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IDENTIFICATION OF KEY HABITATS FOR THE CONSERVATION OF THREE BIRD SPECIES IN THE ECUADORIAN CHOCÓ BIOGEOGRAPHIC REGION: A DIFFUSE OVERLAP APPROACH TO CURRENT AND FUTURE ECOLOGICAL NICHES

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ABSTRACT. Climate change is inducing modifications in species distribution patterns within biodiverse regions such as the Ecuadorian Chocó Biogeographical region. This study identifies priority conservation areas for three key bird species (*Cephalopterus penduliger, Morphnarchus princeps,* and *Bangsia edwardsi*) using ecological niche modeling and fuzzy overlay approaches. MaxEnt software was used to project current and future suitability under the SSP585 scenario (2021 - 2040), integrating bioclimatic and topographic variables with presence records. Validation using TSS and AUC indicated robust model performance. Results project heterogeneous responses to climate change: a critical niche contraction for *Cephalopterus penduliger* (31.4% loss of suitable habitat) and a moderate reduction for *Morphnarchus princeps* (-10.9%), driven by thermal and topographic constraints. In contrast, *Bangsia edwardsi* showed a potential range expansion of 16.6% towards higher altitudes. Fuzzy overlay analysis (Fuzzy Gamma) highlighted the mountainous foothills in the east of the region (800-1,800 m a.s.l.) as priority climate refugia. We conclude that while refugia exist, the viability of these species will depend on the protection of altitudinal corridors against landscape fragmentation.

Identificación de hábitats clave para la conservación de tres especies de aves en el Chocó Biogeográfico Ecuatoriano: Un enfoque de superposición difusa del nicho ecológico actual y futuro

RESUMEN. El cambio climático está induciendo modificaciones en los patrones de distribución de especies en regiones biodiversas como el Chocó Biogeográfico Ecuatoriano. Este estudio identifica áreas prioritarias para la conservación de tres especies de aves clave (*Cephalopterus penduliger, Morphnarchus princeps* y *Bangsia edwardsi*) mediante modelado de nicho ecológico y superposición difusa. Se utilizó el software MaxEnt para proyectar la idoneidad del hábitat actual y futuro bajo el escenario SSP585 (2021 - 2040), integrando variables bioclimáticas, topográficas y registros de presencia. La validación mediante TSS y AUC indicó un desempeño robusto de los modelos. Los resultados proyectan respuestas heterogéneas ante el cambio climático: una contracción crítica del nicho para *Cephalopterus penduliger* (pérdida del 31,4 % de hábitat idóneo) y una reducción moderada para *Morphnarchus princeps* (-10,9 %), impulsadas por restricciones térmicas y topográficas. En contraste, *Bangsia edwardsi* mostró una expansión potencial del 16,6 % hacia zonas de mayor altitud. La superposición difusa (Fuzzy Gamma) destacó las estribaciones montañosas al este de la región (800-1.800 m a.s.l.)

como refugios climáticos prioritarios. Se concluye que, si bien existen áreas de refugio, la viabilidad de estas especies dependerá de la protección de corredores altitudinales frente a la fragmentación del paisaje.

Key words: species distribution, climate change, tropical biodiversity, ornithology.

Palabras clave: distribución de especies, cambio climático, biodiversidad tropical, ornitología.

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1. Introduction

Climate change is causing significant alterations in species distribution patterns globally (Chen *et al.*, 2011). Variations in temperatures, changes in precipitation dynamics, and the increasing frequency of extreme weather events have had a notable impact on biodiversity, affecting not only the structure and functioning of ecosystems, but also the geographical distribution of species, according to the Intergovernmental Panel on Climate Change (IPCC, 2023). These changes have the potential to cause species to move to new areas, alter population dynamics, and even cause local extinctions, underscoring the importance of studying how species respond to these environmental changes (Thomas *et al.*, 2004; Vilela *et al.*, 2020).

In this context, Species Distribution Models (SDMs) are widely used as predictive tools for estimating the geographic distribution of species based on environmental conditions. These models are essential in biogeography, landscape ecology, and conservation biology, as they allow us to predict how species distributions might change in response to changes in climate, land use, or large-scale environmental alterations (Guisan and Thuiller, 2005). SDMs are based on geospatial and ecological data, using the relationship between the locations where a species is present and a series of environmental variables, such as temperature, precipitation, food availability, and vegetation cover, to generate predictions about habitat suitability in unsampled areas or under future climate scenarios (Franklin, 2010).

One of the most robust and widely used approaches within SDMs is the Maximum Entropy (MaxEnt) algorithm, which models the distribution of a species using presence data combined with background points that act as pseudo-absences to estimate environmental suitability (Phillips *et al.*, 2006). This makes MaxEnt a useful tool in situations where presence-absence data are limited or incomplete, which is common for many rare or understudied species (Elith *et al.*, 2011). MaxEnt is based on the principle of maximum entropy, which means that it generates predictions about the potential distribution of the species by seeking the most uniform habitat suitability or ecological niche possible, given the constraints imposed by the input data (Phillips *et al.*, 2006). This makes it a statistically rigorous model, which maximizes the likelihood that predictions reflect reality, even when knowledge about the species' distribution is partial or uncertain.

SDMs also have critical applications in conservation planning and management. These models can be used to identify priority areas for the conservation of endangered species, model the impact of climate change on species, and develop management plans for habitat restoration (Araújo and Peterson, 2012; Moya *et al.*, 2017). Specifically, in the Ecuadorian Chocó, where biodiversity is extremely high and anthropogenic pressure is intense, the use of distribution models can help identify critical areas for conservation and anticipate how climate change will affect habitat availability for species native to the Chocó biogeographic region and the tropical Andes (Fagua and Ramsey, 2019). In addition, SDMs allow for the evaluation of the possibility of invasive species expansion, helping environmental managers and government institutions make proactive decisions to mitigate their impacts (Guisan *et al.*, 2014; Jácome *et al.*, 2019a).

In this context, fuzzy overlap is a technique that allows the results of multiple species distribution models to be combined, assigning degrees of membership that reflect the possibility of coexistence of different species in a specific area (Visser and de Nijs, 2006). Therefore, the objective of this study is to identify priority areas for the conservation of three bird species using SDMs and fuzzy overlap, projecting future habitat changes under the SSP585 scenario (2021-2040).

2. Materials and methods

2.1. Study area

The study focused on the Ecuadorian Biogeographic Chocó (Fig. 1), located in northwestern South America, part of a neotropical ecoregion of high biological importance that extends from Panama to northwestern Peru (Tumbesina Region) (Myers *et al.*, 2000). It is characterized by high rainfall, with an annual range of between 3,000 and 7,000 mm, due to its geographical location on the continent, with an altitudinal range from 0 to 2,082 meters above sea level, covering everything from mangroves to tropical rainforests in the western mountain range (Dodson and Gentry, 1991; Sierra *et al.*, 2002). Temperatures range from 24 to 27 °C in low-lying areas and from 15 to 24 °C in areas adjacent to the mountain range. This area covers 44,478.27 km², according to the geoportal of the Ministerio de Ambiente, Agua y Transición Ecológica (MAATE) (https://www.ambiente.gob.ec/). These characteristics make it a strategic site for scientific research and analysis of ecological processes, especially in the study of biodiversity, as the area faces various anthropogenic pressures such as deforestation, climate change, legal and illegal metal mining, and agricultural expansion.

