains ranges were microrefugia for populations of *Brachycephalus pernix* group (Pie et al., 2018a). While in the Pleistocene (LGM and LIG), our paleomodels indicate vaguely stability of suitable fragmented habitats in the Serras Litorâneas (Santa Catarina). However, the different global circulation models for the paleoclimate show uncertainty of the spatial distribution of suitability habitats. In the sections that follow, we address these results and implications of modelling microendemic species.

4.1 ECOLOGICAL IMPLICATIONS

Our modelling approach with both bioclimatic and a broad set of environmental variables suggest that suitable habitats for species of *Brachycephalus pernix* group could be found within the mountain ranges such as Serra do Mar, Serra Geral and Serras Litorâneas, but the extent of the output of presence-absence map for bioclimatic model overpredict the realized niche for these species. The niche models: overall and uncorrelated, included characteristics or attributes that represent environmental heterogeneity and affect strongly species distributions, such as topography, precipitation, solar radiation, land cover class, and monthly and macro environmental variables (e.g., Buckley & Jetz, 2007; Werner et al., 2007; Reino et al., 2017). These attributes can be considered more realistic to predict suitable habitats than models predicted using only bioclimatic variables (e.g., Raxworthy et al., 2007; Markovic et al., 2012; Pérez & Font, 2012; Cao et al., 2013; Hammond et al., 2016), models based on a single type of variables

might lead under or over fitting of the model (e.g., Pineda & Lobo, 2009; Vasconcelos et al., 2012). Thus, our models with a broad set of environmental variables could simulate microhabitats for microendemic species within topographically complex area predicting their distribution range without overfitting. In comparison with mechanistic models (more details see Kearner & Potter, 2009), studies show the performance between mechanistic and correlative models is similar to predict contemporary ranges (Buckley et al., 2010; Lyons & Kozak, 2019). Moreover, Pie et al. (2013) used model-selection procedures with only bioclimatic variables, the extent of suitable habitats to the south was restricted to Serras Litorâneas in the state of Santa Catarina. However, our approach with many predictors shows the extent of suitable areas to the south has scattered distribution throughout the mountains and foothills in the state of Santa Catarina. The species of *B. pernix* group reported further south are *B. boticario* and *B. fuscolineatus* in Morro do Cachorro and Morro do Baú, respectively from state of Santa Catarina (Ribeiro *et al.*, 2015; Pie et al., 2018b). Therefore, our study uncover new and more suitability areas to *B. pernix* group.

The variable ranking importance based on permutation provides insights about the best environmental variables that could be related with the potential distribution of species of *Brachycephalus pernix* group (e.g., Petitpierre et al., 2016; Searcy & Shaffer, 2016; Zhang & Vincent, 2017). According to this ranking, the variables related to water-soil balance availability in the vegetation and biomass seem to influence the climate niche model of *B. pernix* group, such as P-T alpha, and precipitation. P-T alpha together with precipitation might maintain mesic conditions for these leaf litter frogs (Fontoura et al., 2011), where too much water can disrupt the oxygen diffusion leading to death or stunted development (Ryan et al., 2015). The rate of losing water is higher in smaller amphibians than larger amphibians (Warburg, 1965; e.g., Rowley et al., 2015), thus water-soil balance is important to performance of these leaf litter frogs. Moreover, the topographic variables (i.e. elevation, aspect, slope and roughness) could have an incidence in the solar radiation received at different times of the years due to mountain regions are exposed to a high amount of solar radiation (Amatulli et al., 2018), influencing in the air temperature, humidity, and soil moisture (Desta et al., 2004). The topographic variables create microclimates in patches that shelter isolated populations of species (Hanna et al., 2014). Therefore, *Brachycephalus* depends on topographic complexity and soil-water balance to inhabit microhabitats with suitable conditions.

4.2 PALEOCLIMATE

Our paleomodeling results support to mountains as likely buffers against climate change (glacial-interglacial cycles) providing suitable habitats and speciation via vicariance (Rull, 2009; Carnaval et al., 2014; Condez et al., 2020; e.g., He et al., 2019; Hu et al., 2019). This pattern matches with the climatic variability through the Pleistocene (the last 250 kyr) has influenced the southern AF in creating microrefugia in highlands (Carnaval et al., 2014) similar to our late Pleistocene predictions. Our results emphasize the relationship between mountain and microrefugia in probably preserving species from extinctions during interglacial cycles, and thus affecting the current diversity of the species of *B. pernix* group (Stewart et al., 2010; Pellissier et al., 2014).

The suitable fragmented habitats distributed in mountain ranges during late Pliocene (HadCM3 models) are similar to contemporary distribution of *Brachycephalus pernix* group (Fig. 2; Fig. 3D, E). During late Pliocene, cold (M2) and warm (mPWP) periods, reduced precipitation (Santos et al., 2007; Dolan et al., 2015; Hill, 2015), and wet/dry climatic cycles were predominant in southern AF (Safford, 1999a), although during late Pliocene might have been a gradual increase of humidity (Lara & Patton, 2000). Hence, suitable habitats could have persisted in small pockets with humidity and orographic rain within mountains (Ab'Saber, 1977; 1979). Our past predictions during late Pliocene coincide with one of the rapid diversifications of these species occurred during Pliocene and Pleistocene (Pie et al., 2018a; Condez et al., 2020). Nevertheless, the divergence of *Brachycephalus* dated from Miocene (Pie et al., 2018a; Condez et al., 2020) in which warm and humid conditions predominated (Lara & Patton, 2000).

