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CARRERA INGENIERÍA EN ECOSISTEMAS

Patrones biogeográficos para la conservación de las víboras (Squamata: Viperidae) ecuatorianas, en escenarios de cambio climático futuros

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RESUMEN

El cambio climático acelerado puede alterar la distribución de especies y, por lo tanto, influir en sus rangos biogeográficos. Esta investigación proporciona conocimientos sobre patrones biogeográficos para la conservación de las víboras ecuatorianas bajo escenarios futuros de cambio climático. Los datos sobre la ocurrencia de especies se obtuvieron de repositorios en línea y del Instituto Nacional de Biodiversidad de Ecuador. Los datos ambientales para los dos escenarios futuros (RCP 4.5 y 8.5) se obtuvieron del repositorio WorldClim. Los modelos de nicho ecológico (ENMs) se generaron utilizando el paquete R KUENM. Estos modelos se contrastaron con las regiones naturales de Ecuador y el sistema nacional de áreas protegidas (SNAP) y se calculó el índice de Importancia Ecológica Relativa (REI). En ambos escenarios climáticos, hay una desaparición del nicho ecológico de 10 de las 17 víboras ecuatorianas y una reducción > 65% del nicho de las víboras. En RCP 4.5, el matorral seco y el bosque deciduo experimentan el mayor declive en REI, con disminuciones del 91% y 90%, respectivamente. En RCP 8.5, las regiones del matorral andino y montano occidental exhiben el mayor declive en REI, con disminuciones del 95% y 93%, respectivamente. Además, las áreas de idoneidad para todas las especies de víboras están inadecuadamente conservadas dentro del SNAP. Las regiones montañas y piemontanas son prioritarias en Ecuador para la conservación de las víboras, basándose en la riqueza y especies amenazadas, mientras que el matorral seco es prioritario en función del endemismo en escenarios futuros de cambio climático. En conclusión, este estudio resalta la importancia de estas regiones naturales para la conservación de las víboras bajo escenarios actuales y futuros de cambio climático.

Palabras clave: Patrones biogeográficos, Cambio climático, Conservación, Víboras ecuatorianas, Modelado del nicho ecológico.

ABSTRACT

The rapidly changing climate may alter the distribution of species and thus influence their biogeographic ranges. This research provides knowledge on biogeographic patterns for the conservation of Ecuadorian vipers under future climate change scenarios. The data on Ecuadorian vipers' species occurrence was obtained from online repositories and the National Institute of Biodiversity of Ecuador. The environmental data for the present two future scenarios (RCP 4.5 and 8.5) were obtained from the WorldClim repository. The ENMs were generated using the R package KUENM. Those were later contrasted with Ecuador's natural regions and national protected areas system (SNAP) and the Relative Ecological Importance index was calculated (REI). In both climate scenarios there is a disappearance of the ecological niche of 10 out of the 17 Ecuadorian vipers and a reduction > 65% of the niche of vipers. In RCP 4.5, the dry shrub and deciduous forest experience the largest REI decline, with decreases of 91% and 90% respectively. In RCP 8.5, the Andean Shrub and Western Montane regions exhibit the highest REI decline, with decreases of 95% and 93% respectively. Also, the suitability areas for all viper species are inadequately conserved, inside the SNAP. Ultimately, the montane and foothill are priority in Ecuador for vipers' conservation based on the richness and threatened species, whereas the dry shrub is a priority region based on endemism in future climate change scenarios. In conclusion, the study highlights the importance of this natural regions for the conservation of vipers under current and future climate change scenarios.