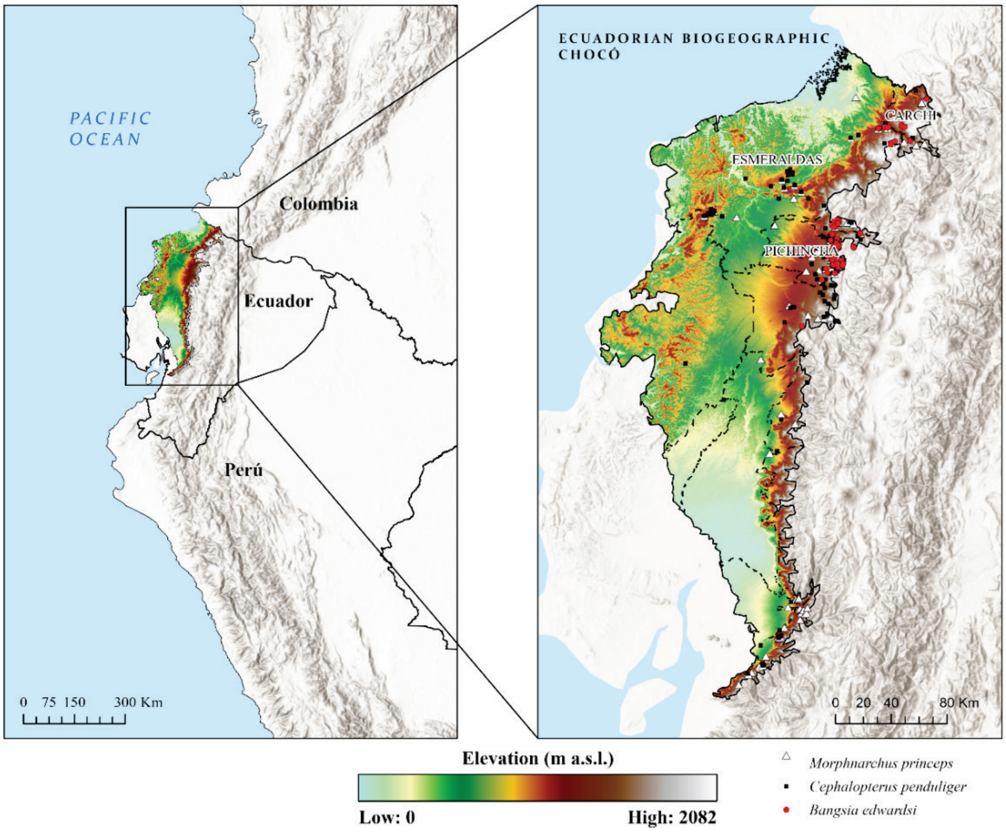

Figure 1. Geographic location of the Ecuadorian Biogeographic Chocó region. Points indicate presence of Cephalopterus penduliger*,* Morphnarchus princeps*, and* Bangsia edwardsi*.*

This site is characterized by remarkably high levels of endemism, as it is estimated to have around 9,000 species of vascular plants, 25% of which are endemic to the area. In the Ecuadorian Chocó, there are an estimated 6,300 species of plants, constituting 25% of the country's flora, 13% of which are endemic. It is also home to animals found nowhere else in the world; birds, including migratory birds, number approximately 830 species, of which 85 (10.2%) are endemic (Myers *et al.*, 2000) However, despite its extraordinary biological wealth, the Chocó faces serious threats due to climate change and an increased rate of deforestation since 2010, driven mainly by agricultural expansion and livestock farming, which endangers a large number of unique species and ecosystems (Fagua and Ramsey, 2019).

2.2. Species of biological importance in the Ecuadorian Chocó Biogeographic Region

The species *Cephalopterus penduliger, Morphnarchus princeps*, and *Bangsia edwardsi* were selected to model their potential distribution in the Ecuadorian Chocó Biogeographic Region due to their ecological relevance, conservation value, and sensitivity to climate change and landscape transformation processes. Although these species are not exclusive to the Chocó and are also distributed in the Tropical Andes, their populations in this region face disproportionate pressure associated with habitat fragmentation and accelerated loss of forest cover. *Cephalopterus penduliger,* categorized as a vulnerable species, is particularly sensitive to deforestation and plays a key role as a seed disperser in mature forests, so its presence reflects the conservation status of forest ecosystems. *Morphnarchus princeps* is considered an umbrella species and one of the top predators, whose persistence depends on large areas of continuous habitat, indirectly contributing to the conservation of multiple species and the regulation of food webs. *Bangsia edwardsi*, on the other hand, has more restricted niche requirements and high sensitivity to microclimatic changes, making it an early indicator of environmental changes associated with climate change. It is also an emblematic species that serves as a symbol of conservation and awareness of the problems facing this region (Freile *et al.*, 2019; Ridgely and Greenfield, 2001; Sergio *et al.*, 2006).

Together, these species represent different trophic levels, ecological functions, and degrees of specialization, allowing for an integrated assessment of the effects of climate change and anthropogenic pressure on the potential distribution of biodiversity in one of the most endemic and biologically diverse regions of the Neotropics. Modeling their current and future distribution provides relevant information for planning conservation and management strategies in the Ecuadorian Biogeographic Chocó.

2.3. Species occurrence data

All occurrence records were obtained from the Global Biodiversity Information Facility (GBIF) (Fig. 1). A data depuration was performed, eliminating duplicates and geographic errors, resulting in a final set of 96 records for *B. edwardsi* (GBIF.org, 2024a), 118 for *C. penduliger* (GBIF.org, 2024b) and 76 for *M. princeps* (GBIF.org, 2024c). Although complementary field visits were made for visual verification of habitats in the study area, the models were constructed exclusively with standardized GBIF data to ensure statistical reproducibility and avoid spatial sampling biases.

2.4. Predictor variables

To characterize the current climate niche, WorldClim v2.1 (https://worldclim.org/) bioclimatic variables corresponding to the historical average for 1970-2000 were used (Fick and Hijmans, 2017). These data have different spatial resolutions; therefore, a resolution of 30 arc-seconds was chosen, corresponding to 1 km2 per pixel. The data were downloaded in a ".zip" file format, which has 19 layers with a GeoTiff extension.

For better model fit and accuracy, biophysical variables based on species ecology were investigated. For this reason, the topographic humidity index (THI) was used, which estimates a relationship between slope and water flow tendency, reflecting an approximation of the potential humidity of the area (Besnard *et al.*, 2013). Consequently, Sierra-Morales *et al.* (2021) indicate that tropical montane cloud forests are characterized by high levels of humidity and high forest density, where species have evolved, and that a decrease in humidity would affect these forests and lead to the extinction of species adapted to these areas. Elevation (Bioe) and slope are variables with a significant impact on the distribution of birdlife, given that the structure and composition of vegetation change according to altitude. This is how local and regional endemism is related to altitudinal gradients, especially in the tropics where evidence suggests that the rate of altitudinal change and direction (upward and downward) is not uniform across all species (Neate-Clegg *et al.*, 2021) Proximity to road infrastructure, such as highways and railways, acts as a physical barrier that limits the dispersion and movement of birds, fragmenting their ecosystems. Finally, a vegetation cover layer was used, as birdlife has certain preferences for habitats, forest structures, the presence of undergrowth, or canopy density, which influence their distribution (Canterbury *et al.*, 2000).

To reduce model overfitting, the collinearity between the predictor variables was evaluated using Pearson's correlation analysis. A threshold of $|r| \geq 0.7$ was applied, eliminating highly correlated variables and retaining only those with values of $|r| < 0.7$, prioritizing their ecological relevance. Subsequently, the Variance Inflation Factor (VIF) was calculated for the reduced set of variables, retaining only those with VIF values ≤ 10 as an additional criterion to minimize redundancies (Jácome *et al.*, 2019b). As a result of this process, highly correlated bioclimatic variables, such as Bio 3, Bio 6, and Bio 10, were eliminated, retaining only those with greater biological relevance and statistical significance for the species under study.

The final set of predictors included bioclimatic and topographic variables (elevation, slope (%) and topographic humidity index (THI)), as well as anthropogenic pressure (distance to road infrastructure). Bioclimatic, topographic, and distance-to-road variables were treated as continuous variables, while land use and land cover (Cob) and forest strata (Estra) were incorporated as categorical variables, assigning each pixel a numerical code corresponding to a specific land use class (Table A1), resulting in the final set of predictors presented in Table 1 (Jácome *et al.*, 2019b).

