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Ecological Niche Modelling of Microendemic Species: Understanding the Distribution of Montane Frogs in the Southern Brazilian Atlantic Forest

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ABSTRACT

Modelling the distribution of microendemic species presents significant challenges due to limited occurrence records and the coarse resolution of available bioclimatic data. This is particularly true for montane regions, which harbour high levels of endemism and environmental heterogeneity. In this study, we modelled the potential distribution of *Brachycephalus pernix* group toadlets to assess their range and identify key environmental drivers of their ecological niches. We applied two correlative modelling approaches—model-selection procedures using MaxEnt and Ensemble Small Models—incorporating a broad suite of environmental predictors beyond traditional bioclimatic variables. Our results highlight that Ensemble Small Models outperformed model-selection procedures (MaxEnt) in predicting suitable habitats for these microendemic species, yielding more spatially precise predictions centred in highland, montane and submontane regions. Suitability was strongly associated with environmental variables related to precipitation and moisture, which play a critical role in shaping the realised niche of the *B. pernix* group. The species exhibited niche conservatism, likely reflecting the retention of ancestral ecological preferences that facilitate persistence in montane environments. This supports the hypothesis that mountain ranges act as long-term refugia during climatic fluctuations. Importantly, models incorporating heterogeneous environmental data outperformed those using only bioclimatic variables, highlighting the value of accounting for topographic and climatic complexity when modelling narrow-range taxa. Despite identifying additional suitable habitats, many of these areas remain unprotected and are increasingly threatened by deforestation and land-use change. Our findings provide new insights into the ecological requirements and distribution dynamics of the *B. pernix* group and emphasise the urgent need for targeted conservation efforts to safeguard their specialised habitats and ensure long-term persistence.

1 | Introduction

The intersection of abiotic and biotic conditions, along with species' dispersal capacities, defines species' ranges (Soberón 2007; Soberón and Nakamura 2009). This intersection represents the realised niche, where organisms can persist (Soberón 2007; Peterson 2011). Species with small ranges often display high habitat specificity at both local and regional scales (Rabinowitz 1981; Franklin and Miller 2009) and are typically constrained by climatic conditions (e.g., Ohlemüller

et al. 2008). This adaptation to specific conditions often leads to narrow endemism, or microendemism. Endemic species tend to be concentrated in limited areas with small population sizes, making these regions centres of endemism and critical for conservation (Orme et al. 2005). Consequently, such species may be especially vulnerable to global warming, experiencing habitat reduction during rapid climate fluctuations, and susceptible to genetic erosion from stochastic events (Malcolm et al. 2006; Honnay and Jacquemyn 2007; La Sorte and Jetz 2010; Allendorf et al. 2013). These characteristics make narrow endemic species a priority for conservation efforts (e.g., López-Pujol et al. 2013).

Ecological niche modelling (ENM) has become a powerful tool for predicting a species' realised niche into geographical space based on statistical relationships between species occurrence and environmental predictors (Guisan and Thuiller 2005; Peterson 2011; Guisan et al. 2013). ENM is crucial for identifying potential habitats for endemic, rare or threatened species and supporting conservation efforts (Guisan et al. 2013). Additionally, ENM offers valuable insights into species ecology, such as identifying variables most influential in defining range boundaries (Searcy and Shaffer 2016; e.g., Pie et al. 2013; Petitpierre et al. 2017; Zhang and Vincent 2017). For endemic species with narrow ranges, however, limited occurrence records can hinder modelling efforts, often leading to model overfitting (Lomba et al. 2010; Breiner et al. 2015). A promising alternative is the use of Ensembles of Small Models (ESMs), designed to address model calibration with small datasets (Breiner et al. 2015, 2018). ESMs perform well by reducing the number of predictor variables, thereby avoiding overfitting without sacrificing explanatory power, and they have proven superior to standard ENMs for species with limited records (Breiner et al. 2015). Despite the potential of these approaches to enhance ENMs for microendemic species, their implementation in empirical studies is still incipient.

Montane regions are often regarded as biodiversity hotspots, harbouring remarkable levels of species richness and endemism (Myers et al. 2000; Rahbek, Borregaard, Antonelli, et al. 2019; Rahbek, Borregaard, Colwell, et al. 2019). Organisms in these regions are particularly vulnerable to rapid climatic fluctuations due to their narrow thermal tolerances and restricted elevational distributions (Janzen 1967; La Sorte and Jetz 2010; Gifford and Kozak 2012; Devitt et al. 2013). These thermal constraints also contribute to the isolation of montane populations, which are typically separated by unsuitable lowland habitats despite being in close geographical proximity (Ghalambor 2006; Rahbek, Borregaard, Antonelli, et al. 2019). Additionally, montane regions exhibit high topographic and habitat heterogeneity, which, in interacting with climatic conditions, creates a range of microhabitats where species can evolve and diversify (Kerr and Packer 1997; Körner 2004; Fjeldså et al. 2012; Antonelli et al. 2018).

The Brazilian Atlantic Forest (BAF) is a recognised biodiversity hotspot, harbouring an extraordinary number of endemic species (Myers et al. 2000; Araujo et al. 2024). This biome encompasses several montane regions that run parallel to Brazil's Atlantic coast. These montane areas display considerable variation in vegetation types (Oliveira-Filho and Fontes 2000; Peres et al. 2020), which create a wide range of habitats and microhabitats. The Serra do Mar mountain range, in particular, is a key area of endemism characterised by persistent microrefugia (Brown and Ab'Saber 1979; Peres et al. 2020), complex topography and high precipitation levels (Safford 1999; Behling 2008). These features, along with dynamic environmental changes over the past 130 000 years (Behling 1997; Behling et al. 2007; Behling and Safford 2010), have contributed to substantial genetic diversity and instances of narrow endemism (Amaral et al. 2013; Carnaval et al. 2014; Ströher et al. 2019).

A notable example of microendemism in the BAF is the genus *Brachycephalus* (Anura: Brachycephalidae), a group of direct-developing anurans that inhabit leaf litter and often exhibit small geographical ranges (Pombal et al. 1994; Pie et al. 2013; Ribeiro et al. 2015; Bornschein, Firkowski, et al. 2016). These small ranges make them highly vulnerable to environmental disturbances. More than half of the 42 known species of *Brachycephalus* (Frost 2024) are classified as Critically Endangered, Endangered or Vulnerable, primarily threatened by deforestation (Bornschein et al. 2019). This conservation crisis is particularly severe in montane regions of the BAF, which are especially at risk due to anthropogenic activities, such as mining and high-altitude agriculture (Martinelli 2007; Rezende et al. 2018; Rosa et al. 2021).

The genus *Brachycephalus* has been divided into three main clades, initially proposed by Clemente-Carvalho et al. (2011) and later adapted by Ribeiro et al. (2015) into three phenetic groups based on morphology and distribution: the *B. didactylus*, *B. ephippium* and *B. pernix* species groups. The monophyly of the *B. ephippium* and *B. pernix* groups has been consistently supported (Pie, Faircloth, et al. 2018; Pie et al. 2019; Condez et al. 2020; Folly et al. 2022), whereas relationships within the *B. didactylus* group remain unresolved (Folly et al. 2022). Notably, the *B. pernix* group exhibits microendemism, being distributed across the Serra do Mar in the southern BAF, where most species inhabit montane and cloud forests on isolated mountaintops (Ribeiro et al. 2015; Pie et al. 2013; Bornschein, Firkowski, et al. 2016). Species within the *B. pernix* group are often considered to exhibit some level of phylogenetic niche conservatism (Pie et al. 2013; Firkowski et al. 2016; Pie, Faircloth, et al. 2018), which refers to the tendency of species to retain and track their ancestral ecological niches. Given the mounting risks associated with climate change and habitat loss, particularly in the montane regions of the Serra do Mar, the *B. pernix* group represents a priority for conservation. Addressing these threats requires a better understanding of their distribution limits and the identification of potential areas for still undescribed species, ultimately helping to preserve both these vulnerable toadlets and the biodiversity of the BAF highlands.

In this study, we use ENMs to predict the potential distribution of species in the *Brachycephalus pernix* group and identify additional areas of suitable habitat across the Serra do Mar mountain range. Given the limited number of occurrence records available for conventional ENMs, we employed a clustering method within two ENM approaches: a model-selection procedure using MaxEnt and ESMs. We compare our approach with that of Pie et al. (2013), who relied solely on bioclimatic variables, by

incorporating a broader set of environmental predictors to evaluate which approach yields more reliable ecological predictions for microendemic species. To better capture the biological attributes of these toadlets, we integrated climatic, mesoclimatic and macroclimatic variables to account for topographic complexity and abiotic interactions at a local scale (Dobrowski 2011). We also assessed the most influential environmental variables to understand their biological relevance in shaping niche space. Lastly, we used niche similarity tests to explore whether species in the *B. pernix* group exhibit climatic niche conservatism, thereby providing insights into the ecological and evolutionary mechanisms driving their distribution.

2 | Materials and Methods

The potential geographical distribution of members of the *Brachycephalus pernix* species group was estimated using correlative niche modelling (Beerling et al. 1995; Robertson et al. 2003; Elith et al. 2010), based on the association of occurrence records with a broad set of candidate environmental variables. We compared these results with an alternative model based solely on the commonly used 19 bioclimatic variables (Fick and Hijmans 2017), as done in Pie et al. (2013). For brevity, we refer to the models using the broad set of environmental variables as the 'Full-model', and the models using the 19 bioclimatic variables as the 'Bio-model' (see *Model comparisons*).

2.1 | Environmental Variables

We compiled a set of environmental datasets, including bioclimatic variables, as well as maximum, minimum and mean measures of solar radiation, wind speed and water vapour from a monthly dataset (Fick and Hijmans 2017). Additionally, we included variables related to cloud cover (mean annual and seasonality concentration) (Wilson and Jetz 2016) and soil moisture (Saiter et al. 2016; Brown et al. 2017). Solar radiation, wind speed, water vapour, cloud cover and soil moisture are important factors that reflect suitable microclimate habitats and help define climatic constraints on the distribution of organisms (Kearney and Porter 2009; Kearney et al. 2014). We also incorporated macro-environmental variables suggested as key drivers of species distribution (e.g., Hu and Jiang 2018), such as annual actual evapotranspiration, annual aridity index, annual potential evapotranspiration, net primary productivity (as a proxy for ecosystem functioning) and Priestley-Taylor alpha coefficient (P–T alpha) (Trabucco and Zomer 2019). P–T alpha coefficient is the ratio of annual actual evapotranspiration to annual potential evapotranspiration (Trabucco and Zomer 2019). For the topographic features, we use a 30 m resolution elevation raster (STRM NASA) and calculated aspect, slope, topographic position index, terrain ruggedness index, roughness, northness and eastness using the R packages 'raster' 3.4.5 (Hijmans et al. 2019) and 'spatialEco' 1.1.0 (Evans 2023). Topographic variables can serve as proxies for microclimates (e.g., Mota-Vargas et al. 2013; Kübler et al. 2016). All variables were resampled to a spatial resolution of ~1 km^2 (30 arc-seconds) using bilinear interpolation with the function *resample* in 'raster' package. In total, 51 predictors were included in the environmental dataset, with further details provided in Table S1.