The variation between different global circulation models was pronounced for the past producing uncertainty in modeling the climate, some global circulation models predicted similar distribution of suitable habitats for LGM (Oscillayers, CCSM and MIROC), and for Mid-Holocene (WorldClim: CCSM, PaleoClim: CCSM and MIROC), while others predicted dissimilar distribution of suitable habitats for LIG (CCSM vs. Oscillayers), mPWP and M2 (HadCM3 vs. Oscillayers). These discordant predictions could be due to each model was derived from different mechanisms or climatic conditions for its simulation (Weber et al., 2007; Fordham et al., 2011). To contrast these caveats, could be employed a multi global circulation model ensemble to create predictions with optimal performance (Fordham et al., 2011; e.g., Lyons & Kozak, 2019). However, the

most of our past models have realistic predictions that coincide with the current distribution of *Brachycephalus pernix* group.

5. CONCLUSIONS

In this paper, we demonstrate how an approach based on model-selection procedures with a broad set of environmental variables may simulate a distribution with accuracy for microendemic frogs in mountain ranges (Sky islands). Mainly, we demonstrate that mountains maintain suitable habitats in response to warming climates (contemporary climate) acting as microrefugia. Thus, our approach can be relevant to many others microendemic species such as birds of the genus *Scytalopus* (Pulido-Santacruz et al., 2016). However, our analyses should be interpreted with caution because they are estimates of suitability habitat, we considered many environmental variables to simulate potential new habitats that harboring suitable conditions for *Brachycephalus pernix* group. Additionally, our paleomodels highlight an important role of the mountains as microrefugia during glacial-interglacial cycles preserving species from extinctions. Particularly, in the late Pliocene the mountains were buffers against abrupt climate changes during climatic fluctuations. Thus, species of *B. pernix* group could have tracked their ancestral niche and speciated via vicariance. We indicate that use of different global circulation models could have caveats to predict to past conditions, thus use a multi global global circulation model ensemble. Finally, we suggest two analyses: (i) examine the distribution of *B. pernix* group to predict the responses to climate change in the future whether the mountains act as microrefugia, and (ii) evaluate in a microevolutionary level the genetic diversity with phylogeographic approach within these Sky islands.

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TABLES:

Table 1. Localities of records of species of *Brachycephalus pernix* group. The numbers correspond to records shown in the Fig. 1.

No.	Species	Locality	Latitude	Longitude	Elevation (m)	Source
1	<i>B. acteus</i>	Braço do Norte, municipality of Itapoá, Santa Catarina	-26.1247	-48.73	240	Monteiro et al., 2018a
2	<i>B. acteus</i>	Centro de Estudos e Pesquisas Ambientais da Univille (CEPA), Vila da Glória, Distrito do Saí, municipality of São Francisco do Sul, Santa Catarina	-26.2275	-48.6919	120	Monteiro et al., 2018a
3	<i>B. acteus</i>	Estrada do Saí, Distrito do Saí, municipality of São Francisco do Sul, Santa Catarina	-26.2017	-48.6936	100	Monteiro et al., 2018a
4	<i>B. acteus</i>	Fazenda Morro Grande, Morro Grande, Ilha de São Francisco, municipality of São Francisco do Sul, Santa Catarina	-26.2964	-48.6194	60	Monteiro et al., 2018a
5	<i>B. acteus</i>	Fazenda Palmito Juriti, municipality of Itapoá, Santa Catarina	-26.1358	-48.7317	100–170	Monteiro et al., 2018a
6	<i>B. acteus</i>	Serra da Palha, Laranjeiras, Ilha de São Francisco, municipality of São Francisco do Sul, Santa Catarina	-26.2972	-48.6744	20–90	Monteiro et al., 2018a
7	<i>B. acteus</i>	Serra da Tiririca, municipality of Itapoá, Santa Catarina	-26.1283	-48.7422	170–530	Bornschein et al., 2016a; 2019b
8	<i>B. albolineatus</i>	Morro Azul, on the border between the municipalities of Pomerode and Rio dos Cedros, Santa Catarina	-26.7644	-49.2055	725–740	Bornschein et al., 2019a

9	<i>B. albolineatus</i>	Morro Boa Vista, on the border between the municipalities of Jaraguá do Sul and Massaranduba, Santa Catarina	-26.5161	-49.0539	835	Bornschein et al., 2016b; 2018
10	<i>B. albolineatus</i>	Morro do Garrafão, municipality of Corupá, Santa Catarina	-26.4730	-49.2658	500–530	Teixeira et al., 2018
11	<i>B. albolineatus</i>	Morro do Schmidt, municipality of Pomerode, Santa Catarina	-26.6653	-49.2153	810–870	Bornschein et al., 2019a
12	<i>B. auroguttatus</i>	Pedra da Tartaruga, municipality of Garuva, Santa Catarina	-26.0058	-48.9236	1070–1100	Firkowski, 2013; Ribeiro et al., 2015; Bornschein et al., 2016a; Firkowski et al., 2016; Pie et al., 2018a
13	<i>B. boticario</i>	Morro do Cachorro, boundary of the municipalities of Blumenau, Gaspar, and Luiz Alves, Santa Catarina	-26.7785	-49.0324	685–795	Bornschein et al., 2016a; Ribeiro et al., 2015; Firkowski et al., 2016; Pie et al., 2018a; Firkowski, 2013
14	<i>B. brunneus</i>	Abrigo 1, municipality of Campina Grande do Sul, Paraná	-25.2247	-48.8547	1440–1640	Bornschein et al., 2019a; Firkowski et al., 2016; Pie et al., 2018a
15	<i>B. brunneus</i>	Camapuã, Serra dos Órgãos, boundary of the municipalities of Campina Grande do Sul and Antonina, Paraná	-25.2664	-48.8377	1595	Pie et al., 2013; Firkowski et al., 2016; Pie et al., 2018a; Firkowski, 2013; Fontoura et al., 2011
16	<i>B. brunneus</i>	Caranguejeira, Serra da Graciosa, municipality of Quatro Barras, Paraná	-25.3408	-48.9086	1095–1110	Bornschein et al., 2016a; Firkowski, 2013
17	<i>B. brunneus</i>	Caratuva, Serra dos Órgãos, municipality of Campina Grande do Sul, Paraná	-25.2426	-48.8345	1300–1770	Pie et al., 2013; Firkowski et al., 2016; Pie et al., 2018a; Ribeiro et al., 2005; Clemente-Carvalho et al., 2009; Campos,