Table 1. Variables considered in the distribution modeling.

Variables	**Description**
Bio 1	Average annual temperature
Bio 2	Average daily range of monthly average maximum temperature-minimum temperature
Bio 7	Annual temperature range (BIO5-BIO6)
Bio 12	Annual precipitation
Bio 13	Precipitation in the wettest month
Bio 16	Precipitation in the wettest quarter
Bio 18	Precipitation in the warmest quarter
Topographic Humidity Index (ith)	Potential humidity
Elevation (Bioe)	Digital Elevation Model
Slope (%)	Terrain inclination
Land use and land cover (Cob)	Classifies the territory into discrete units of occupation
Forest strata (Estra)	Classifies the area into zoogeographic belts
Transportation routes (Vías)	Proximity to road infrastructures

These biophysical variables were obtained from the Land Cover and Use Map (Ministerio del Ambiente de Ecuador, 2020) at a scale of 1:100,000, rasterized at 30 meters and subsequently rescaled to match the bioclimatic resolution and considering that they influence bird distribution (Table 1) (Ramesh *et al.*, 1999; Rosas *et al.*, 2023). All predictor variables (bioclimatic and biophysical) were reprojected, cropped to the study area, and standardized to a final spatial resolution of 1 km² (30 arc-seconds) (Singh *et al.*, 2020).

2.5. Climate change scenarios

A short-term time horizon (2021–2040) was selected under the SSP585 scenario to assess the most immediate climate impacts on species distribution. This represents a precautionary approach to explore early climate impacts under a high-emission scenario, providing relevant insights for short-term conservation decision-making. This approach is aligned with global and regional initiatives aimed at identifying priority areas for conservation, such as Target 3 of the Convention on Biological Diversity [CBD] (2022), which proposes the protection of at least 30% of terrestrial ecosystems.

This time horizon allows for the identification of areas that could experience significant changes in their environmental suitability in the near future, which is especially relevant in highly vulnerable regions such as the Ecuadorian Biogeographic Chocó, where high rates of deforestation and anthropogenic pressure increase the susceptibility of ecosystems to climate change (IPCC, 2023). In addition, the HadGEM3-GC31-LL climate model was chosen due to its high efficiency and predictive performance in tropical areas and climate variability in South America with ecological niche models (Calvas *et al.*, 2024; Medrano-Vizcaíno *et al.*, 2020). Topographic and anthropogenic variables were kept constant across scenarios, assuming that these present marginal changes at the regional scale in the short term, which allows the effect of climate variations on the potential distribution of species to be isolated and specifically evaluated. This methodological approach is widely used in species distribution models to reduce the uncertainty associated with projecting future changes in land use, which depend on multiple socioeconomic factors that are difficult to predict accurately. However, some studies have pointed out that the explicit incorporation of future land use scenarios, although relevant in certain contexts, can introduce an additional source of uncertainty into projections, given that these changes are conditioned by highly variable economic, political, and demographic assumptions (Araújo and New, 2007; Franklin, 2010). Consequently, numerous studies choose to keep non-climatic variables constant and focus the analysis on the response of species to future climatic conditions, recognizing that this decision seeks to isolate the climatic signal without eliminating other possible sources of variability (Elith and Leathwick, 2009). In this way, the results obtained mainly reflect the sensitivity of species to changes in climatic conditions, regardless of other sources of environmental variability.

2.6. Potential distribution modeling

MaxEnt 3.4.4 software was used, which is one of the most widely used in the field of ecology to determine the potential distribution of species due to its predictive power and ease of interpretation. MaxEnt is based on the principle of maximizing entropy, which seeks the most uniform distribution possible in the study area given the constraints imposed by environmental predictors. It generally uses a logistic scale with values ranging from 0 to 1, where a value close to 0 indicates low suitability, while a value close to 1 reveals high habitat suitability (Phillips *et al.*, 2006; Rivera *et al.*, 2021).

Finally, to evaluate the modeling performance, 25% of the data was defined for testing and 75% for training using a logistic output format. The software options were configured with a random test of 20 and 5,000 maximum interactions, a convergence threshold of 0.001, and 10,000 background points were generated randomly (Jácome *et al.*, 2019b). The final design of the maps was carried out in ArcGIS Pro-3.0.2.

2.7. Model evaluation

Two metrics were used to validate the model: Area Under the Curve (AUC) and True Skill Statistics (TSS). The AUC is based on the ROC (Receiver Operating Characteristic) curve, which allows the predictive accuracy of the model to be evaluated, where values close to one indicate good performance. The categorization given by (Araújo *et al.*, 2005) was followed: excellent (1–0.9), good (0.9–0.8), acceptable (0.8–0.7), poor (0.7–0.6), and finally, invalid (0.6–<0.5). In addition, the True Skill Statistics (TSS) index is used to determine the performance of species distribution models due to its rigor (Allouche *et al.*, 2006). Fielding and Bell (1997), indicate the procedure for obtaining this value, generating a confusion matrix formed by the number of correct and incorrect predictions applied to the areas of absence and presence. Subsequently, accuracy, specificity, and sensitivity were calculated based on the matrix. Finally, TSS is defined as sensitivity + specificity -1. Because the matrix is determined by a threshold value, it is recommended to use a value that increases the sum of sensitivity and specificity (Yoon and Lee, 2023) The R software (R Core Team, 2025) was used for the research through the RStudio interface, and the Presence-Absence Model Evaluation package (Freeman and Moisen, 2008; version 1.1.11), which includes functions to determine the optimal threshold, confusion matrix, sensitivity, specificity, and TSS.

2.8. Optimization of species distribution models using fuzzy overlay

Once the current and future distribution had been modeled, the suitability layer was used to identify areas of high niche congruence between species (Hattab *et al.*, 2013). Diffuse overlap allows multiple suitability models to be integrated into a continuous index from 0 to 1, reflecting the joint possibility of occurrence (Zabihi *et al.*, 2017).

To identify these areas with high joint environmental suitability for the three species, the habitat suitability raster layers (continuous values from 0 to 1) resulting from the MaxEnt models for each scenario (current and future 2021–2040) were combined. This integration was performed using the Fuzzy Overlay tool in ArcGIS Pro software (version 3.0.2), applying the Fuzzy Gamma operator (Zabihi *et al.*, 2017; Michael and Collins, 2021).

The Fuzzy Gamma operator is defined as an algebraic combination of the fuzzy sum and fuzzy product operators, and is expressed as:

$$\mu_{\gamma} = (\mu_{Sum})^{\gamma} \times (\mu_{Product})^{(1-\gamma)} \quad (1)$$

where γ is a control parameter that varies between 0 and 1 and allows the balance between both operators to be adjusted. In this study, a value of $\gamma = 0.9$ was selected to obtain a result that balances the tendency of the sum operator to overestimate and that of the product operator to underestimate the joint suitability. This approach is useful for identifying areas where multiple criteria (in this case, suitability for each species) coincide at high values (Esri, 2023). The result is a continuous map with values in the range (0, 1) for each scenario. Values close to 1 indicate high combined environmental suitability, i.e., areas that are simultaneously suitable for *C. penduliger, M. princeps,* and *B. edwardsi*.

3. Results

3.1 Contribution of variables and model evaluation

The Jackknife test (Fig. S1, Supplementary Material) and percentage contribution analysis identified three key predictors for each species. For detailed analysis of the response curves (Fig. S2, Supplementary Material), the most influential variables were selected, prioritizing the identification of gradients and physiological thresholds (climatic and topographic) that limit distribution.

Elevation (Bioe) remained the dominant cross-cutting factor. For *Cephalopterus penduliger*, elevation (Bioe) defined the main range of suitability. The most influential secondary variables were the annual temperature range (Bio 7) and the mean annual temperature (Bio 1). The response curves of these thermal variables show a marked preference for environments with seasonal stability (Bio 7 low) and a specific average thermal regime, indicating that suitability decreases rapidly if the average temperature deviates from its optimum or if annual variability increases.