To avoid collinearity among variables, we used Pearson's correlation coefficient to select biologically relevant and non-correlated variables, applying a threshold of less than |0.75| (Dormann et al. 2013; Figure S1). This approach resulted in a final dataset of 16 environmental variables, which formed the Full-model: annual potential evapotranspiration (PET), aspect, mean annual cloud cover, mean solar radiation, roughness, topographic position index (TPI), net primary productivity, P–T alpha, maximum wind speed, minimum temperature of the coldest month, temperature annual range, precipitation of the wettest month, precipitation of the driest month, moisture index seasonality, mean moisture index of the wettest quarter and mean moisture index of the coldest quarter.

2.2 | Occurrence Records

Building upon previous compilations (Pie et al. 2013; Bornschein, Firkowski, et al. 2016; Bornschein et al. 2019), we added new occurrence records from the literature since their publication until December 2021 (Figure 1A; Table S2). At the time of our analyses, the *Brachycephalus pernix* species group included 19 species: *B. actaeus* Monteiro et al. (2018); *B. albolineatus* Bornschein, Ribeiro, et al. (2016); *B. auroguttatus* Ribeiro et al. (2015); *B. boticario* Pie, Bornschein, Firkowski, Belmonte-Lopes and Ribeiro 2015; *B. brunneus* Ribeiro et al. (2005); *B. coloratus* Ribeiro et al. (2017); *B. curupira* Ribeiro et al. (2017); *B. ferruginus* Alves et al. (2006); *B. fuscolineatus* Pie, Bornschein, Firkowski, Belmonte-Lopes and Ribeiro 2015; *B. izecksohni* Ribeiro et al. (2005); *B. leopardus* Ribeiro, Firkowski and Pie 2015; *B. mariaeterezae* Bornschein, Morato, Firkowski, Ribeiro and Pie 2015; *B. mirissimus* Pie, Ribeiro, et al. (2018); *B. olivaceus* Bornschein, Morato, Firkowski, Ribeiro and Pie 2015; *B. pernix* Pombal et al. (1998); *B. pombali* Alves et al. (2006); *B. quiririensis* Pie and Ribeiro 2015; *B. tridactylus* Garey et al. (2012); and *B. verrucosus* Ribeiro, Firkowski, Bornschein and Pie 2015. Many of these species are microendemic, with narrow distributions of suitable habitats (Bornschein et al. 2019). In total, we included 50 occurrence records for 19 species (Table S2).

The spatial scale is a critical factor in defining endemism (Peterson and Watson 1998; Daru et al. 2020) as some species may be endemic to large areas, while others are restricted to smaller areas (Evans et al. 2022). Species with small range sizes often exhibit high habitat specificity at local and regional scales (Rabinowitz 1981; Franklin and Miller 2009) and are typically regionally constrained by climatic conditions (e.g., Ohlemüller et al. 2008). This type of narrow endemism is known as microendemism (Caesar et al. 2017; Médail and Baumel 2018; Helmstetter et al. 2021). Due to their high level of microendemism within the *Brachycephalus pernix* group, conducting species-level ENM is unfeasible. A plausible solution is to cluster the distribution records based on their climatic similarity (e.g., Pie et al. 2013).

We employed model-based clustering with Gaussian mixture models, implemented in the R package 'mclust' 5.4.6 (Scrucca et al. 2023), to identify the optimal clustering structure that best fits our environmental dataset. These models estimate cluster parameters using the iterative Expectation–Maximisation (EM) algorithm for maximum-likelihood estimation

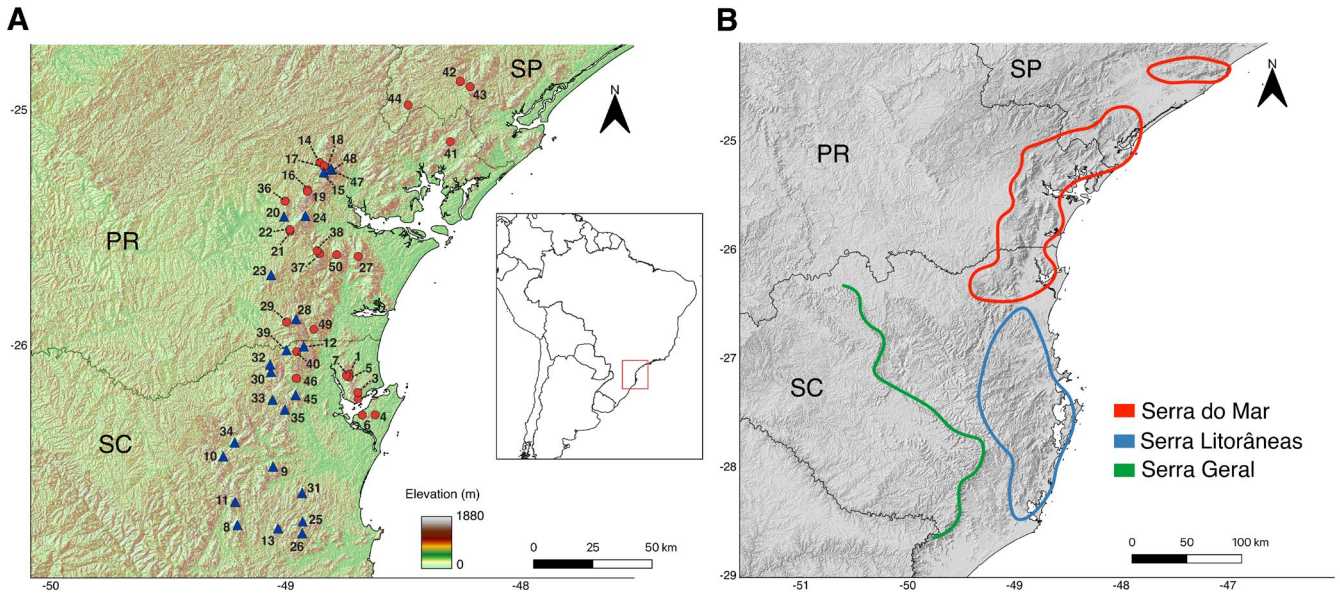

FIGURE 1 | Map showing the distribution of occurrence records for species in the *Brachycephalus pernix* group (A). Numbers correspond to localities listed in Table S2. Red circles represent Cluster 1, and blue triangles represent Cluster 2. Map showing the major mountain ranges of the southern Atlantic Forest (B). Acronyms indicate Brazilian states: PR, Paraná; SC, Santa Catarina; SP, São Paulo.

(Ezard et al. 2010; Fraley et al. 2012; Kassambara 2017). This approach improves accuracy by assessing clusters based on geometric parameters in multivariate space: shape (covariance structure), volume (cluster dispersion) and orientation (principal axes of variation), allowing for a more precise representation of divergence between groups (Fraley et al. 2012). The best model was selected according to Bayesian Information Criterion (BIC) (Ezard et al. 2010; Kassambara 2017). To perform the clustering, we first scaled the 16 environmental variables and extracted the corresponding values for each occurrence record. We then performed a principal component analysis (PCA) to reduce dimensionality, selecting the retained components using the broken-stick criterion (Borcard et al. 2011). The first three principal components (PCs) were used in our clustering analysis (Table S3). Two clusters were identified: Cluster 1 with 27 records and Cluster 2 with 23 records (Table S2; Figures 1A and S2). These two clusters were treated as distinct 'species' for further analysis.

2.3 | Ecological Niche Modelling

We generated ENMs for each cluster using two strategies: model-selection procedures (M-PR) and Ensemble of Small Models (ESMs). First, for M-PR, we used MaxEnt 3.4.1 (Phillips et al. 2006, 2017) through the 'ENMeval' 2.0 (Muscarella et al. 2014; Kass et al. 2021) and 'dismo' 1.3.2 (Hijmans et al. 2017) R packages. MaxEnt uses presence-background data to estimate a relative probability distribution, indicating the environmental suitability of the species (Phillips et al. 2006; Phillips and Dudík 2008). We inspected variable rankings based on permutation importance within a model-selection procedure, a method empirically supported by Pie et al. (2013) and Searcy and Shaffer (2016) as an effective estimate of climatic determinants of species ranges. Permutation importance is calculated by randomly permuting the values of variables among the training presence and background points and measuring the resulting decrease in the training area under the curve (AUC). A large decrease indicates that the model depends heavily on that variable (Searcy and Shaffer 2016; Phillips et al. 2017). We used 10 000 random background points within a polygon of presence localities, buffered by two degrees in all directions. Cluster 1 (27 records) was evaluated using the k-fold cross-validation method, which randomly partitions the dataset into training and testing subsets across five bins (Peterson 2011; Muscarella et al. 2014). In contrast, for Cluster 2 (23 records), we used the jackknife method (leave-one-out), where each occurrence was tested individually while the remaining records were used for training in each iteration (Muscarella et al. 2014). The choice of partitioning method was based on dataset size. The k-fold cross-validation method was applied to Cluster 1 because it provides a reliable estimate of model performance when a moderate number of records is available. However, for smaller datasets (< 25 records), such as Cluster 2, the jackknife method is preferred because it enables a robust evaluation of predictive ability with limited data. These data partitioning methods follow the recommendations of Muscarella et al. (2014) and Shcheglovitova and Anderson (2013). To select the best-fitting model, we tuned models with two settings: feature classes, which define the response curve shape between occurrence records and environmental variables, and regularisation multipliers, which help reduce overfitting (Phillips et al. 2006; Merow et al. 2013; Shcheglovitova and Anderson 2013; Muscarella et al. 2014). We tested six combinations of feature classes as follows: (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 regularisation multipliers, we tested values ranging from 0.5 to 5 in 0.5 increments.