								2011; Pombal and Izecksohn, 2011; Firkowski, 2013; Clemente-Carvalho et al., 2011; Fontoura et al., 2011; Pie et al., 2017
18	<i>B. brunneus</i>	Getúlio, Serra dos Órgãos, municipality of Campina Grande do Sul, Paraná	-25.2383	-48.8369	1310–1490			Bornschein et al., 2016a; Pie et al., 2013
19	<i>B. brunneus</i>	Mãe Catira, Serra da Graciosa, municipality of Quatro Barras, Paraná	-25.3476	-48.9069	1135–1405			Bornschein et al., 2019a; Pie et al., 2013; Firkowski et al., 2016; Firkowski, 2013
20	<i>B. coloratus</i>	Estância Hidroclimática Recreio da Serra, Serra da Baitaca, municipality of Piraquara, Paraná	-25.4538	-49.0075	1145–1230			Ribeiro et al., 2017
21	<i>B. curupira</i>	Morro do Canal, municipality of Piraquara, Paraná	-25.5153	-48.9821	1320			Bornschein et al., 2019a; Bornschein et al., 2016a; Firkowski et al., 2016; Firkowski, 2013
22	<i>B. curupira</i>	Morro do Vigia, municipality of Piraquara, Paraná	-25.5090	-48.9827	1250			Bornschein et al., 2016a; Pie et al., 2013; Firkowski et al., 2016; Pie et al., 2018a; Firkowski, 2013
23	<i>B. curupira</i>	Serra do Salto, Malhada District, municipality of São José dos Pinhais, Paraná	-25.7020	-49.0622	1095–1160			Bornschein et al., 2016a; Pie et al., 2013; Firkowski et al., 2016; Pie et al., 2018; Ribeiro et al., 2017; Firkowski, 2013
24	<i>B. ferruginus</i>	Olimpo, Serra do Marumbi, municipality of Morretes, Paraná	-25.4508	-48.9163	965–1470			Pie et al., 2013; Firkowski et al., 2016; Pie et al., 2018a; Alves et al., 2006;

								Clemente-Carvalho et al., 2009; Pombal & Izecksohn, 2011; Firkowski, 2013; Clemente-Carvalho et al., 2011
25	<i>B. fuscolineatus</i>	Morro Braço da Onça, municipality of Luiz Alves, Santa Catarina	-26.7494	-48.9280	525–530			Bornschein et al., 2019c
26	<i>B. fuscolineatus</i>	Morro do Baú, municipality of Ilhota, Santa Catarina	-26.7994	-48.9297	640–790			Ribeiro et al., 2015; Pie et al., 2013; Firkowski et al., 2016; Pie et al., 2018; Firkowski, 2013
27	<i>B. izecksohni</i>	Torre da Prata, Serra da Prata, boundary of the municipalities of Morretes, Paranaguá, and Guaratuba, Paraná	-25.6236	-48.6919	980–1340			Pie et al., 2013; Firkowski et al., 2016; Pie et al., 2018; Ribeiro et al., 2005; Clemente-Carvalho et al., 2009; Firkowski, 2013; Clemente-Carvalho et al., 2011
28	<i>B. leopardus</i>	Morro dos Perdidos, municipality of Guaratuba, Paraná	-25.8894	-48.9561	1340–1420			Ribeiro et al., 2015; Pie et al., 2013; Firkowski et al., 2016; Firkowski, 2013
29	<i>B. leopardus</i>	Serra do Araçatuba, municipality of Tijucas do Sul, Paraná	-25.9018	-48.9964	1640–1645			Ribeiro et al., 2015; Pie et al., 2013; Firkowski et al., 2016; Firkowski, 2013
30	<i>B. mariaeterezae</i>	Reserva Particular do Patrimônio Natural Caetezal, top of the Serra Queimada, municipality of Joinville, Santa Catarina	-26.1141	-49.0626	1265–1270			Ribeiro et al., 2015; Pie et al., 2013; Firkowski et al., 2016; Firkowski, 2013; Pie et al., 2018a

31	<i>B. mirissimus</i>	Morro Santo Anjo, municipality of Massaranduba, Santa Catarina	-26.6280	-48.9305	470–540	Pie et al., 2018b
32	<i>B. olivaceus</i>	Base of the Serra Queimada, municipality of Joinville, Santa Catarina	-26.0825	-49.0663	985	This study; Ribeiro et al., 2015
33	<i>B. olivaceus</i>	Castelo dos Bugres, municipality of Joinville, Santa Catarina	-26.2323	-49.056	850	This study; Ribeiro et al., 2015; Pie et al., 2013; Firkowski et al., 2016; Firkowski, 2013; Monteiro et al., 2018b
34	<i>B. olivaceus</i>	Morro do Boi, municipality of Corupá, Santa Catarina	-26.4134	-49.2175	650–920	Bornschein et al., 2016a; Pie et al., 2013; Pie et al., 2018
35	<i>B. olivaceus</i>	Pico Jurapé, municipality of Joinville, Santa Catarina	-26.2741	-49.0036	650–780	Bornschein et al., 2019a
36	<i>B. pernix</i>	Anhangava, Serra da Baitaca, municipality of Quatro Barras, Paraná	-25.3885	-49.0041	1135–1405	Pie et al., 2013; Firkowski et al., 2016; Pie et al., 2018a; Da Silva et al., 2007; Clemente-Carvalho et al., 2009; Campos, 2011; Pombal et al., 2011; Firkowski, 2013; Clemente-Carvalho et al., 2011; Pombal et al., 1998; Campos et al., 2010; Wistuba, 1998; Pires et al., 2005; Ribeiro et al., 2014
37	<i>B. pombali</i>	Morro dos Padres, Serra da Igreja, municipality of Morretes, Paraná	-25.6110	-48.8560	1060–1300	Pie et al., 2013; Firkowski et al., 2016; Pie et al., 2018a; Alves et al., 2006; Clemente-Carvalho et al.,