In the case of *Morphnarchus princeps*, in addition to elevation, the model highlighted the importance of mean annual temperature (Bio 1) and slope (%). The curves show that, unlike the other species, this taxon responds strongly to the physical structure of the terrain (rugged topography) combined with a specific range of average temperature, avoiding lowlands that are too warm and peaks that are too cold.

Finally*, Bangsia edwardsi* exhibited a restricted niche dominated by elevation, annual temperature range (Bio 7), and mean annual temperature (Bio 1). Its curves indicate a critical intolerance to annual temperature variability and a strict dependence on a constant mean temperature, confirming its high degree of specialization in the middle strata of the Andean slope. The effectiveness of the species distribution models was evaluated using the True Skill Score (TSS) and Area Under the Curve (AUC), confirming the accuracy of the projections and obtaining good values for the species studied (Table 2).

Table 2. Validation of species distribution models.

Especies	**TSS**	**AUC**
Cephalopterus penduliger	0.71	0.89
Morphnarchus princeps	0.70	0.87
Bangsia edwardsi	0.85	0.97

3.2 Current and future distribution

Cephalopterus penduliger: Based on current climate data and the distribution model generated (Fig. 2), the largest area of suitability for *Cephalopterus penduliger*, known as the umbrella bird, is distributed in northwestern Pichincha and near the western mountain range and the border of the Ecuadorian Chocó, an area with several birding and ornithological research sites due to its high bird richness and diversity. This species, which depends on tropical rainforests at medium altitudes, currently finds its ideal distribution in some primary forests in the central and western parts of the biogeographic area, where high humidity levels and dense forest cover provide the ecological conditions necessary for a suitable habitat for the species.

The future projection model for *C. penduliger*, based on extreme climate change conditions and increased anthropogenic activities according to the chosen scenario, shows a reduction in the distribution range throughout the study area, as this species faces a significant decline in suitable habitat, particularly at low altitudes, where an almost total loss of suitability is projected due to rising temperatures and ecosystem fragmentation. Refuge areas will be limited to higher altitudes within the mountainous zone and the transition zone from low to high areas, which are geographically understudied and little known. High and very high suitability is also identified in Pichincha, in the Andean Chocó, because this species prefers warm temperatures and is occasionally recorded in the foothills of the Andes at altitudes of up to 1,800 m a.s.l.

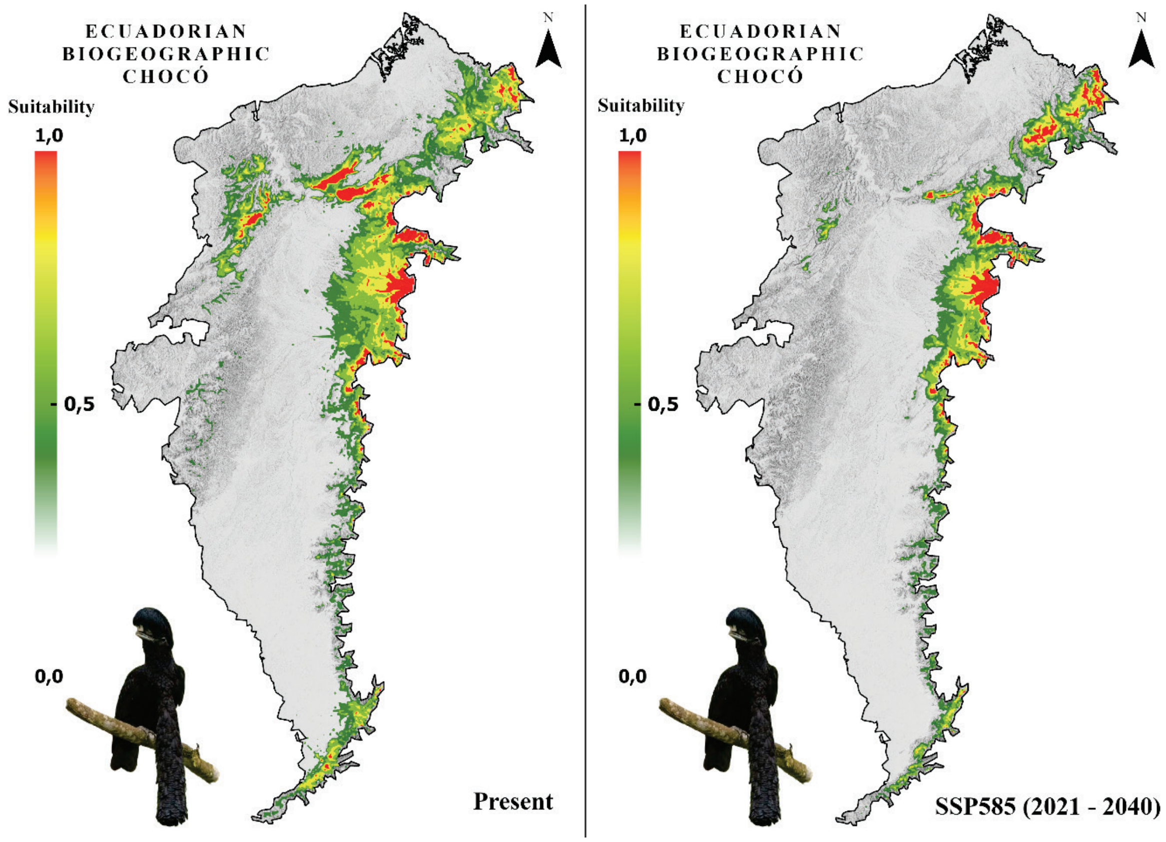

Figure 2. Current and future distribution (SSP585 scenario, 2021–2040) of Cephalopterus penduliger.

Morphnarchus princeps: As shown in the distribution model (Fig. 3), the very high, high, and medium suitability of the Barred Hawk is mainly distributed in the eastern part of the Chocó and the lower Andes mountain range, with the largest area of suitability in the province of Pichincha, southeast of the province of Esmeraldas, and the southern border of the province of Carchi, areas with a predominance of low montane evergreen ecosystems of the western mountain range and high montane ecosystems. This bird of prey has a preference for the edges of both primary and secondary rainforests. The mountainous topography of the region, together with the average altitude, creates favorable conditions for this species. The high availability of prey in these well-preserved forest areas is a factor contributing to their current suitability.

For *M. princeps*, projections indicate a notable decrease in its suitable habitat under the SSP585 scenario. Therefore, it is observed that the suitable areas for the species will shift to higher elevations, and although this species is more resilient, it will also experience a contraction in its potential distribution. The currently suitable areas in the northeastern regions will significantly increase their optimal habitat area for this species due to the altitudinal range and the ability of this location to maintain the most suitable climatic conditions in the future.