To simplify our models for both cluster 1 and 2, we employed a stepwise approach, successively omitting variables with zero or the lowest permutation importance values. We then calculated the corrected Akaike Information Criterion (AICc) for each

model and selected the one with the lowest AICc value as the best-fitting model (Muscarella et al. 2014). To evaluate model performance, we calculated the area under the curve (AUC) of the receiver operating characteristic (ROC) curves, which represents the probability that a randomly selected presence site will be ranked higher than a randomly selected background site (Phillips and Dudík 2008; Merow et al. 2013). AUC scores greater than 0.75 are considered informative, and scores above 0.9 indicate high accuracy (Phillips and Dudík 2008). Validation AUC values were calculated using the test data subset generated during cross-validation to assess the model's ability to distinguish between presence and background points (Muscarella et al. 2014; Kass et al. 2021). Furthermore, we estimated the maximum true-skill statistic (MaxTSS), as a presence-absence measure (Allouche et al. 2006) and used the Boyce index to evaluate model consistency with the observed distribution of presence data in the evaluation dataset. The Boyce index values range from −1 to 1, with values near 1 indicating high consistency, values near 0 suggesting no difference from a random model, and negative values highlighting counter-predictions (Boyce et al. 2002; Hirzel et al. 2006). The Boyce index was calculated using the R package 'ecospat' 3.1 (Di Cola et al. 2017). To distinguish between suitable and unsuitable areas, we applied the maximum training sensitivity and specificity logistic threshold (TSS threshold), chosen for its high predictive performance (Liu et al. 2005; Cao et al. 2013) and ability to minimise commission errors, which could otherwise lead to misidentification of suitable areas (Loiselle et al. 2003; Pie et al. 2013; Meyer et al. 2014).

The second set of models was constructed using ESM, a method designed for reliable species distribution modelling with limited occurrence data (less than 30 records; Lomba et al. 2010; Breiner et al. 2015; Di Cola et al. 2017). ESM calibrates all possible bivariate combinations of environmental variables, building small, bivariate models which are then averaged into a weighted ensemble (Breiner et al. 2015, 2018). In this study, we employed artificial neural networks (ANN), gradient boosting machines (GBM) and generalised linear models (GLM) to calibrate bivariate models for each cluster. Parameters were tuned according to Breiner et al. (2018): for ANN, we used a size of 8 and decay of 0.001; for GBM, 1000 trees, a tree complexity of 4 and shrinkage of 0.005; and for the GLM, a quadratic model type, an interaction level of 0, and a maxit of 1000. The other parameters remained as default.

Each ESM ran 10 replicates, using 80% of the occurrence data for calibration and the remaining 20% for evaluating, along with 10 000 pseudo-absences. ESMs were implemented using the R packages 'ecospat' 3.1 (Di Cola et al. 2017) and 'biomod2' 3.4.6 (Thuiller et al. 2019). We built an ensemble prediction by averaging across the three ESM methods, weighted by Somers' D (Breiner et al. 2015), excluding bivariate models with Somers' D below 0. The output of averaging the three ESM techniques is an ensemble prediction (EP), which was used to assess model reliability and project habitat suitability (Breiner et al. 2015). We evaluated ESM predictions with the function *ecospat.ESM.EnsembleEvaluation*, which provides a cross-validation pool of Boyce index, AUC and MaxTSS scores (Boyce et al. 2002; Hirzel et al. 2006; Collart et al. 2021). The variable contributions for each ESM were assessed using the function *ecospat.ESM.VarContrib*. Binary projections (presence/absence) were determined using the TSS threshold, calculated with the function *ecospat.ESM.threshold*. All these procedures were conducted using the R package 'ecospat' 3.1 (Di Cola et al. 2017).

To assess the distribution of suitable habitats within Integral Protection Conservation Units, we used binary maps derived from the best-performing Full and Bio models, based on the most accurate techniques for predicting both habitat suitability and the extent of suitable areas between M-PR and ESMs (see *Model comparisons*). Conservation unit boundaries were obtained from TerraBrasilis (Assis et al. 2019). We also examined the percentage and area of predicted suitable habitats located in regions affected by land conversion—such as deforestation, urbanisation or agriculture—across different elevation zones. These zones were classified according to Veloso et al. (1991) as follows: lowlands (5–30 m a.s.l.), submontane (30–400 m a.s.l.), montane (400–1000 m a.s.l.) and highlands (> 1000 m a.s.l.) (Figure S3A). In addition, we calculated the percentage of presence records distributed across these altitudinal zones. Land cover and land use data were sourced from Vancine et al. (2023), while deforestation data were obtained from TerraBrasilis (Assis et al. 2019). Finally, we evaluated and summarised the predicted habitat areas where species occurrence data is lacking. This involved identifying locations that the model predicts as suitable for the species but where no direct evidence (e.g., occurrence records or observations) confirms the species' presence.

2.4 | Model Comparisons

To evaluate whether a broader set of candidate environmental variables (hereafter referred to as the Full-model) could outperform models using only the 19 bioclimatic variables (Fick and Hijmans 2017), we built ENMs using these bioclimatic variables (referred to as the Bio-model) for both clusters. We applied the same modelling strategies, M-PR and ESMs, as described in the Ecological niche modelling section, following the procedures in Pie et al. (2013) to compare the performance of Full-models and Bio-models.

We assessed the effects of different modelling techniques (M-PR, ANN, GBM, GLM and EP) within and between Full-model and Bio-model frameworks in predicting habitat suitability and the spatial extent of suitable areas across variable altimetric ranges, using generalised linear models. Estimating suitable area allowed us to assess how modelling choices influence the identification of potentially new or expanded areas of suitable habitat. Elevation zones followed the classification of Veloso et al. (1991): lowlands (5–30 m a.s.l.), submontane (30–400 m a.s.l.), montane (400–1000 m a.s.l.) and highlands (> 1000 m a.s.l.) (Figure S3A).

Habitat suitability, used as a proxy for the probability of species occurrence in areas that best match their ecological niche (more details see Hirzel and Le Lay 2008), served as an indicator of model accuracy. Models predicting occurrence probabilities close to 1 were considered to have high predictive accuracy. To extract suitability values, we identified suitable pixels (binary value = 1) in the binary maps and retrieved corresponding values from continuous logistic maps using the R package 'terra' 1.7.78 (Hijmans et al. 2025). This was performed separately for each modelling technique across elevation zones, and the results

were aggregated to compute the mean suitability per zone. To quantify the spatial extent of suitable habitat across elevational zones, we calculated the total area (km^2) of suitable pixels (presence = 1) by intersecting binary maps with the elevation zones. Per-pixel areas were estimated using the *cellSize* function, and total areas per zone were computed with the *zonal* function from 'terra' package (Hijmans et al. 2025).

To test the effects of modelling techniques and elevation zones on mean habitat suitability and suitable area (km^2) in both Full and Bio models, we fitted Generalised Linear Models (GLMs) using the R package 'glmmTMB' 1.1.10 (Brooks et al. 2017). Mean habitat suitability was modelled assuming a Beta distribution (habitat suitability ~ modelling technique + elevation zone), while suitable area was modelled assuming a Gamma distribution with a log link (suitable area ~ modelling technique + elevation zone) (Ferrari and Cribari-Neto 2004; Zuur et al. 2009). Post hoc pairwise comparisons among techniques and zones were performed using Tukey's HSD test.

To compare the predictive performance of the Full and Bio models in terms of habitat suitability, we fitted Generalised Linear Mixed Models (GLMMs). We treated mean habitat suitability as the response variable, model type (Full or Bio) as a fixed effect, and modelling technique as a random effect (habitat suitability ~ model + (1|modelling technique)). Model performance (Full-model vs. Bio-model) was evaluated using AUC and Boyce index metrics (MaxTSS was highly correlated with AUC; Pearson's $r > 0.8$). For evaluation metrics, we again treated model type as a fixed effect and technique as a random effect (evaluation metric ~ model) + (1|modelling technique). GLMMs were fitted assuming a Beta distribution and a logit link (Zuur et al. 2009) using the 'glmmTMB' package (Brooks et al. 2017).

2.5 | Assessing Phylogenetic Climatic Niche Conservatism

Previous research suggests that climatic niche conservatism may be a key process underlying the speciation and geographical distribution of *Brachycephalus* species (Firkowski et al. 2016; Pie, Faircloth, et al. 2018). To investigate niche conservatism in the *Brachycephalus pernix* group, we quantified niche overlap between two identified clusters (see *Occurrence records*) using the approach by Broennimann et al. (2012). This approach employs a kernel density smoother to calculate species occurrence and environmental density within a reduced environmental space. Here, the reduced environmental space was composed of the first three principal components used in our model-based clustering. To delineate the geographic region associated with each cluster, we created a 2 km polygon around each occurrence point, taking into account the small range size of most species. We then applied the niche equivalency test (Warren et al. 2008), which randomly relocates the occurrences of both clusters between their ranges, generating a null distribution at which observed niche overlap is compared (Broennimann et al. 2012). We used 1000 background points for density calculations and repeated the randomisation process 200 times to ensure high confidence. We selected the equivalency test over the similarity test because most of the geographical distribution of the clusters overlap in space. Therefore, correcting for differences in densities of the environment is not necessary (Broennimann et al. 2012). The degree of niche overlap was measured using Schoener's *D* and Hellinger's *I* similarity indices (Warren et al. 2008), which vary between 0 (no overlap) and 1 (complete overlap). If the observed overlap falls outside the density of 95% of the simulated values, the null hypothesis of niche equivalency is rejected. Niche overlap analyses were carried out using the R packages 'ecospat' 3.2 (Di Cola et al. 2017) and 'ENMTools' 1.0.5 (Warren et al. 2021).

3 | Results

3.1 | Clustering Analysis

The first three axes of the PCA, derived from 16 environmental variables, were retained based on the broken-stick criterion (Table S3; Figure S4). Examination of the highest factor loadings for each PC axis indicates that PC1 is positively influenced by annual cloud cover and moisture index of the coldest quarter, PC2 is positively influenced by temperature annual range and negatively by moisture seasonality and precipitation of the wettest month, and PC3 is negatively influenced by solar radiation, aspect and P–T alpha (Table S3). The percentage contributions of PCs 1–3 were 25%, 24% and 14%, respectively (Table S3). PC1 and PC2 together contribute nearly half (49%) of the variation, which suggests that moisture availability (cloud cover and coldest quarter moisture) and temperature range with moisture seasonality are highly influential in shaping the ecological space. Based on model-based clustering using the first three PCs, the best-fitting model identified two environmental clusters (Figure S2; see above in *Locality records*), with the highest score of BIC (Figure S5). The best-fitting model indicates that the two clusters share equal volume and shape but differ in orientation, meaning that their main axes of variation point in different directions in multivariate space. In the paired plot of the clustering method (Figure S2), the two clusters are distinct, with less overlap along the PC2 axis compared to the other PCs.