38	<i>B. pombali</i>	trail to Morro dos Padres, municipality of Morretes, Paraná	-25.5994	-48.8659	845–1060	2009; Firkowski, 2013; Clemente-Carvalho et al., 2011 Pie et al., 2013
39	<i>B. quiririensis</i>	Serra do Quiriri, municipality of Campo Alegre, Santa Catarina	-26.0213	-48.9963	1240–1270	Bornschein et al., 2016a; Pie et al., 2013; Firkowski et al., 2016; Pie et al., 2018a; Firkowski, 2013; Pie & Ribeiro, 2015
40	<i>B. quiririensis</i>	Serra do Quiriri, municipality of Garuva, Santa Catarina	-26.0282	-48.9529	1320–1380	Pie et al., 2013; Monteiro et al., 2018b
41	<i>B. tridactylus</i>	Serra do Morato, Reserva Natural Salto Morato, municipality of Guaraqueçaba, Paraná	-25.1360	-48.3000	805–910	Bornschein et al., 2016a; Firkowski et al., 2016; Garey et al., 2012; Bornschein et al., 2019d
42	<i>B. verrucosus</i>	Morro da Tromba, municipality of Joinville, Santa Catarina	-26.2122	-48.9579	455–945	Bornschein et al., 2016a; Ribeiro et al., 2015; Pie et al., 2013; Firkowski et al., 2016; Pie et al., 2018a; Firkowski, 2013
43	<i>Brachycephalus</i> sp.	Morro do Bisel, Serra do Guaraú, municipality of Cajati, São Paulo	-24.9025	-48.2158	800–1060	This study
44	<i>Brachycephalus</i> sp.	Pedra Branca do Araraquara, Serra do Araraquara, municipality of Guaratuba, Paraná	-25.9333	-48.8805	1000	Bornschein et al., 2016a
45	<i>Brachycephalus</i> sp.	Pico Paraná, Serra dos Orgãos, municipality of Antonina, Paraná	-25.2527	-48.8088	1880	Bornschein et al., 2019a
46	<i>Brachycephalus</i> sp.	Serra Canasvieiras, boundary of the municipalities of Guaratuba and Morretes, Paraná	-25.6162	-48.7831	1080	Bornschein et al., 2016a; Pie et al., 2018b;

47	<i>Brachycephalus</i> sp.	Serra do Pico, municipality of Joinville, Santa Catarina	-26.1419	-48.9552	410–720	Firkowski et al., 2016; Firkowski, 2013
48	<i>Brachycephalus</i> sp.	Serra Pelada, municipality of Barra do Turvo, São Paulo	-24.9805	-48.4791	1130–1140	This study
49	<i>Brachycephalus</i> sp.	Torre Embratel, municipality of Cajati, São Paulo	-24.8794	-48.2575	960–990	This study
50	<i>Brachycephalus</i> sp.	Tupipiá, Serra dos Órgãos, municipality of Antonina, Paraná	-25.2536	-48.8055	1560	Bornschein et al., 2019a; Pie et al., 2013; Firkowski et al., 2016; Pie et al., 2018a; Firkowski, 2013

Table 2. Environmental variables for each best model with the lowest value of AIC, the AUC test dataset (AUC_{TEST}), the AUC of training and testing data (AUC_{DIFF}), 10% training omission rate (OR_{10}) and permutation importance

Model	AICc	AUC_{TEST}	AUC_{DIFF}	OR_{10}	Variables	Permutation importance
Overall model	830.55	0.9932	0.00215	0.12	P-T alpha	67.64
					Precipitation of July	10.41
					Solar radiation of June	9.92
					Elevation	8.64
					Net primary productivity	1.57
					Roughness	1.54
					Deciduous Broadleaf Trees	0.21
					Aspect	0.03
Bioclimatic model	865.44	0.9901	0.00283	0.14	Precipitation seasonality (BIO 15)	25.25
					Precipitation of wettest month (BIO 13)	24.36
					Mean diurnal range (BIO 2)	18.19
					Precipitation of coldest quarter (BIO 19)	17.19
					Precipitation of driest quarter (BIO 17)	8.70
					Min temperature of coldest month (BIO 6)	6.28
					Aspect	0.03
Uncorrelated model	868.69	0.9914	0.00394	0.14	Precipitation of warmest quarter (BIO 18)	27.73
					Solar radiation of September	27.51
					Vapor pressure of January	23.63
					Net primary productivity	10.49
					Annual actual evapotranspiration	3.55
					Temperature annual range (BIO5-BIO6)	3.20
					Slope	2.86
					Precipitation of December	1.00
					Aspect	0.03
					Evergreen Broadleaf Trees	0.003

Table 3. Summary of comparisons of logistic output model predictions in geographic space for paleomodels over time of species of *Brachycephalus pernix* group.