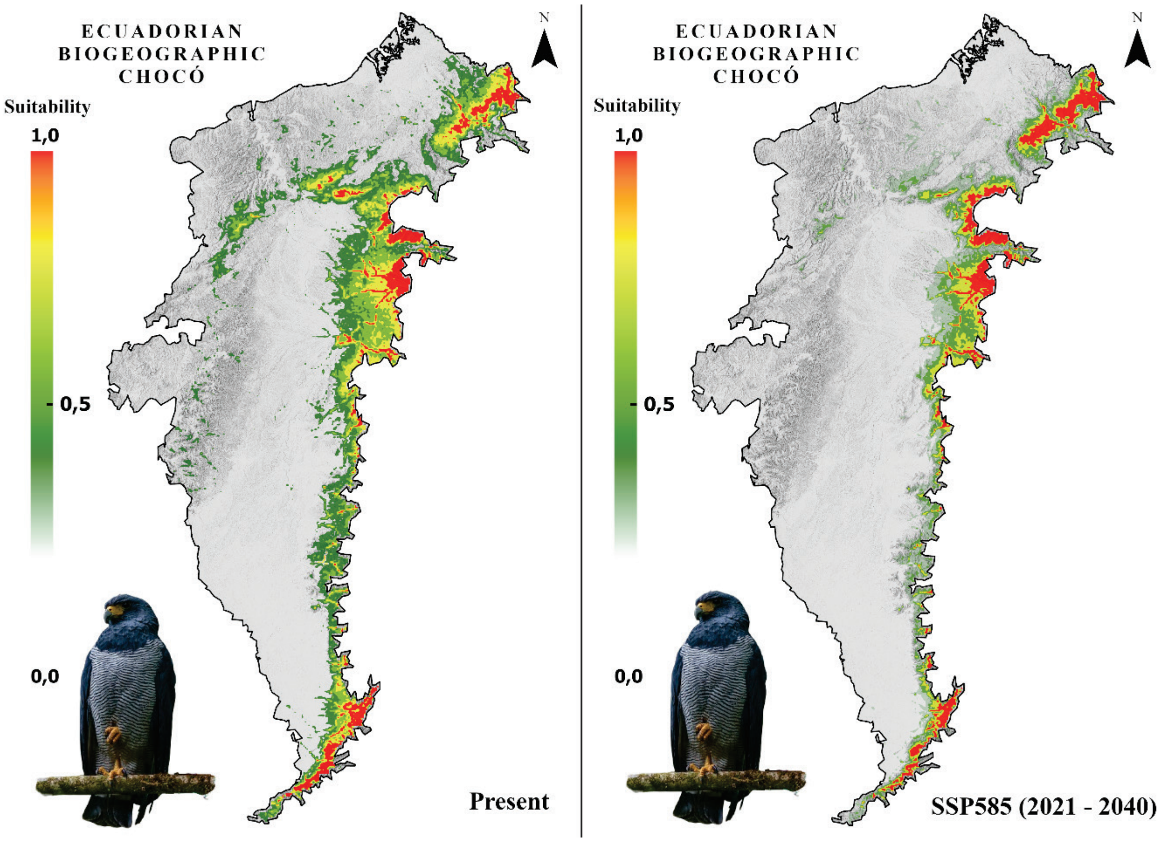

Figure 3. Current and future distribution (SSP585 scenario, 2021–2040) of Morphnarchus princeps.

Bangsia edwardsi: The ecological niche of this species (Fig. 4) has a wider distribution range throughout the lower part of the Andes mountain range or western part of the Tropical Andes region, referring to the Ecuadorian Chocó. This species is classified as endemic to this region, as it inhabits humid forest areas at medium altitudes. Its current habitat is closely linked to humidity conditions and the presence of dense vegetation, which are determining factors for its survival.

As for *B. edwardsi*, the model projects a spatial redistribution of its ecological niche, with a loss of suitability in lowland areas but a net expansion (+16.6%) towards higher elevations for the period 2021-2040, positioning it as one of the most vulnerable species under this scenario, with an almost total loss of suitable habitat in lowland areas. However, like the other species analyzed, it could benefit in specific areas of the northeastern Chocó Biogeographic Region, where climatic conditions would remain favorable at higher altitudes.

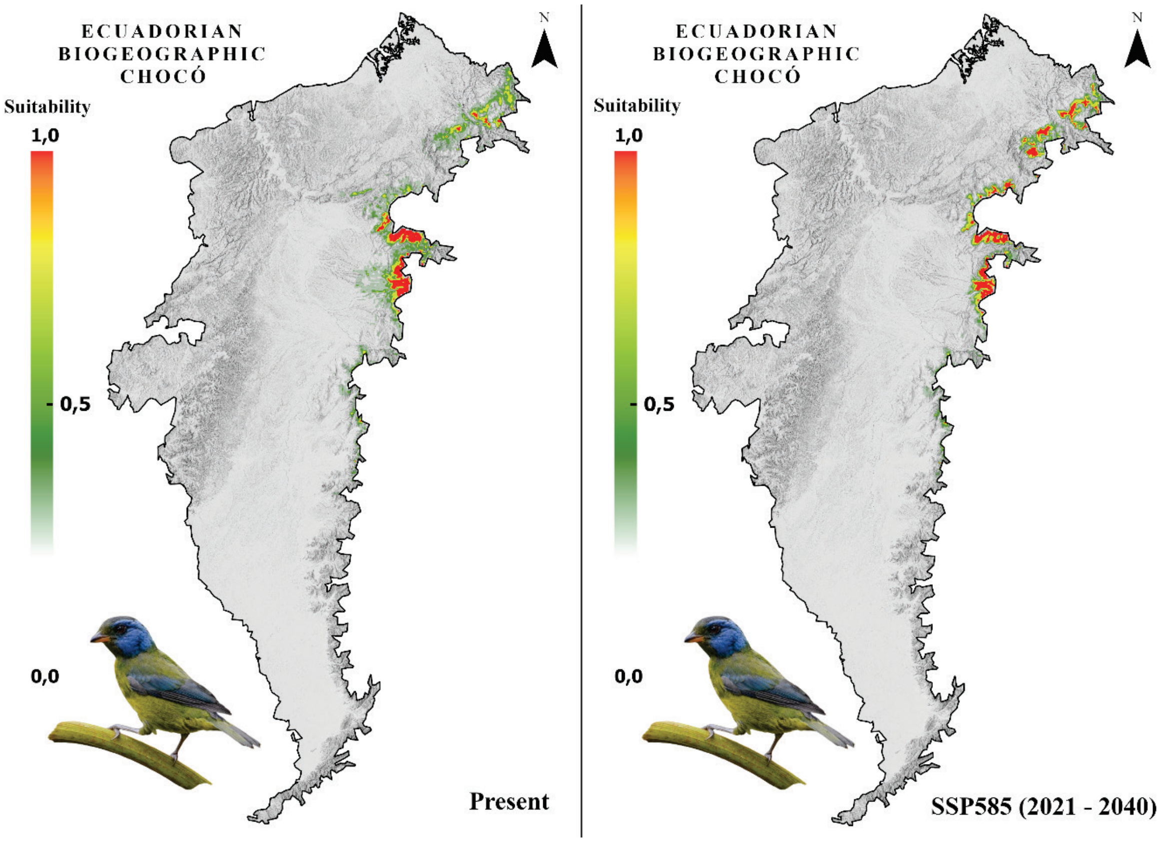

Figure 4. Current and future distribution (SSP585 scenario, 2021–2040) of Bangsia edwardsi.

Finally, analysis of current and future distribution areas under the SSP585 scenario (Table 3) indicates an overall reduction in suitable areas for the three species studied, while there is a significant increase in areas considered unsuitable or non-existent. The distribution areas for the current and future scenarios were reclassified into five suitability categories based on natural thresholds established on the MaxEnt suitability scale (0–1): Null (0–0.2), Low (0.2–0.4), Medium (0.4–0.6), High (0.6–0.8), and Very High (0.8–1). This reclassification allows for a more intuitive interpretation of changes in the extent of suitable habitat. For *C. penduliger*, the very high and high suitability categories are reduced by 19.45% (869 km² to 700 km²) and 37.12% (1,829 km² to 1,150 km²) respectively, while areas with no suitability (zero) increase considerably by 14% (32,177 km² to 36,680 km²). For the species *M. princeps*, there is a mixed projection, with an increase of 6.71% (1,281 km² to 1,367 km²) in the very high suitability category but similarly shows a reduction in the remaining categories and an increase of 8.16% in the null category areas (31,917 km² to 34,520 km²). In the case of *B. edwardsi*, very high suitability experienced an increase of 19.60% (250 km² to 299 km²), and the high category also experienced an increase in area of 13.82% (275 km² to 313 km²), although the medium and low categories are reduced alarmingly. In addition, there is an increase of 2.50% (39,760 km² to 40,749 km²) in areas without suitability, reflecting greater restriction in the future.