3.2 | Ecological Niche Models and Assessment of Environmental Variables

The predictions generated by ESMs (ANN, GBM, GLM and EP) and M-PR (MaxEnt) demonstrated high performance based on AUC and MaxTSS values for both the Full and Bio models (Table 1). Additionally, our predictions were consistent with known presence occurrences, as indicated by Boyce index values ranging from 0.9 to 1 (Table 1). In the context of M-PR, the best-fitting models—identified by the lowest AICc values (Table 1)—included linear and quadratic feature classes with regularisation multipliers of 1.5, incorporating six environmental variables for Cluster 1 (Figure 2A), and linear feature classes with regularisation multipliers of 0.5, using seven variables for Cluster 2 (Figure 2B).

Niche projections indicated that the high environmental suitability predicted for members of the *Brachycephalus pernix* species group is distinctly concentrated in mountain ranges (Figures 3–5). Suitable habitats cover the Serra do Mar in the states of São Paulo, Paraná and Santa Catarina, as well as the Serra Geral and the coastal mountain chains of Santa Catarina

TABLE 1 | Performance metrics for model-selection procedures (M-PR, using MaxEnt) and ensemble of small models (ESMs) used to evaluate each model within each cluster. Metrics include Area Under the Curve (AUC), Maximum True-Skill Statistic (MaxTSS) and Boyce index. For M-PR, only the best models with the lowest AICc are shown. The Full-model incorporates a broad set of environmental variables (including topography, temperature, precipitation, etc.), while the Bio-model includes only bioclimatic factors. Modelling techniques: ANN, Artificial Neural Networks; EP, Ensemble Prediction; GBM, Gradient Boosting Machines; GLM, Generalised Linear Models and M-PR, Model-Selection Procedures via MaxEnt.

Ecological niche modelling	Cluster	AUC	Max TSS	Boyce index	AICc
Model-selection procedures (M-PR)					
Full-model	1	0.9941	0.981	0.871	455.37
	2	0.9953	0.977	0.973	381.52
Bio-model	1	0.9923	0.961	0.934	448.52
	2	0.9932	0.959	0.867	407.86
Ensembles of small models (ESMs)					
Full-model					
GLM	1	0.9941	0.969	0.923	
	2	0.9912	0.932	0.945	
GBM	1	0.9946	0.974	0.993	
	2	0.9867	0.897	0.986	
ANN	1	0.9959	0.970	0.993	
	2	0.9940	0.952	0.942	
EP	1	0.9958	0.976	0.952	
	2	0.9919	0.936	0.976	
Bio-model					
GLM	1	0.9919	0.955	0.926	
	2	0.9802	0.896	0.978	
GBM	1	0.9890	0.917	0.9	
	2	0.9768	0.923	0.89	
ANN	1	0.9949	0.973	0.933	
	2	0.9874	0.936	0.96	
EP	1	0.9940	0.965	0.958	
	2	0.9847	0.932	0.987	

("Serras Litorâneas") (Figures 1B, 3–5). Of the 50 presence records, only 2% were found in lowlands (1 record), 14% in submontane areas (7 records) and the majority—84%—were distributed evenly between montane (42%) and highland (42%) zones (21 records each) (Table S2; Figure S3B), highlighting a strong association with higher elevation habitats, consistent with model predictions.

Some potentially suitable habitats are located within Integral Protection Conservation Units in São Paulo, Paraná and Santa Catarina (Figure 5C). In São Paulo, these areas include Estação Ecológica Juréia-Itatins, Parque Estadual do Rio Turvo and Parque Estadual Lagamar de Cananeia. In Paraná, they encompass Reserva Biológica Bom Jesus, Parque Nacional Guaricana and Parque Nacional de Saint-Hilaire/Lange. In Santa Catarina, they include Parque Natural Municipal Morro do Baú, Parque Natural Municipal Morro dos Stinghen, Parque Natural Municipal Freymund Germer, Parque Nacional da Serra do Itajaí, Refúgio de Vida Silvestre de Itapema, Parque Estadual da Serra do Tabuleiro, Parque Nacional de São Joaquim and Reserva Biológica Estadual do Aguaí.

The projection of suitable habitats across land cover and land use types was derived from the GLM technique, which performed strongly in capturing broader areas of moderate suitability (see *Model comparisons and climatic niche conservatism evaluation*) within the Full-model framework. Forest Formation emerged as the dominant land cover type within predicted suitable areas across submontane, montane and highland zones (Figure 6A). In the submontane zone, forest formation accounted for 86.3% of the area (2220.16 km^2), followed by mosaics of use (7.9%; 203.11 km^2) and forest plantations (3.0%; 76.55 km^2). The montane zone was even more

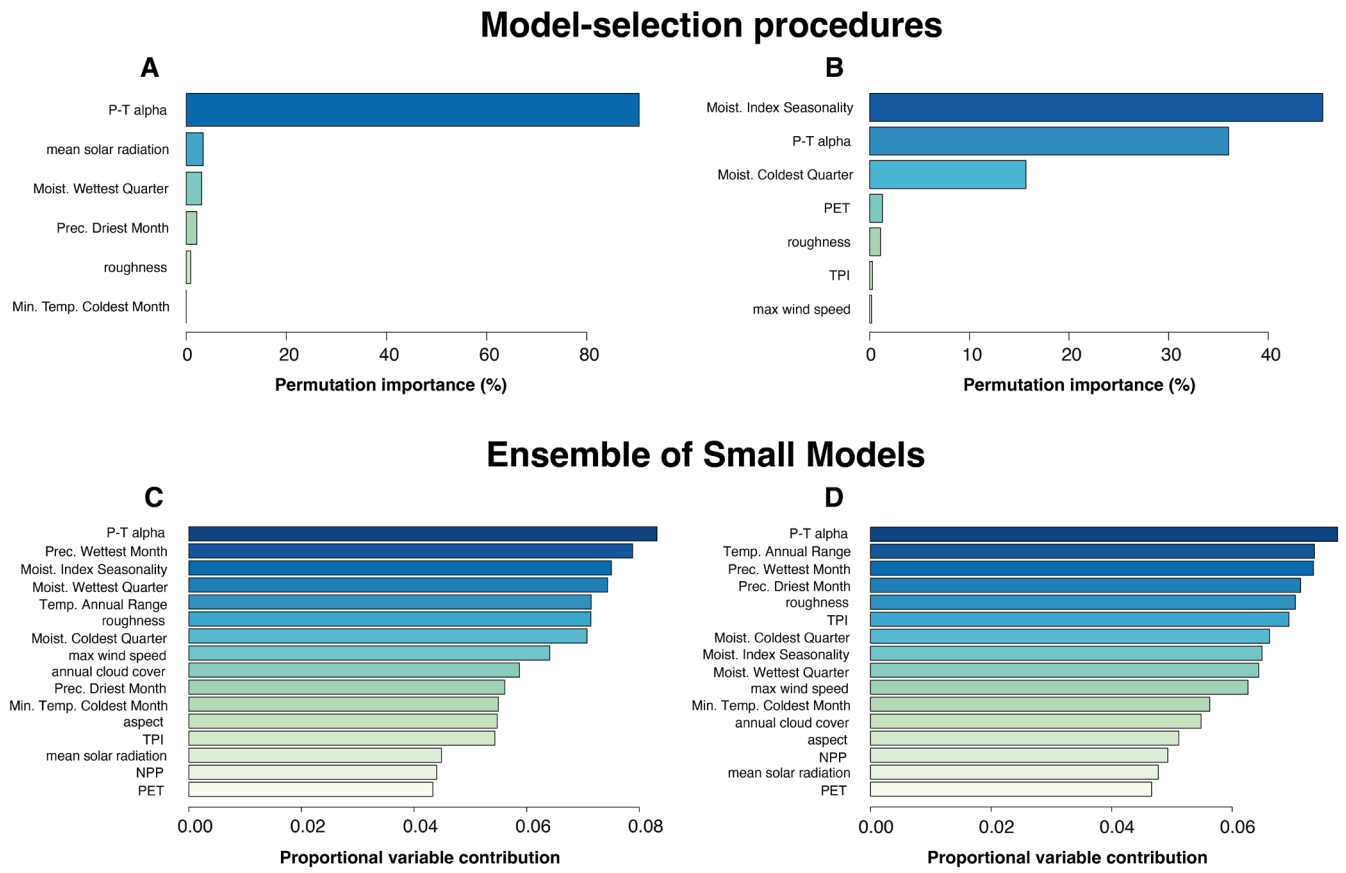

FIGURE 2 | Bar plots showing the environmental variable contributions used in the Full-model for each strategy (M-PR and ESMs) for Cluster 1 (A, C, respectively) and Cluster 2 (B, D). For M-PR, the environmental variables are displayed with their permutation importance from the best-fit models. For ESMs, the proportional variable contributions represent the weighted means of all models into a single ensemble model.