Scenario	Paleomodel		Schoener's <i>D</i>
Mid-Holocene	CCSM (PaleoClim)	MIROC	0.33
	CCSM (WorldClim)	MIROC	0.50
	CCSM (PaleoClim)	CCSM (WorldClim)	0.45
LGM	CHELSA	Oscillayers	0.08
	CCSM	MIROC	0.35
	CHELSA	CCSM	0.15
	CHELSA	MIROC	0.04
	CCSM	Oscillayers	0.38
	Oscillayers	MIROC	0.37
LIG	CCSM	Oscillayers	0.11
mPWP	HadCM3	Oscillayers	0.06
M2	HadCM3	Oscillayers	0.22

FIGURES:

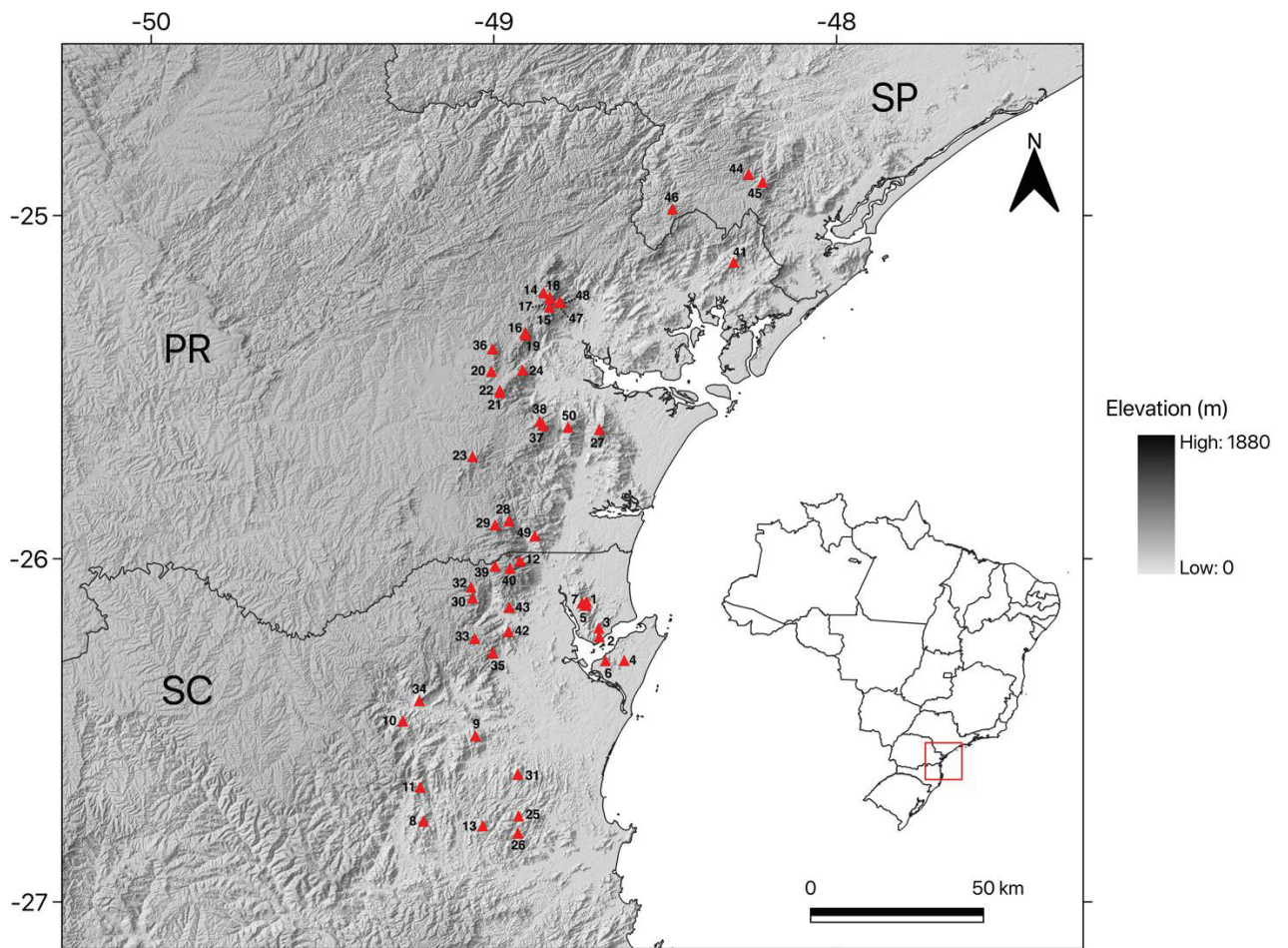


Figure 1. Map of distribution of species of the *Brachycephalus pernix* group. SP = São Paulo, PR = Paraná and SC = Santa Catarina. The numbers represent the localities listed in the Table 1.