Table 3. Comparison of the extent (km² and percentage of variation) of suitability categories between the current and future scenarios (SSP585, 2021–2040).

Suitability Category	Current km² (A)	Future km² (A)	Current km² (B)	Future km² (B)	Current km² (C)	Future km² (C)
Very High (0.8 – 1)	869	700	1,281	1,367	250	299
High (0.6 – 0.8)	1,829	1,150	1,865	1,437	275	313
Medium (0.4 – 0.6)	3,073	1,545	2,575	1,826	585	348
Low (0.2 – 0.4)	4,184	2,165	4,502	3,108	1,322	553
None (0 – 0.2)	32,177	36,680	31,917	34,520	39,760	40,749
Total Suitable Area (Very High + High)	2,698	1,850	3,146	2,804	525	612
Net Variation (%)	(A) – 31.4 %		(B) – 10.9 %		(C) + 16.6 %	

A: *Cephalopterus penduliger,* B: *Morphnarchus princeps,* C: *Bangsia edwardsi*. The net change represents the percentage change in suitable area (sum of High and Very High categories) in the future scenario compared to the current scenario.

3.3 Fuzzy overlap

The fuzzy logic approach applied to habitat models allowed us to combine the results of the current and future distributions of *Cephalopterus penduliger, Morphnarchus princeps*, and *Bangsia edwardsi*, helping to identify key areas for conservation (Fig. 5). Thus, the current environmental overlap shows areas with values close to 1 in much of the Ecuadorian Chocó Biogeographic Region, specifically in the eastern and northeastern parts, showing a high degree of overlap in areas of high suitability in the middle and higher altitude parts of the area, as well as in forested areas. These areas include well-preserved forest habitats that benefit these species.

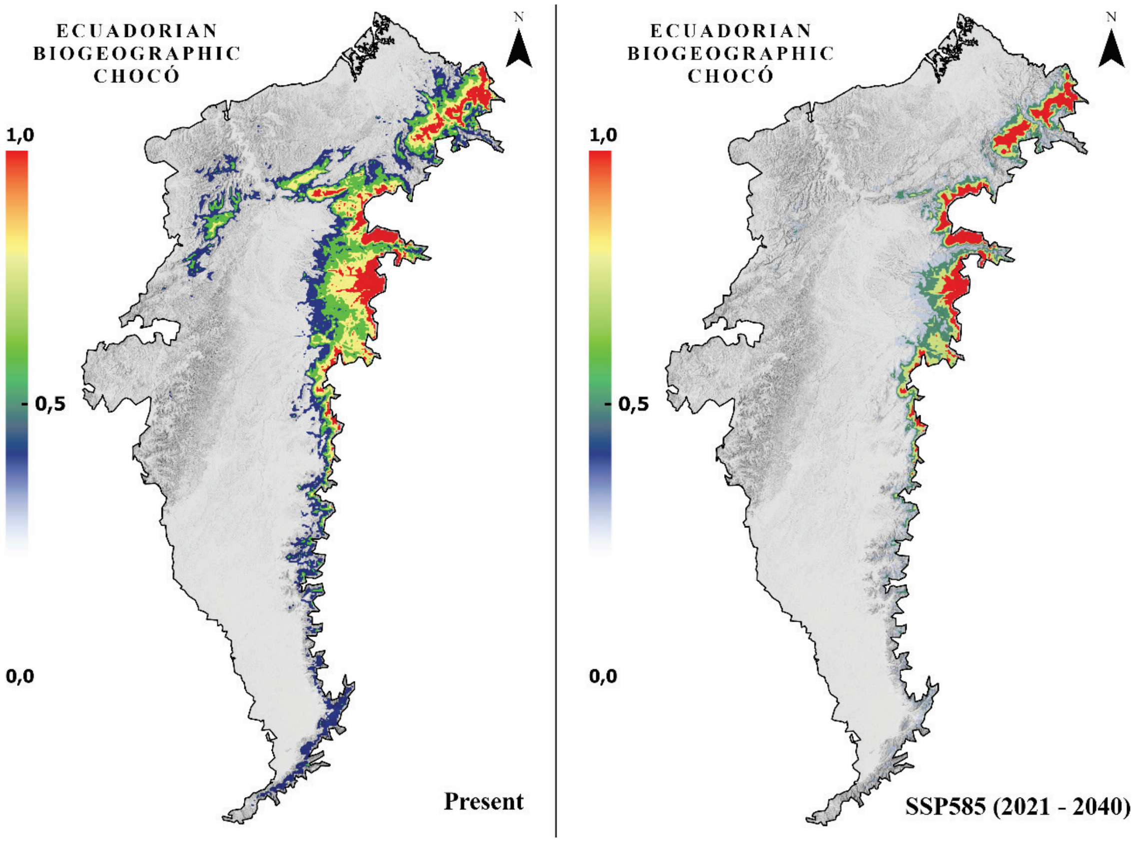

Figure 5. Environmental suitability zoning based on the diffuse overlap of the models for the three species studied.

On the other hand, the future model shows a general decrease in the suitability of environments for species throughout the study area, with the exception of some specific areas at higher altitudes, where a relative improvement in conditions is observed. These areas could play a key role in the persistence of species by offering more stable microclimates in the face of extreme climate change scenarios. In contrast, low-lying areas show a significant loss of suitable habitats, reinforcing the need for conservation approaches that prioritize ecological connectivity and the preservation of strategic mountainous areas.

4. Discussion

Under the SSP585 climate scenario, all the models for the three species predict a significant decline in optimal habitat over the next decade, reflecting the sharp increase in greenhouse gas emissions projected by the IPCC, which would exacerbate climate change, specifically in sensitive regions such as the Ecuadorian Chocó (IPCC, 2023). The focus on the biogeographic area allowed for a more detailed observation of the spatial dynamics of these changes in key areas of the Ecuadorian Chocó, which has been affected by anthropogenic activities that have not only local but also global impacts, with direct effects on species distributions (Feng *et al.*, 2024). The response of the species was not homogeneous. The models indicate an altitudinal shift toward higher elevation areas, a pattern widely documented in various taxonomic groups as a response to global warming. However, the magnitude of these shifts and the loss of suitable areas vary among species, reflecting differences in their niche breadth and climate tolerance. This generates competition for resources and causes ecological effects that modify environmental conditions, which in turn can affect the distributions of other organisms (Calvas *et al.*, 2024; Lenoir *et al.*, 2008; Uribe, 2015).

4.1. Current distribution of species

The results confirm that elevation (Bioe) is the primary environmental filter for the birdlife of the Chocó, defining the fundamental limits of distribution. The response curves (Fig. S2, Supplementary Material) indicate that suitability peaks are concentrated between 500 and 1,800 m a.s.l., coinciding with the strip of piedmont and low montane forests where moisture condensation is highest (Snow *et al.*, 2020). However, detailed analysis of secondary variables reveals differentiated ecological strategies. For *Morphnarchus princeps*, the association with mean annual temperature (Bio 1) and slope (%) suggests habitat selection is based not only on climate but also on topography. The preference for steep slopes favors the updrafts necessary for gliding flight and hunting by raptors, while average temperature acts as a physiological barrier that excludes warm, deforested lowland plains (Bierregaard *et al.*, 2020). On the other hand, *Cephalopterus penduliger* and *Bangsia edwardsi* showed a critical dependence on thermal stability, determined by the mean annual temperature (Bio 1) and the annual temperature range (Bio 7). The sharp decline in their suitability in response to deviations in mean temperature or increases in seasonality (Bio 7) confirms their stenothermic nature, which posits that tropical mountain species evolve under constant thermal regimes, preventing them from colonizing areas with marked seasonal variability. This physiological restriction means that these species are particularly vulnerable to global warming, as their thermal niche is rigid and limited (Richart and Burns, 2020). These results validate the ability of our models to represent the basic ecological requirements of each species.