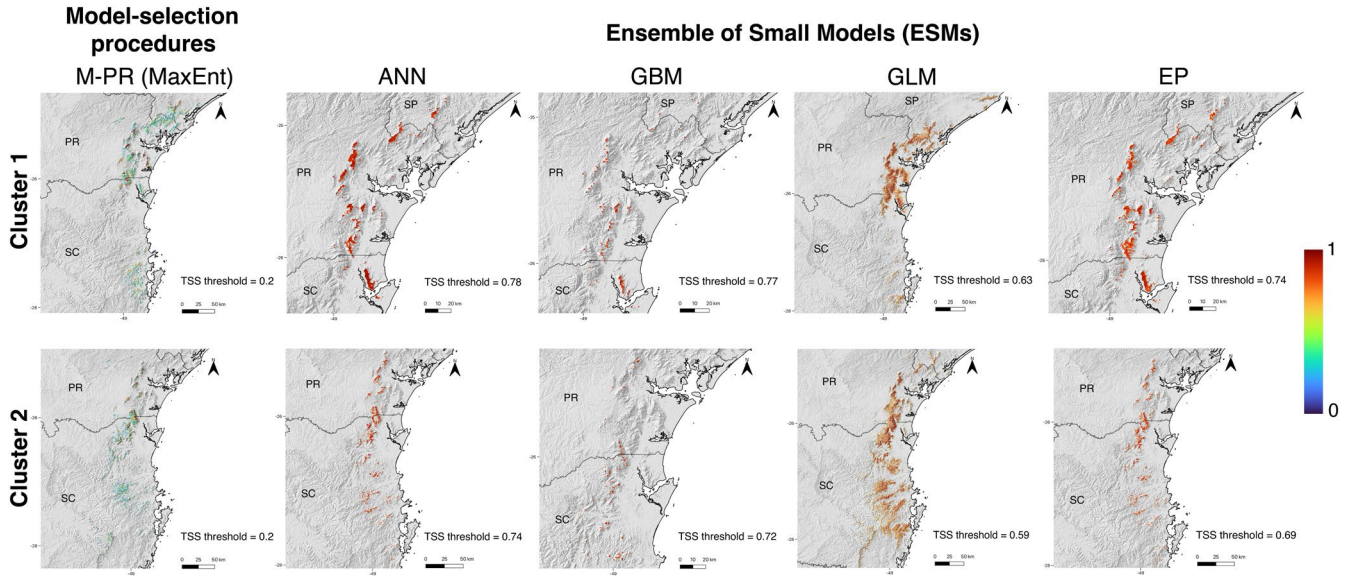

FIGURE 3 | Predicted distribution of suitable habitats under the Full-model for species of the *Brachycephalus pernix* group, split into clusters using the M-PR and ESMs (ANN, GBM, GLM and EP) strategies. The model maps are visualised using logistic probability values, with values below the TSS threshold for each technique not displayed. Presence probability is shown on a scale from 0 to 1, with the highest values shown in red. The Full-model incorporates a broader set of environmental variables, including topography, temperature and precipitation. Modelling techniques: ANN, Artificial Neural Networks; EP, ensemble prediction; GBM, Gradient Boosting Machines; GLM, Generalised Linear Models and M-PR = Model-Selection Procedures via MaxEnt.

strongly dominated by forest formation, covering 90.9% (4852.80 km^2), with mosaics of use (3.6%; 192.95 km^2) and forest plantations (2.9%; 157.02 km^2) comprising the next most extensive categories. In the highland zone, forest formation also prevailed (80.3%; 760.11 km^2), while rocky outcrops (7.8%; 73.43 km^2) and mosaics of use (3.8%; 35.95 km^2) were also present. Other land use types such as pasture, grassland and agricultural areas represented smaller proportions (< 4%) across all zones (Table S4). Although forest formation was dominant, small portions of the predicted suitable areas had already been cleared, totaling approximately 8.91 km^2 (0.35%) in the submontane zone, 3.30 km^2 (0.06%) in the montane zone, and 0.42 km^2 (0.04%) in the highland zone (Figure 6B).

Based on an assessment of the relative importance of environmental variables in the Full-model niche models for our two clusters, the permutation importance of M-PR and the variable contribution of ESMs (Figure 2) were aligned, with P–T alpha, precipitation of the wettest month, moisture index seasonality, moisture index of the wettest and coldest quarters, and temperature-related variables (including annual range and the coldest month) showing the highest contributions across clusters. Specifically, inspecting permutation variable importance within M-PR for each cluster, P–T alpha was the most important variable defining the environmental space of Cluster 1, while for Cluster 2, the key variables were moisture index seasonality, P–T alpha, and moisture index of the coldest quarter (Figure 2A,B). For the proportional variable contribution in ESMs, P–T alpha was a major contributor for both clusters, along with precipitation of the wettest month (Figure 2C,D). High-contribution variables for Cluster 1 included moisture index seasonality and moisture index of the wettest quarter (Figure 2A,C), whereas for Cluster 2, they included temperature annual range, precipitation of the driest month, roughness and TPI (Figure 2B,D). In contrast, the Bio-model assessment based solely on bioclimatic variables highlighted precipitation-related factors (including seasonality, the wettest month and the driest quarter) and temperature variables (diurnal and annual range) as the most significant contributors for both clusters (Figure S6).

3.3 | Model Comparisons and Climatic Niche Conservatism Evaluation

Generalised Linear Models (GLMs) revealed significant differences in both habitat suitability and suitable area (km^2) across modelling technique and elevation zones (Figure 7). For habitat suitability, all modelling techniques significantly outperformed M-PR in both the Full and Bio models (GLM: $p < 0.001$, Table 2; Tukey's HSD: $p < 0.001$, Table S5; Figure 7A,B), with ANN yielding the highest suitability estimates (Full-model: $\beta = 2.63$; Bio-model: $\beta = 2.67$; both $p < 0.001$). Highland areas exhibited 45% (Full) and 32% (Bio) higher suitability than lowlands ($p = 0.001$–0.002; Table 2), while montane and submontane zones showed intermediate values, with marginally significant differences in the Full-model ($p = 0.06$–0.08) and non-significant differences in the Bio-model ($p = 0.54$–0.69).

In contrast, for suitable area, M-PR predicted substantially larger extents than other techniques (Full: 159 km^2, Bio: 742 km^2, back-transformed from the model intercepts; both $p < 0.001$; Table 2; Tukey's HSD: $p < 0.001$, Table S6; Figure 7C,D). GLM predicted slightly larger areas than M-PR (Full: $\beta = 0.48$, $p = 0.058$; Bio: $\beta = 0.48$, $p = 0.462$), though these differences were not statistically significant. ANN and GBM predicted the smallest suitable areas, with reductions of 89%–98% compared to M-PR ($p < 0.001$, Figure 7C,D). Montane zones contained 24.3× (Full) and 17.7× (Bio) more suitable area than lowlands ($p < 0.001$, Table 2; Tukey's HSD: $p < 0.001$, Table S6), and both highlands and submontane zones also showed significantly greater extents (Full: 8–9×, $p < 0.001$; Bio: 4.4×, $p = 0.029$).

These statistical results were reflected in the spatial predictions, which consistently indicated that suitable habitats are concentrated in mountain ranges. ANN, which produced the highest suitability scores, predicted more spatially restricted areas within montane and highland zones under both the Full and Bio models (Table 2; Figures 3,4 and 7A–D). Similarly, GBM and EP yielded high suitability estimates with smaller predicted areas. The combination of high suitability and limited spatial extent in ANN, GBM and EP suggests greater discriminative power and more ecologically plausible predictions. For example, ANN predictions precisely identified optimal habitats, with a particularly high probability of new records in the Serras of Parque Nacional da Serra do Itajaí, Santa Catarina (Figure 5A). In contrast, GLM and M-PR exhibited weaker predictive performance: GLM produced moderate suitability estimates, while M-PR had the lowest scores (Figure 7A,B). Additionally, both techniques predicted broader suitable areas, with extensive coverage across submontane, montane and highland zones, and overestimated suitability in lowland regions—particularly in the Bio-model (Figures 4 and 7C,D).

Our results from the generalised linear mixed-effects indicated that the Full-model outperformed the Bio-model in predicting suitable areas ($p < 0.001$; Table S7; Figure S7A). This finding suggests that, in terms of accuracy, the Full-model provided more reliable predictions for habitat suitability, thereby minimising both commission and omission errors. Regarding evaluation metrics, the Full-model performed significantly better than the Bio-model in terms of AUC, demonstrating superior discriminatory ability ($p = 0.019$; Table 3). However, neither model showed a clear advantage based on the Boyce index (Table 3; Figure S7B).

The niche equivalency test revealed variation in the level of niche conservatism across the PCs for the two clusters (Table 4). The test indicated high niche overlap between PC1 and PC2, suggesting that both Cluster 1 and Cluster 2 share a significant amount of similarity regarding cloud cover and moisture availability (PC1), and temperature/moisture seasonality and precipitation (PC2). Moisture availability conditions appear to govern the niche space of these toadlets, resulting in their niche conservatism, a finding further supported by the selected environmental variables (see above). A moderate niche overlap was also observed between PC2 and PC3, along gradients of temperature annual range, moisture seasonality, precipitation (PC2) and solar radiation, aspect, P–T alpha (PC3). However, niche equivalency between PC1 and PC3 was rejected, with differences along gradients related to solar radiation, aspect, and P–T alpha (PC3)

TABLE 2 | Analysis of generalised linear models evaluating the performance of modelling techniques (ANN, GBM, GLM, EP, AND M-PR) within the Full and Bio models in predicting habitat suitability and the spatial extent of suitable areas across different altitudinal zones. Habitat suitability and suitable area (km^2) models were fitted using beta and gamma distributions, respectively. The Full model includes a broad set of environmental variables (topography, temperature, precipitation, etc.), while the Bio model uses only bioclimatic factors. Observations refer to the total number of data points used in model fitting. Bold values indicate statistically significant results ($p < 0.05$). Modelling techniques: ANN, Artificial Neural Networks; GBM, Gradient Boosting Machines; GLM, Generalised Linear Models; EP, Ensemble Prediction and M-PR, Model-Selection Procedures via MaxEnt.