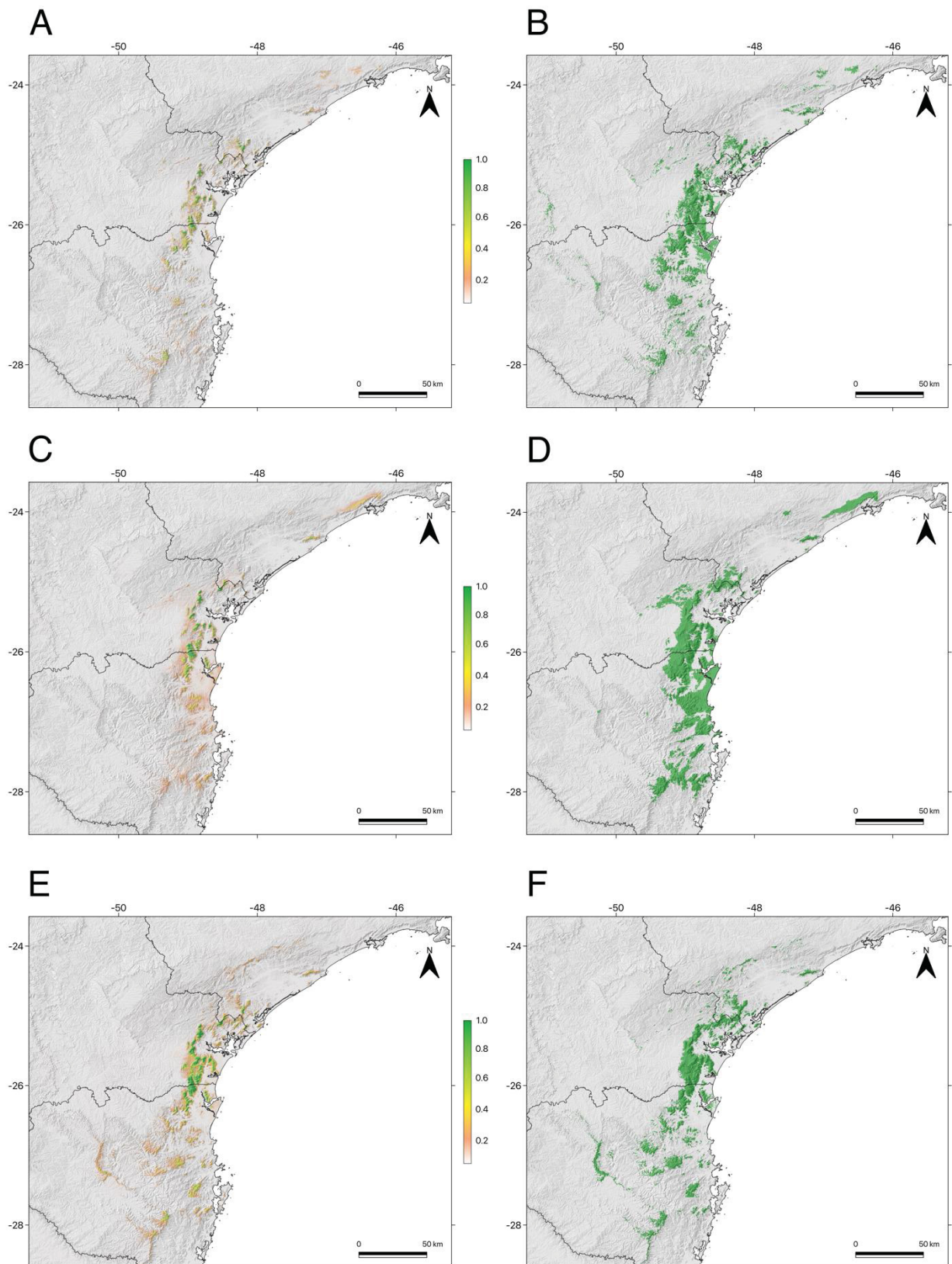


Figure 2. Predicted distribution of suitable habitats for species of *Brachycephalus pernix* group. Models were visualized using logistic probability values (right), and converted to presence-absence maps using maximum-training-sensitivity-and-specificity logistic (left; green indicates presence). Species distribution models for overall model (A, B); for bioclimatic model (C, D); and for uncorrelated model (E, F).