4.2. Future projections under the SSP585 scenario

Our projections under the SSP585 scenario (2021–2040) predict a significant contraction of suitable habitat for species, particularly in the Chocó lowlands (Table 3). The projected changes vary by species, with one notable finding being the potential expansion of 16.6% for *Bangsia edwardsi*. This increase is due to the emergence of new climatically favorable areas at higher elevations (climate refuges) as a result of global warming. However, this theoretical gain should be interpreted with caution: the effective occupation of these new areas will depend strictly on the connectivity of the montane forest and the species' ability to disperse through fragmented landscape matrices, factors that often act as insurmountable barriers despite climatic suitability (Neate-Clegg *et al.*, 2021; Şekercioğlu *et al.*, 2012). *Cephalopterus penduliger* faces the most critical scenario with a 31.4% contraction of its suitable habitat, which, combined with its critical dependence on seasonal stability (Annual Temperature Range - Bio 7), suggests a high risk of attrition by lowlands. This implies that optimal thermal conditions are shifting toward the tops of mountains faster than the species can migrate or adapt (Renjifo *et al.*, 2014; Snow *et al.*, 2020). *Morphnarchus princeps* shows lower vulnerability (-10.9%), possibly because its dependence on topographic structure (slope %) allows it to persist on steep slopes that maintain microclimates, although the increase in average annual temperature (Bio 1) reduces its available area in low-lying areas and shifts its niche to higher altitude areas that are currently geographically limited (Fagua and Ramsey, 2019; Hansen *et al.*, 2020).

Despite the decline in suitability in lowlands, our models project an increase in habitat at medium and high elevations, located mainly in the eastern and northeastern sectors of the bioregion. These areas could act as climatic refuges for the species studied, a phenomenon that is particularly evident for *M. princeps*. This pattern of altitudinal displacement is consistent with reports from other studies, where tropical mountainous areas have served as evolutionary refuges and are projected to be key sites for the survival of vulnerable species (Şekercioğlu *et al.*, 2012; Ramírez-Alán *et al.*, 2015). However, it is important to consider that the ability of species to colonize these new potential habitats may be limited by geographical barriers and landscape fragmentation due to anthropogenic activities (road construction, agricultural expansion, urban development) (Huntley *et al.*, 2008; Uribe, 2015). For endemic tropical birds that are sedentary or have low dispersal capacity, access to these altitudinal refuges may not be feasible, increasing the risk of local extinction (Loarie *et al.*, 2009). Therefore, the identification of these climatic refuges must be complemented by strategies that ensure landscape connectivity to facilitate the climatic migration of species.

It is important to consider the inclusion of various environmental factors, such as temperature, altitude, vegetation cover, water availability, and influential anthropogenic activities to determine the quality and quantity of suitable new areas that species will obtain due to climate change (Bellard *et al.*, 2012). Another fundamental point is to understand the ecology of species, such as habitat requirements, population structure, biological interactions, reproductive strategies, and climate tolerances, as these components influence the adaptive capacity of species (Buckley and Roughgarden, 2004; Jetz *et al.*, 2007). However, the lack of studies on the consequences of climate change on entire bird communities in tropical regions, such as the Ecuadorian Chocó, characterized by its high endemism and biodiversity, together with the few bird families evaluated in their entirety, reveal a significant lack of knowledge (Feng *et al.*, 2024).

4.3. Fuzzy overlay as a tool for conservation

The analysis of the diffuse overlap between current and future species distribution models reveals a trend of loss of synchrony between the distribution areas of the three species in lowlands, indicating that optimal conditions for their coexistence will decline over the next decade. However, the middle and high zones could offer ideal conditions for multiple bird species in the future, particularly in areas of the eastern mountain range, as they are located in a mountainous area, which is key to conservation. The coincidence of these areas with protected areas such as Cotacachi-Cayapas National Park reinforces their strategic importance for regional conservation (Zapata-Ríos and Araguillin, 2013).

These results highlight the value of integrating species distribution models with fuzzy overlap techniques as an effective tool for identifying potential climate refuge areas and supporting spatial conservation planning under climate change scenarios, overcoming approaches based exclusively on current distribution. This is particularly relevant in mega-diverse regions such as the Chocó, where critical habitats are already being fragmented by human activities. Areas closest to the western mountain range should be considered conservation priorities, as they are projected to be refuge sites for multiple species in the short and medium term. In this case, higher altitude sites emerge as strategic areas for the planning of ecological corridors, which are essential for contributing to species dispersal, maintaining ecological interactions, and thus helping to minimize the impacts of climate change (Jenkins *et al.*, 2013).

It is also essential to promote habitat restoration and management policies that include the protection of watersheds and the control of agricultural expansion. Connectivity between forest fragments will be essential to allow species to move as the climate becomes more inhospitable in lowland areas. Efforts should be directed toward the conservation of mountainous areas and their adjacent habitats, promoting the resilience of the ecosystem to climate change and its long-term impacts (Armenteras and Rodríguez, 2014).

Conclusions

The integration of ecological niche modeling with fuzzy overlap proved to be a robust methodology for identifying priority conservation areas in the Chocó Biogeographic Region, allowing us to overcome traditional binary uncertainty (presence/absence) and prioritize areas according to their convergent suitability gradient.

The models showed robust performance, with AUC values above 0.90 and TSS above 0.7, indicating high accuracy in predicting current niches. With regard to altitude, optimal habitats are currently concentrated between 500 and 1,800 m a.s.l. and would migrate to higher altitudes under the SSP585 climate scenario (2021-2040).

Projections under the SSP585 scenario (2021-2040) revealed a predominant trend toward contraction of suitable habitat, although with heterogeneous impacts among taxa. *Cephalopterus penduliger* is identified as the most vulnerable species, facing a critical loss of 31.4% of its current optimal area, driven by its strict dependence on stable temperature ranges. Similarly, *Morphnarchus princeps* shows a reduction of 10.9%, restricted by the alteration of its topographic and thermal requirements in lowlands. In contrast, *Bangsia edwardsi* exhibits a potential niche expansion of 16.6%, suggesting a possible shift to higher-altitude climatic refuges. However, this optimistic scenario is conditional on the existence of effective ecological connectivity. The fragmentation of the piedmont and lower montane forest could be a significant limitation, reducing the probability of colonization of new climatically favorable areas. Consequently, it is recommended to prioritize the protection of altitudinal corridors connecting lowlands with the Andean foothills, ensuring the biological flow necessary for the adaptation of these species. This study highlights the urgency of incorporating physiological variables (such as mean temperature and annual range) into management plans, as thermal filters could represent significant constraints to local persistence, even beyond short-term loss of vegetation cover.