	Full-model						Bio-model					
	Habitat suitability			Suitable area (km^2)			Habitat suitability			Suitable area (km^2)		
Predictors	**Estimates**	**Std. error**	***p***	**Estimates**	**Std. error**	***p***	**Estimates**	**Std. error**	***p***	**Estimates**	**Std. error**	***p***
(Intercept)	−1.37	0.13	**< 0.001**	5.07	0.23	**< 0.001**	−0.95	0.10	**< 0.001**	6.61	0.54	**< 0.001**
ANN	2.63	0.16	**< 0.001**	−2.22	0.25	**< 0.001**	2.67	0.12	**< 0.001**	−3.79	0.75	**< 0.001**
GBM	2.54	0.15	**< 0.001**	−3.51	0.25	**< 0.001**	2.09	0.11	**< 0.001**	−3.92	0.76	**< 0.001**
GLM	1.92	0.14	**< 0.001**	0.48	0.25	0.058	1.70	0.10	**< 0.001**	0.48	0.65	0.462
EP	2.32	0.15	**< 0.001**	−2.17	0.25	**< 0.001**	2.22	0.11	**< 0.001**	−2.97	0.75	**< 0.001**
Submontane	0.23	0.13	0.077	2.11	0.22	**< 0.001**	0.04	0.10	0.694	1.48	0.68	**0.029**
Montane	0.25	0.13	0.060	3.19	0.23	**< 0.001**	−0.06	0.10	0.540	2.88	0.73	**< 0.001**
Highlands	0.47	0.14	**0.001**	2.27	0.23	**< 0.001**	0.32	0.11	**0.002**	2.43	0.79	**0.002**
Observations	20			20			20			20		
R^2	0.956			0.992			0.973			0.950		

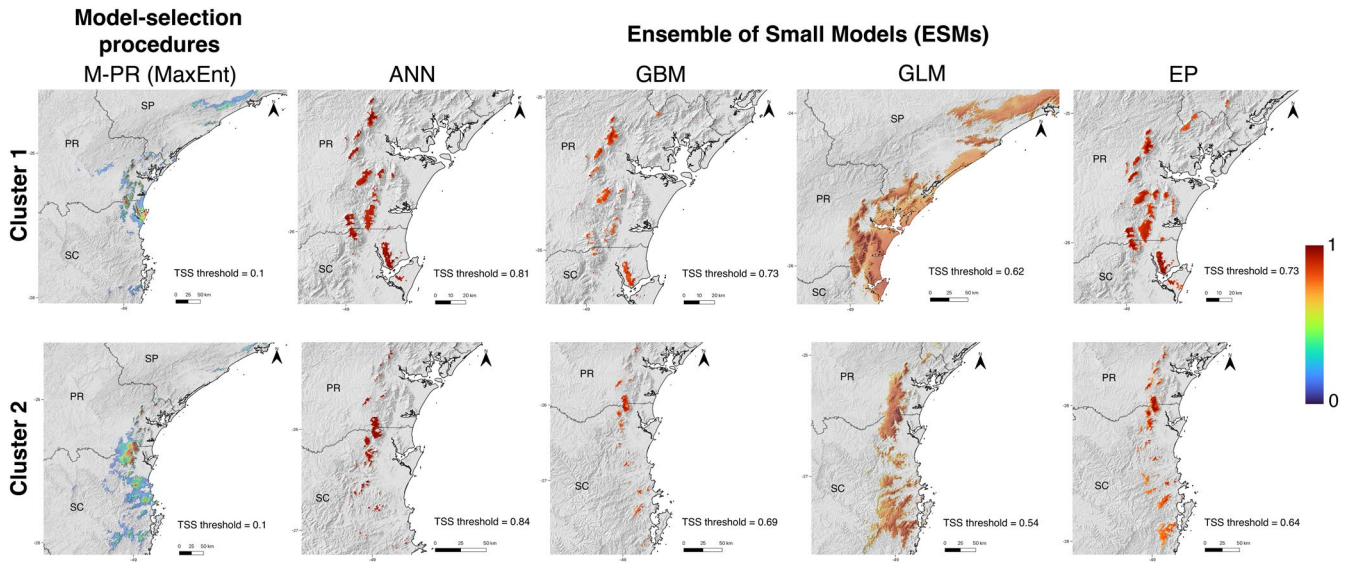

FIGURE 4 | Predicted distribution of suitable habitats under the Bio-model for species of the *Brachycephalus pernix* group, split into clusters using the M-PR and ESMs (ANN, GBM, GLM and EP) strategies. The model maps are visualised using logistic probability values, with values below the TSS threshold for each technique not displayed. Presence probability is shown on a scale from 0 to 1, with the highest values shown in red. The Bio-model includes only bioclimatic factors. Modelling techniques: ANN = Artificial Neural Networks; EP, Ensemble Prediction; GBM, Gradient Boosting Machines; GLM, Generalised Linear Models and M-PR, Model-Selection Procedures via MaxEnt.

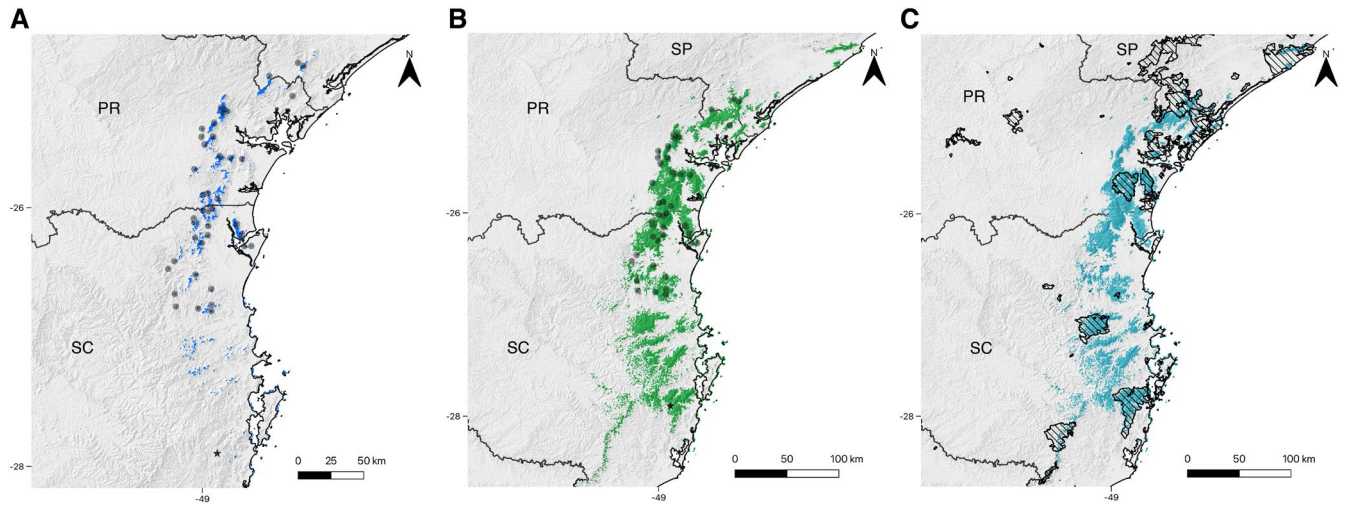

FIGURE 5 | Binary presence/absence maps from the best-performing Full-model (using a broad set of environmental variables), based on ESMs using the most accurate technique (ANN, with the highest suitability estimates) and the technique that predicted the largest suitable areas (GLM). Maps were thresholded using the maximum training sensitivity plus specificity (TSS) logistic threshold. Predicted presences are shown in blue (ANN; A) and green (GLM; B). Black points represent known occurrences; the star indicates *Brachycephalus tabuleiro* (Mângia et al. 2023), not included in model calibration (see *Discussion* for more details). The combined binary map (C) shows areas predicted by either ANN or GLM, highlighting suitable habitat (cyan) within Integral Protection Conservation Units. Modelling techniques: ANN, Artificial Neural Networks and GLM, generalised linear models.

and cloud cover, moisture index (PC1). Both metrics, Schoener's *D* and Hellinger's *I*, yielded similar results.

4 | Discussion

The niche projections generated in this study, using both modelling strategies: model-selection procedures via MaxEnt (M-PR) and Ensemble small models (ESMs) (Figures 3 and 4), highlight the critical importance of mountain ranges as suitable habitats while also revealing new potential areas for species within the *Brachycephalus pernix* group (Figure 5). Both modelling strategies demonstrated strong performance, particularly for microendemic species with few occurrence records. This was evidenced by high AUC (average values: M-PR = 0.994; ESMs = 0.990) and MaxTSS metrics (mean values: M-PR = 0.970; ESMs = 0.944). These values reflect robust predictive power and accuracy in distinguishing presence from absence points (Table 1). Predictions were further validated using the Boyce index, which indicated strong

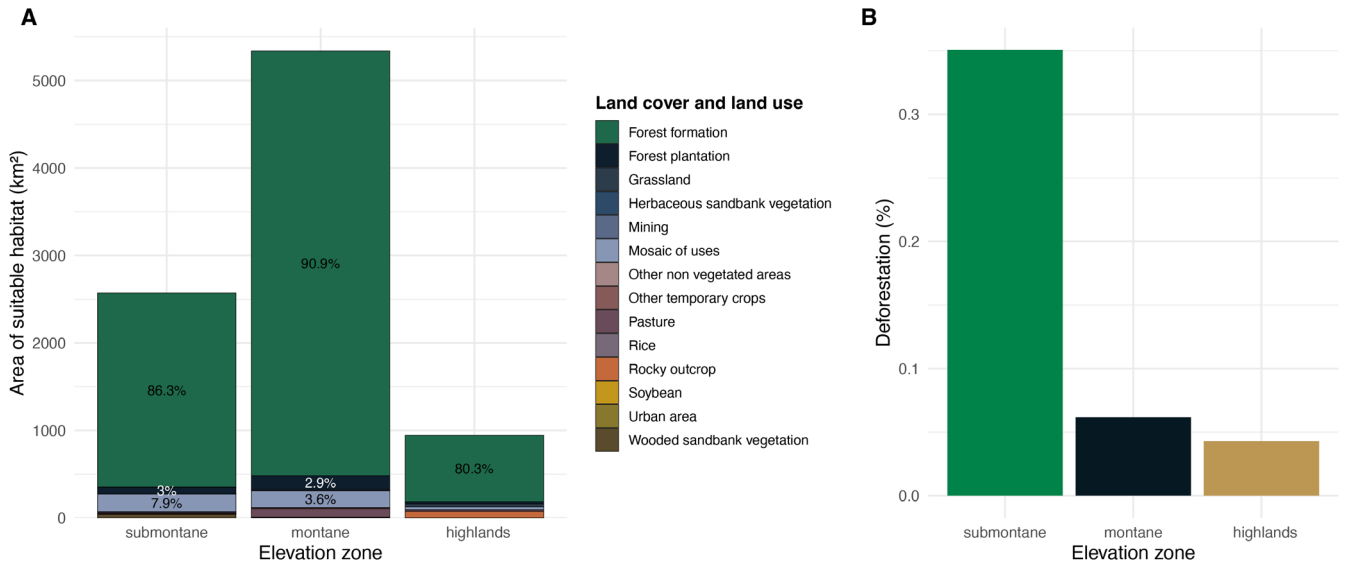

FIGURE 6 | Stacked bar chart showing the composition of land cover and land use within predicted suitable habitats across elevation zones (A). Bar heights represent the total area (in km^2) of suitable habitat, with colours indicating the percentage contribution of each land use type. Corresponding percentages and areas are detailed in Table S4. Bar chart illustrating the percentage of suitable habitat lost (deforestation) across elevation zones (B). Colours represent different zones, and bar heights indicate the total percentage of habitat loss in each.