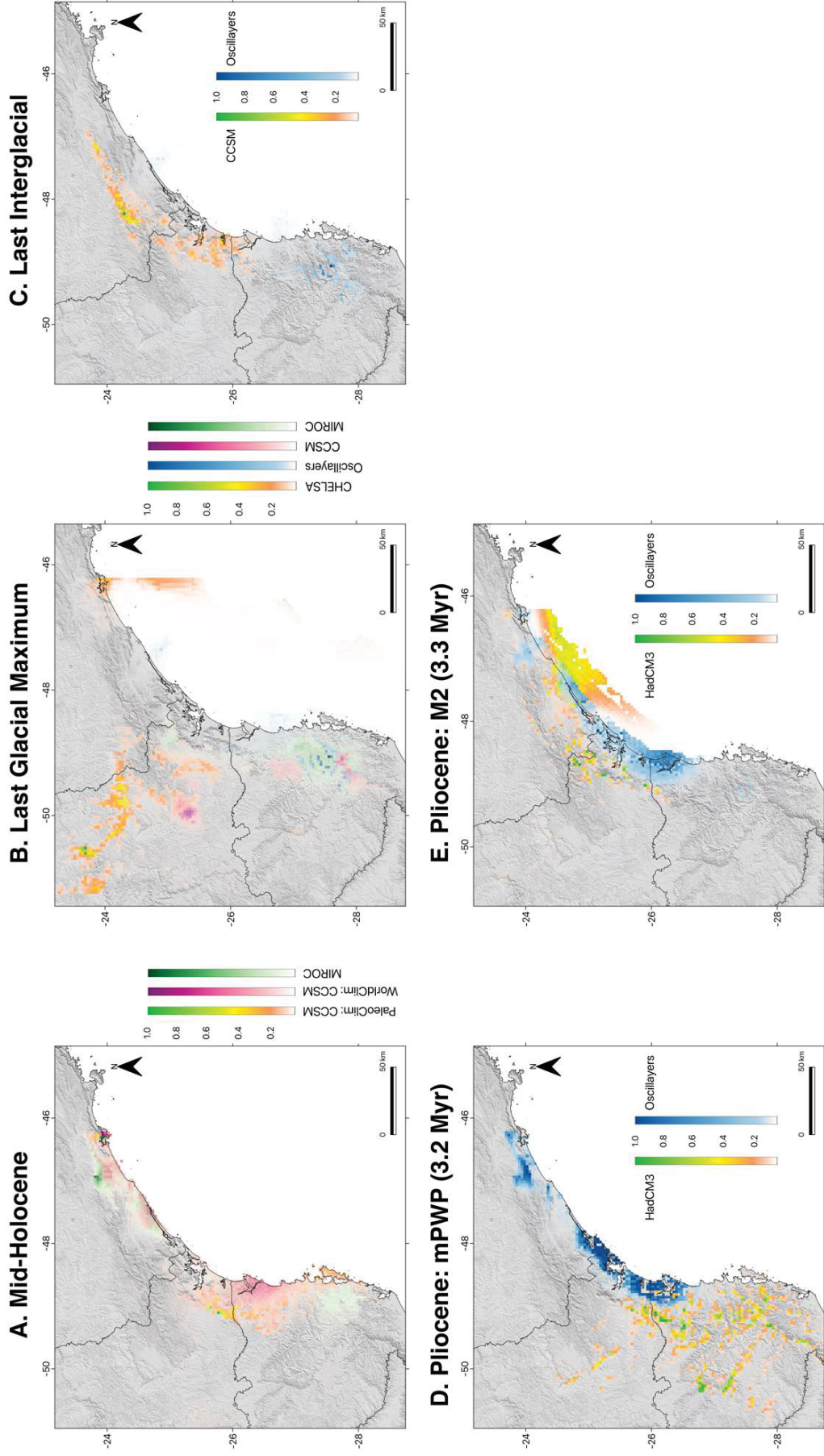


Figure 3. Distribution of suitable habitats of *Brachycephalus pennix* group in different time periods: 6 kyr (Mid-Holocene); 20 kyr (LGM); 130 kyr (LIG); 3.2 Myr (mPWP); and 3.3 Myr (M2).

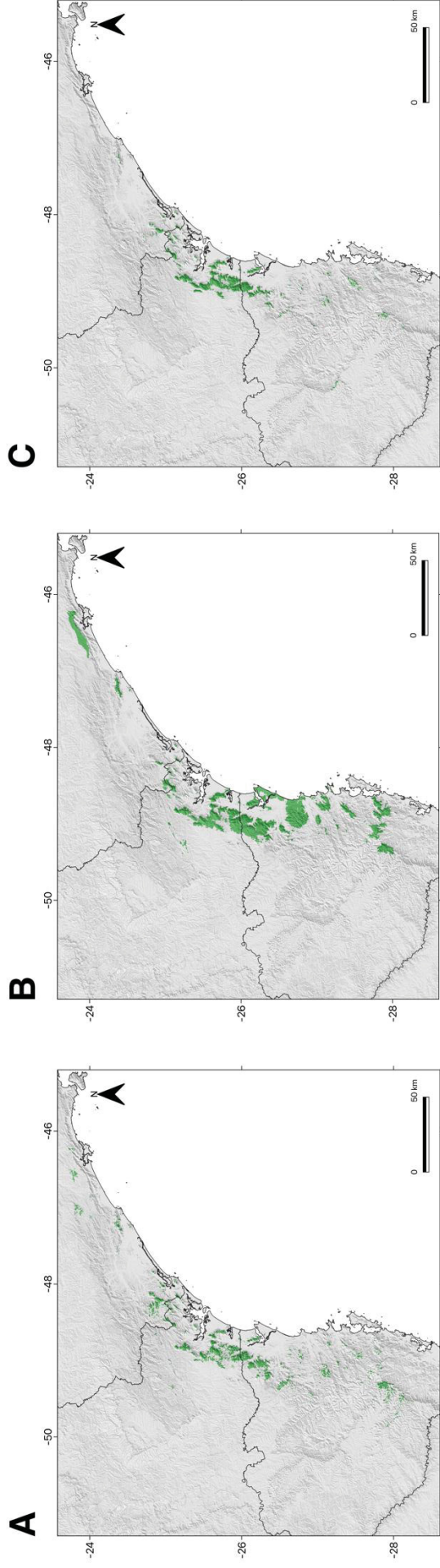
APPENDIX

Table S1. Environmental layers used for niche modelling with their data source.