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Supplementary Material

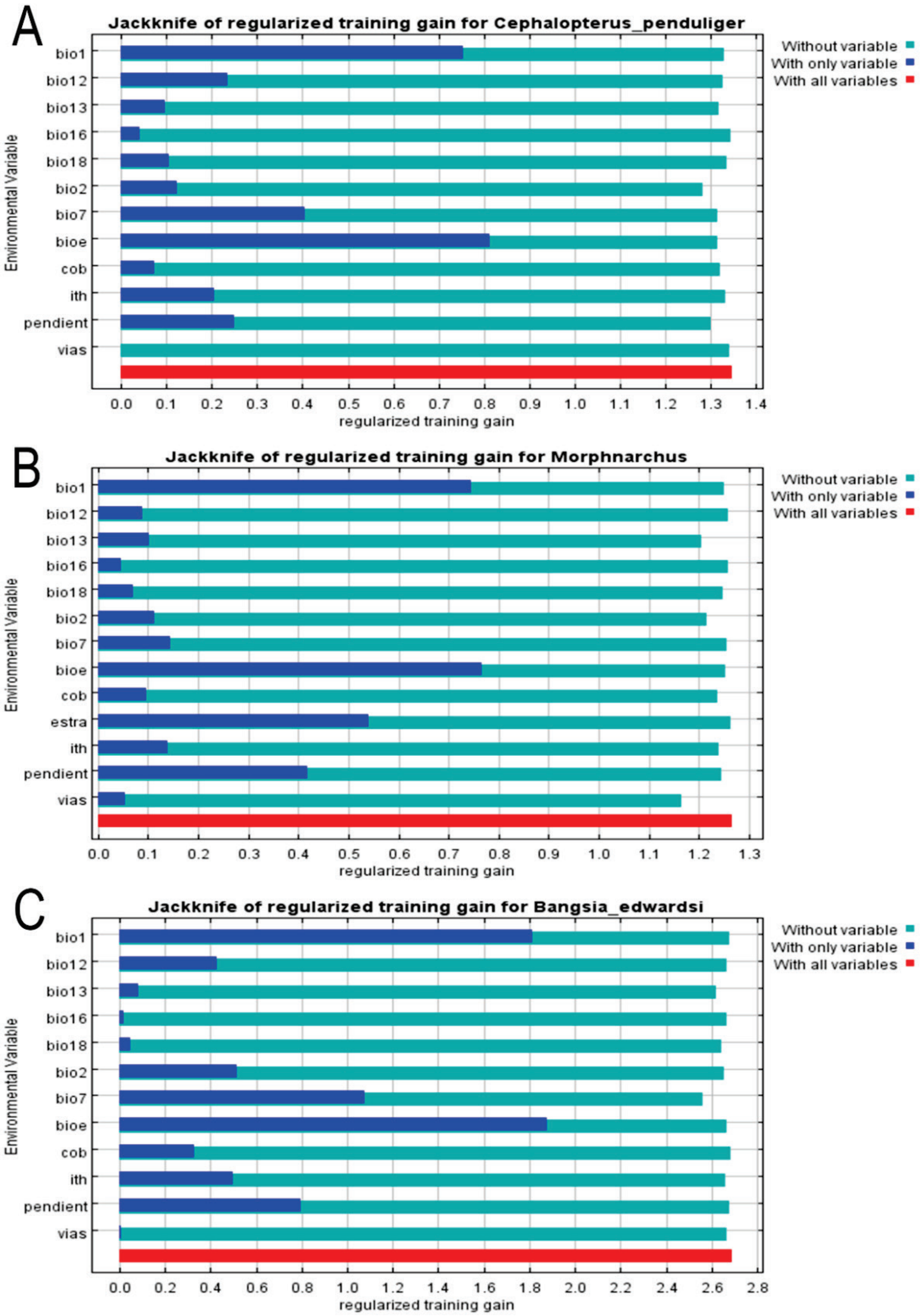

Figure S1. A: Cephalopterus penduliger, *B:* Morphnarchus princeps, *C:* Bangsia edwardsi**.** *Jackknife test results indicating the contribution of environmental variables to the species distribution models.*

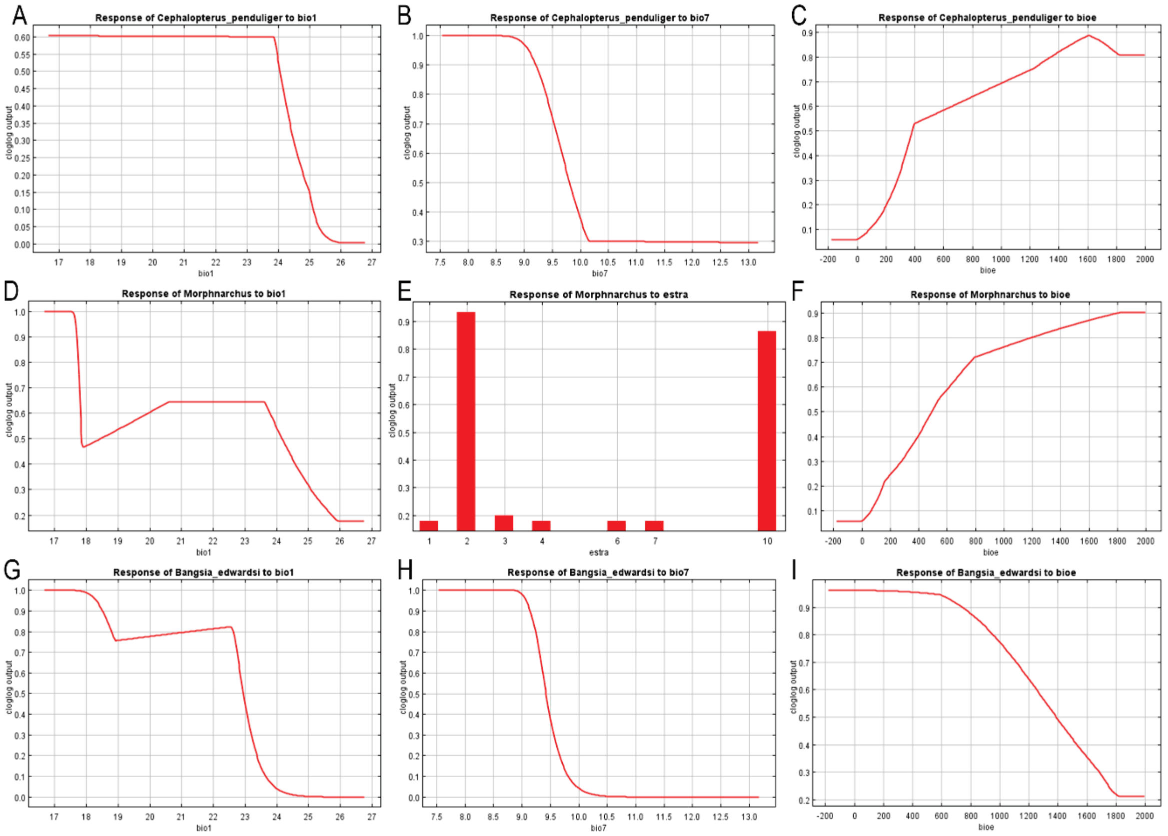

Figure S2. Response curves of the environmental variables with the highest contribution to the distribution models. Row 1 (A, B, C): Graphs for Cephalopterus penduliger *(Bio1, Elevation (Bioe), Bio7). Row 2 (D, E, F): Graphs for* Morphnarchus princeps *(Bio1, Forest strata (Estra), Elevation (Bioe)). Row 3 (G, H, I): Graphs for* Bangsia edwardsi *(Bio1, Elevation (Bioe), Bio7).*

Table A1. Description and coding of the categorical environmental variables: land use and land cover (Cob) and forest strata (Estra).

Variable	**Code**	**Category**	**Ecological/functional description**
Forest strata (estra)	1	Andean evergreen forest of the Andean brow	Humid montane belt; structurally complex forest
	2	Andean montane evergreen forest	Montane belt; closed canopy and developed understory
	3	Non-forest	Open or transformed areas; simplified plant structure
	4	Mangrove	Coastal plain; floodplain forest
	5	Montane cloud forest	High montane belt; high humidity and vertical complexity
	6	Chocó lowland evergreen forest	Lowland level; tropical rainforest
	7	Seasonal rainforest	Low to intermediate elevation; marked seasonality
	8	Humid scrub	Transitional belt; secondary vegetation
	9	Floodplain forest	Low belt; forest associated with wet areas
	10	Andean evergreen foothill forest	Transitional zone between lowlands and montane zone
Land use and land cover (cob)	1	Native forest	Preserved forest cover, closed canopy
	2	Shrub and herbaceous vegetation	Open natural cover
	3	Grassland	Livestock use
	4	Agricultural crops	Permanent or annual agriculture
	5	Agricultural mosaic	Heterogeneous and fragmented landscape
	6	Forest plantation	Planted forests
	7	Anthropic zone / infrastructure	Urbanized or developed areas
	8	Natural water bodies	Rivers, lagoons, and water bodies water