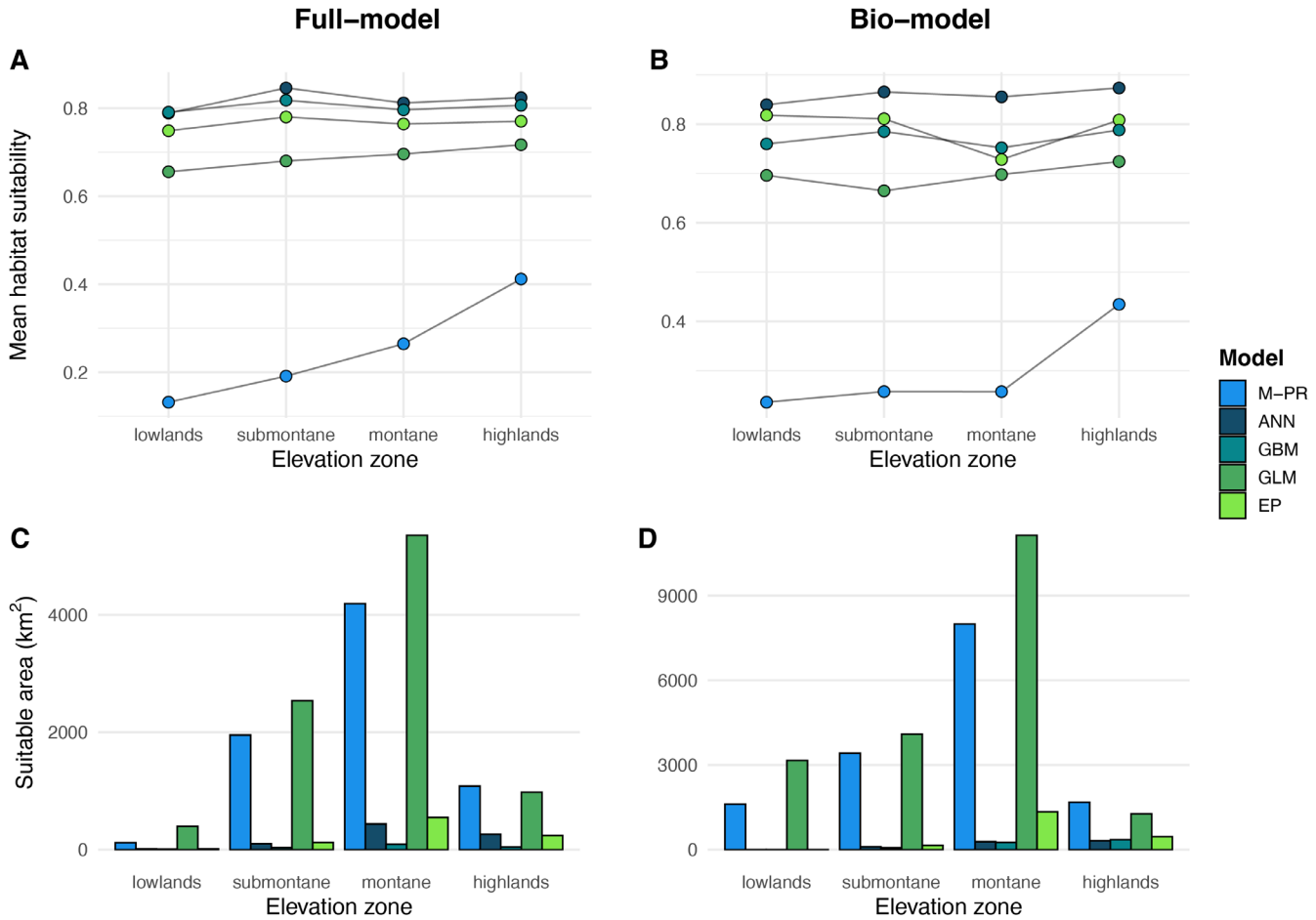

FIGURE 7 | Comparisons of habitat suitability and suitable area (km^2) across elevation zones for Full (A, C) and Bio (B, C) models. Line and point plots (A, B) show mean suitability across modelling techniques; bar plots (C, D) show corresponding suitable areas. Colours represent different technique types. The Full model incorporates a comprehensive set of environmental predictors, while the Bio model includes only bioclimatic variables. Modelling techniques: ANN, Artificial Neural Networks; EP, Ensemble Prediction; GBM, Gradient Boosting Machines; GLM, generalised linear models; and M-PR, Model-Selection Procedures via MaxEnt.

TABLE 3 | Analysis of generalised linear mixed-effects models evaluating the performance of Full and Bio models using two metrics: Area Under the Curve (AUC) and Boyce index. The models were evaluated with the Full model, which incorporates a broad set of environmental variables (topography, temperature, precipitation, etc.), and the Bio model, which uses only bioclimatic factors. Modelling techniques (ANN, GBM, GLM, EP and M-PR) were included as random effects to account for the variability across different model types. The AUC and Boyce index were used to assess model performance, with AUC representing the discriminatory ability of the model and the Boyce index measuring the consistency of predictions with observed occurrences. Random effects were included to account for the variation in model predictions across different techniques. The Observations refer to the total number of model comparisons evaluated in the analysis. Bold values indicate statistically significant results ($p < 0.05$). Modelling techniques: ANN, Artificial Neural Networks; EP, Ensemble Prediction; GBM, Gradient Boosting Machines; GLM, Generalised Linear Models; M-PR, Model-Selection Procedures via MaxEnt.

	AUC			Boyce index		
Predictors	**Estimates**	**Std. error**	***p***	**Estimates**	**Std. error**	***p***
(Intercept)	4.49	0.13	**<0.001**	2.65	0.23	**<0.001**
Full-model	0.45	0.19	**0.019**	0.48	0.33	0.144
Random effects						
σ^2		0.00			0.00	
τ_{00}		$0.00_{strategy}$			$0.07_{strategy}$	
ICC		0.47			0.98	
N		$10_{strategy}$			$10_{strategy}$	
Observations		20			20	
Marginal R^2/Conditional R^2		0.999/1.000			0.471/0.990	

TABLE 4 | Results of the niche equivalency tests for clusters 1 and 2, evaluating the level of niche overlap and conservatism using Schoener's *D* and Hellinger's *I* metrics. The loadings for each principal component (PC) are displayed in Table S3.

	Schoener's *D*	**Hellinger's *I***	***p* value *D***	***p* value *I***
PC1 vs. PC2	0.64	0.78	0.73	0.65
PC1 vs. PC3	0.33	0.51	0.03	0.04
PC2 vs. PC3	0.44	0.6	0.31	0.27

agreement between predicted suitable areas and observed occurrences (average: M-PR = 0.911; ESMs = 0.953; Table 1). Notably, ESM techniques (ANN, GBM, GLM and EP) outperformed M-PR (MaxEnt) in predicting suitable habitats, with predictions more concentrated in highland, montane and submontane zones. In contrast, GLM and M-PR predicted broader suitable areas, likely overestimating habitat suitability in lowland regions where environmental conditions are less favourable (Table 2; Figure 7). Our findings indicate that the inclusion of a broader set of environmental variables—beyond bioclimatic factors—improved niche predictions across all modelling techniques, surpassing the performance of bioclimatic variables alone, as shown by comparisons using our generalised linear models (Tables 3, S7; Figure S7). Specifically, models incorporating variables related to precipitation and moisture consistently yielded better predictions, as highlighted in permutation importance for M-PR and variable contributions in ESMs (Figure 2). These factors appear to play a crucial role in determining the realised niche of this species group. Importantly, support for niche equivalency (e.g., PC1 vs. PC2: *p*-value Schoener's $D = 0.73$; *p*-value Hellinger's $I = 0.65$; Table 4) suggests niche conservatism in its strict sense (Warren et al. 2008; Broennimann et al. 2012). This reinforces the idea that mountain ranges may act as long-term refuges, buffering suitable habitats during climatic fluctuations. In the sections that follow, we address these results.

4.1 | Evaluating Niche Predictions for Microendemic Montane Species

Our Full-model niche outperformed the Bio-model niche in predicting suitable areas ($p < 0.001$; Table S7) and demonstrated superior discriminatory ability in distinguishing between areas of species presence and absence (AUC: $p = 0.019$; Table 3). This improvement was achieved by incorporating a broader range of environmental factors, including topography, temperature, precipitation, solar radiation, soil moisture, wind speed and monthly and macro environmental variables. These factors capture environmental heterogeneity and help define the boundaries of species distributions, constraining potential habitats within the fundamental niche space. This is particularly critical for species with restricted ranges, such as those in the *Brachycephalus pernix* group. Several studies suggest that incorporating a diverse set of environmental variables can enhance the accuracy of habitat suitability predictions compared to models based solely on bioclimatic variables, thereby minimising both commission and omission errors (e.g., Raxworthy et al. 2007; Markovic et al. 2012; Pérez and Font 2012; Cao et al. 2013; Hammond et al. 2016; Cobos et al. 2019). Models relying on a single type of variable risk underfitting or overfitting niche predictions (e.g., Pineda and

Lobo 2009; Vasconcelos et al. 2012) and may fail to capture sufficient information about a species' niche, particularly for species with small geographic ranges, which are more vulnerable to inaccurate distribution models. Although including more variables in the Full-model increases the potential for overfitting, we addressed this concern by reducing dimensionality and selecting biologically relevant variables, which improved model performance (Farrell et al. 2019). Our modelling strategies also include safeguards against overfitting. For instance, M-PR via MaxEnt was fine-tuned by optimising regularisation parameters using cross-validation, which involved splitting the data into training and testing subsets (Merow et al. 2013; Cobos et al. 2019; Farrell et al. 2019). Similarly, ESMs mitigate overfitting by averaging simple small models into an ensemble (Breiner et al. 2015, 2018).