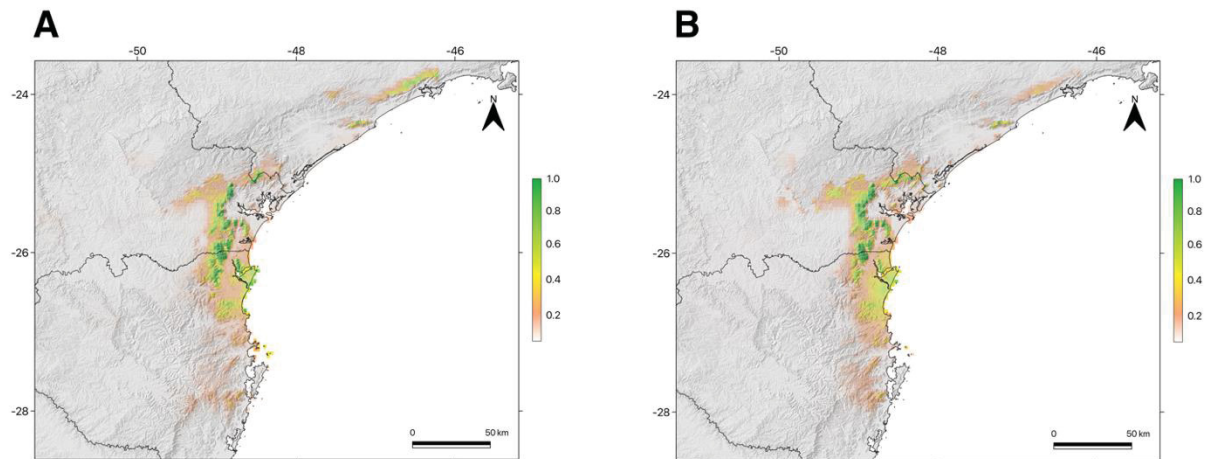
Type variable data	No. variables	Environmental variables
Climate		
	19	Bioclimatic variables ^a
	12	Monthly climate data of minimum temperature (°C) ^a
	12	Monthly climate data of maximum temperature (°C) ^a
	12	Monthly climate data of average temperature (°C) ^a
	12	Monthly climate data of precipitation (mm) ^a
	12	Monthly climate data of solar radiation (kJ m ⁻² day ⁻¹) ^a
	12	Monthly climate data of wind speed (m s ⁻¹) ^a
	12	Monthly climate data of water vapor pressure (kPa) ^a
Macro-environmental		
	1	Annual actual evapotranspiration ^b
	1	Annual aridity index ^b
	1	Annual potential evapotranspiration ^b
	1	Priestley-Taylor alpha coefficient (P-T alpha) ^b
	1	Net primary productivity ^c
Habitat heterogeneity		
	1	Coefficient of variation ^d
	1	Evenness ^d
	1	Range ^d
	1	Shannon ^d
	1	Simpson ^d
	1	Standard deviation ^d
	1	Contrast ^d
	1	Correlation ^d
	1	Dissimilarity ^d
	1	Homogeneity ^d
	1	Maximum ^d
	1	Uniformity ^d
	1	Variance ^d
Land cover classes		
	1	Evergreen Broadleaf Tree ^e
	1	Deciduous Broadleaf Trees ^e
	1	Mixed/Other Trees ^e
	1	Shrubs ^e
	1	Herbaceous Vegetation ^e
Soil		
	1	Soil properties and classes ^f
Topographic		

	1	Elevation ^g
	1	Roughness ^h
	1	Slope ^h
	1	Aspect ⁱ

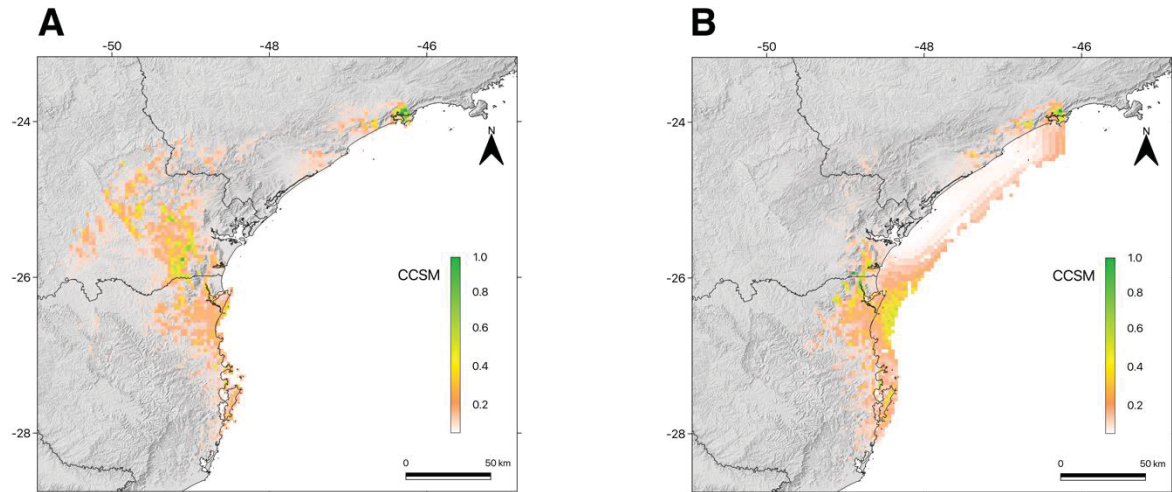
Data sources: ^aWorldClim v. 2 database (Fick & Hijmans, 2017; www.worldclim.org/version2); ^bConsortium for Spatial Information (Trabucco & Zomer, 2019; <http://www.cgiar-csi.org>); ^cNASA Earth Observations (NEO) dataset (for the month of November 2016; <https://neo.sci.gsfc.nasa.gov>); ^dEarthEnv (Tuanmu & Jetz, 2015; <https://www.earthenv.org/texture>); ^eEarthEnv (Tuanmu & Jetz, 2014; <https://www.earthenv.org/landcover>); ^fSoilGrids v. 0.5.3 (SoilGrids, 2018; <https://soilgrids.org>); ^gConsortium for Spatial Information (CGIAR-CSI) database (Jarvis *et al.*, 2008; <http://srtm.csi.cgiar.org/srtmdata>); ^hEarthEnv using median value (Amatulli *et al.*, 2018; <https://www.earthenv.org/topography>); ⁱAspect was computed using the function *terrain* from our elevation layer with the RASTER package (Hijmans *et al.*, 2019) in R v. 3.6.0 (R Core Team, 2019).



Appendix 1. Binary predictions of species distribution models of *Brachycephalus pernix* group using the threshold 10th percentile training presence (green indicates presence). (A) overall model, (B) bioclimatic model, and (C) uncorrelated model.



Appendix 2. Predicted distribution of suitable habitats for species of *Brachycephalus pernix* group. Logistic probability maps used to model to past climate. (A) Present-day model to Holocene and Pleistocene; and (B) Present-day model to Pliocene.



Appendix 3. Species distribution models of *Brachycephalus pernix* group for Late Holocene (A) and Early Holocene (B).