The modelling techniques used in Ensemble small models (ESMs), including ANN (Artificial Neural Networks), GBM (Gradient Boosting Machines), GLM (Generalised Linear Models) and EP (Ensemble Prediction), have proven to be more effective for modelling microendemic species (Breiner et al. 2015) compared to model-selection procedures using MaxEnt (M-PR) under both the Full-model and Bio-model approaches (Table 2; Figure 7). Projections from our ESMs consistently identified highland, montane and submontane zones as the most suitable habitats, with highlands exhibiting 32%–47% higher suitability than lowlands and significantly greater predicted habitat area at both montane and submontane elevations. These results are supported by the Boyce index, which indicated strong concordance between predicted suitability and observed occurrences in elevated regions (Figure S3B). This pattern aligns with previous research demonstrating that species in the *Brachycephalus pernix* group are restricted to high-elevation habitats (Pie et al. 2013). The use of the Boyce index to evaluate our predictive models is a reliable approach and critical for identifying new populations without overestimating potential suitable areas (Hirzel et al. 2006; Breiner et al. 2015, 2018). This is particularly important for microendemic and threatened species with presence-only data, such as the *B. pernix* group (Bornschein et al. 2019; e.g., Engler et al. 2004; Scherrer et al. 2019).

4.2 | Predicting Suitable Habitats in Montane Environments: Insights From Modelling Techniques

Despite the overall effectiveness of the ESMs, individual modelling techniques within ESMs varied in sensitivity and specificity. ANN and GBM produced more conservative predictions, identifying smaller areas of suitable habitat. In particular, ANN demonstrated high predictive power, suggesting precise identification of optimal habitats. This strength lies in its ability to identify correlated patterns without requiring prior assumptions about underlying distributions, enabling it to capture complex relationships in the data while minimising overfitting (Goethals et al. 2007; Kulhanek et al. 2011). In contrast, EP, an ensemble approach that averages predictions from multiple techniques, showed robust performance but did not outperform top techniques like ANN, a finding consistent with previous studies (Breiner et al. 2015).

GLM predicted moderate suitability estimates, accompanied by a broader spatial extent of suitable habitat, particularly across submontane and montane zones. While this broader extent could be interpreted as an overestimation due to the relatively moderate suitability values, the model's predictions align with the known distribution of *Brachycephalus tabuleiro*, a recently described species from the Serras Litorâneas (Mângia et al. 2023). This species inhabits montane regions also identified as suitable by GLM, lending further support to the model's reliability (Figures 5B and S3B). This pattern can be attributed to GLM's capacity to assess species-habitat relationships (Austin 1987), corroborating the preference of these toadlets for montane environments.

Although M-PR predicted the largest suitable areas, it consistently produced the lowest suitability values (Figure 7). This pattern may be linked to the use of the AIC criterion in selecting the best-performing niche model within the M-PR framework. AIC balances model fit and complexity to optimise explanatory power in ecological space, but it does not directly assess predictive accuracy in geographic space (Velasco and González-Salazar 2019). This limitation may explain why M-PR identified broad areas of suitability with relatively low estimated habitat quality. As is noted by Breiner et al. (2018), no single modelling technique is universally superior. The performance of each technique depends on the particularities of data that affect model prediction (Thibaud et al. 2014; Qiao et al. 2015).

4.3 | Scattered Montane Habitats and Climatic Drivers of *Brachycephalus* Distribution

Pie et al. (2013) provided a reasonable estimate of suitable habitats, reporting that areas to the south were restricted to the Serras Litorâneas in the state of Santa Catarina, southern Brazil. Species of the *Brachycephalus pernix* group found further south include *B. boticario*, *B. fuscolineatus* and *B. tabuleiro*, occurring in Morro do Cachorro, Morro do Baú and Serra do Tabuleiro, respectively, within Santa Catarina (Ribeiro et al. 2015; Pie, Ribeiro, et al. 2018; Mângia et al. 2023). Our niche models, incorporating heterogeneous predictors (Full-model), indicate additional suitable habitats with a scattered distribution across the mountains and foothills of Santa Catarina, extending northward into São Paulo. This broadens the potential range of the *B. pernix* group (Figures 1B and 5). These predicted habitats are concentrated in the Serras Litorâneas (spanning submontane and montane zones) and the Serra Geral (spanning montane and highland zones) in Santa Catarina, with further unexplored areas identified in the mountainous region of the Estação Ecológica Juréia-Itatins in São Paulo, encompassing submontane, montane and highland zones.

The most influential environmental variables selected in our models, particularly those related to moisture and precipitation, highlight the importance of water availability for the occurrence of *Brachycephalus* toadlets in montane environments (Figure 2). The mountain regions (submontane, montane and highland zones) of the southern BAF correspond to Dense Ombrophilous Forests (Veloso et al. 1991), which are characterised by high moisture levels due to fog interception, frequent

cloud cover, high humidity and low evapotranspiration (Bruijnzeel and Proctor 1995; Scheer and Mocochinski 2009; Meireles and Shepherd 2015). These montane conditions are critical for *Brachycephalus* species, which depend on moist leaf litter for activities such as egg-laying (Haddad and Prado 2005) and exhibit behavioural adaptations to minimise water loss, such as pressing their ventral surface against wet substrates (Mari et al. 2022).

4.4 | Climatic Niche Conservatism

As expected, our niche equivalency results (Table 4) supported niche conservatism in species of the *Brachycephalus pernix* group (Firkowski et al. 2016; Pie, Faircloth, et al. 2018). Specifically, our niche equivalency approach compares clusters that were separated based solely on climatic data, even across phylogenetically distant species. The k-means method partitions points such that the difference between clusters was maximised. Taken together, those factors may inflate estimates of niche divergence between clusters, leading to conservative estimates of climatic niche overlap.

Our findings indicate that more pronounced niche overlap among these toadlets is related to moisture availability (cloud cover and moisture index) and temperature ranges (e.g., Table 4: PC1 vs. PC2), variables typical of mountain climates, as mentioned earlier. The retention and tracking of ancestral ecological niches, particularly with regard to moisture conditions across mountainous regions, appear to provide suitable survival conditions that may be under selection. Under the niche conservatism scenario, we attribute the role of the southern mountains of BAF in providing persistent small pockets with humidity and orographic rain as microrefugia against climate change (Brown and Ab'Saber 1979; Carnaval and Moritz 2008), thereby helping to preserve these toadlets from extinction over time. Additionally, we support the evolutionary scenario proposed by Pie, Faircloth, et al. (2018), in which these toadlets speciated in allopatry within microrefugia, with multiple scenarios of secondary contact during periods of connectivity, evolving within a sky-islands system (McCormack et al. 2009; Pie, Faircloth, et al. 2018).

4.5 | Conservation Challenges for *Brachycephalus* Habitats

Our model predictions reveal that while Forest Formation remains the dominant land cover type within predicted suitable habitats for the *Brachycephalus pernix* group, portions of these habitats have already been lost to deforestation. Although the total cleared area is relatively small, it represents the irreversible loss of microhabitats restricted to montane regions—conditions essential for the persistence of these microendemic species due to their narrow thermal tolerances and limited distributions (Ribeiro et al. 2015). Deforestation in these montane habitats primarily reduces soil moisture and disrupts local microclimates, potentially leading to drier, semi-arid conditions (Doumenge et al. 1995; Ataroff and Rada 2000; Lawton et al. 2001; Martinelli 2007).

While some suitable habitats fall within Integral Protection Conservation Units, such as Parque Nacional da Serra do Itajaí and Parque Nacional de São Joaquim, a substantial portion lies outside protected areas, particularly in the states of Paraná and Santa Catarina (Figure 5C; e.g., Sales and Pires 2023). These states have experienced some of the highest deforestation rates in southern Brazil between 2002 and 2023—2.4% in Paraná and 3.9% in Santa Catarina (globalforestwatch.org)—mainly driven by agriculture (Bornschein et al. 2019). The ongoing habitat loss outside protected areas, especially in montane zones, highlights the urgent need for targeted conservation efforts. Identifying and preserving remaining suitable habitats—particularly those not covered by current protection frameworks—should be a conservation priority for this group of microendemic species.

5 | Conclusion

This study highlights the critical importance of submontane, montane and highland habitats in shaping the ecological niches and distribution patterns of the *Brachycephalus pernix* group. By applying Ensemble of small models (ESMs) with a comprehensive set of environmental predictors (Full-model), we accurately identified potential areas of suitable habitat for range-restricted species. Moisture- and precipitation-related variables emerged as key determinants of habitat suitability for these microendemic toadlets. Our findings emphasise the importance of incorporating diverse environmental predictors to improve niche model accuracy and minimise both commission and omission errors, particularly for narrowly distributed and threatened species. This modelling framework may also be applicable to other microendemic taxa, such as *Scytalopus* birds (Pulido-Santacruz et al. 2016). The strong performance metrics of our models underscore their reliability in identifying suitable habitats, even when occurrence data are limited.

The modelling techniques ANN and GLM demonstrated good performance in modelling the ecological niches of species within the *Brachycephalus pernix* group. ANN exhibited higher discriminative power and produced more ecologically plausible predictions, accurately identifying areas with a high probability of containing new records of these toadlets. In contrast, GLM performed optimally in predicting broader spatial extents with moderate suitability values, an important feature for informing conservation planning where some false positives are acceptable. While each method offers distinct strengths, the complementary use of ANN for precision and GLM for broader habitat detection provides valuable insights into the environmental preferences of these microendemic amphibians.

Importantly, the projections not only reaffirmed known montane regions as key habitats but also revealed previously unexplored highland zones with high suitability, followed by montane and submontane areas. These insights refine our understanding of the ecological requirements of the *B. pernix* group and underscore the role of mountain ranges as long-term climatic refugia. This pattern is consistent with climatic niche conservatism, particularly related to moisture availability, which appears to have facilitated the persistence and diversification of these microendemic toadlets within humid montane microrefugia.

Lastly, significant portions of the predicted suitable habitats remain unprotected and are increasingly threatened by deforestation and agricultural expansion, particularly in Paraná and Santa Catarina. These findings underscore the urgent need for targeted conservation strategies to safeguard critical habitats, preserve ecological integrity and ensure the long-term survival of these unique microendemic species.

Author Contributions

C. Daniel Rivadeneira: conceptualization, data curation, formal analysis, investigation, methodology, validation, writing – original draft, writing – review and editing. **Andreas Schwarz Meyer:** conceptualization, data curation, formal analysis, investigation, methodology, validation, writing – original draft, writing – review and editing. **Marcos R. Bornschein:** conceptualization, methodology, writing – original draft, writing – review and editing. **Luiz F. Ribeiro:** conceptualization, methodology, writing – original draft, writing – review and editing. **Marcio R. Pie:** conceptualization, investigation, methodology, project administration, supervision, writing – original draft, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data necessary to repeat our analyses is available.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.