Keywords: Biogeographical patterns, Climate Change, Conservation, Ecuadorian Vipers, Ecological Niche Modeling

1. INTRODUCTION

Anthropogenic climate change has been extensively documented, and it is predicted that without a significant reduction in greenhouse gas emissions, it could lead to an increase in global temperatures by over 4°C within this century (Huang et al., 2013). As ectothermic animals, vipers snakes depend on external heat sources to carry out their physiological processes, and a rise in temperatures has been observed to increase their activity time, metabolic rate, digestive function, and activity levels, thus impacting their survival and reproduction (Carrillo et al., 2005). With increasing temperatures, the habitats inhabited by vipers are undergoing heightened aridity and reduced hospitability (Ducatez & Shine, 2017). As suitable environmental conditions shift within the geographic space, vipers grapple with the challenge of swiftly adjusting to rapid changes in global scenarios(Needleman et al., 2018).

The rapidly changing climate may alter the distribution of species and thus influence their biogeographic ranges (Guedes et al., 2018). These changes will inevitably affect global biodiversity, thus ecosystem function and services (Weiskopf et al., 2020). While the effects of climate change are indeed widespread and intricate, they do not distribute uniformly across all regions, nor do they impact all species groups in the same manner. (Crews, 1988). This divergence is particularly pronounced, Tropical and montane ecosystems are highly vulnerable to the impacts of climate change (Eguiguren et al., 2016;Tovar et al., 2013 ;Pepin et al., 2022). These ecosystems act as isolated islands that foster the development of endemic species, which are particularly vulnerable to climate change due to their limited ability to migrate and adapt (Herzog et al., 2012).Likewise, in the case of vipers, as many species have already exhibited sensitivity to alterations in temperature and precipitation patterns(Wu, 2016).

The majority of viper species are found in the tropics and subtropics, where some are already experiencing temperatures above their optimal physiological range (Weiskopf et al., 2020). Among all the megadiverse countries in the world, Ecuador, despite being the smallest, boasts the highest number of reptile species per unit of area (<https://bioweb.bio/faunaweb/reptiliaweb/>). The nation boasts a rich variety of reptiles, encompassing an impressive total of 502 species, with seventeen belonging to the Viperidae Family (<https://bioweb.bio/faunaweb/reptiliaweb/>) (Adhikari et al., 2018) .

Among Ecuadorian vipers' species, one is endemic and considered as Endangered (EN) (*Porthidium arcossae*) and three are considered as Vulnerable (VU) (*Bothrocophias campbelli*, *Bothrops lojanus*, *Bothrops osbornei*) by IUCN (Carrillo et al., 2005). However, making the use of ecological niche models a practical tool for this purpose (Ortega et al., 2021; McPherson et al., 2008). The high diversity of species in Ecuador can be attributed to the country's location within the intertropical convergence zone and the presence of diverse altitudinal levels in the Andes (Esquerré et al., 2019). These conditions create a wide range of physical, climatic, and biological environments that contribute to the diversity of natural regions in Ecuador, each with unique characteristics and supporting a variety of endemic species (Hazzi et al., 2018)

Vipers stand out as terrestrial vertebrates hosting one of the highest numbers of threatened species (Ducatez & Shine, 2017). Regrettably, vipers have faced indiscriminate depletion and population decline, largely influenced by their historical characterization as enigmatic and feared creatures. (Pandey et al., 2016). They play a crucial role in maintaining healthy ecosystems as predators that control the populations of prey species (Crews, 1988), thus contributing to the balance of the trophic chain. From a public health standpoint, there exists a notable risk in the likelihood of snakebite incidents attributable to climate change. This risk arises from heightened species migration, shifts in geographical distribution, and the extension of envenomation-prone seasons. (Yáñez et al., 2021). In this context, proteins isolated from snake venom have practical applications in pharmaceuticals, making it imperative to protect these invaluable natural resources (Kumar et al., 2002).

Vipers and other reptiles demonstrate heightened vulnerability to habitat loss, climate change, and enduring environmental shifts. This susceptibility positions them as valuable bioindicators, offering insights into the processes that influence ecosystems. (Shine & Bonnet, 2000). Furthermore, this attribute positions them as excellent models for evaluating the potential impacts of climate change on terrestrial ectotherms (Rautsaw et al., 2022). Moreover, studies have shown that Viperidae species and ecosystems where they are distributed are vulnerable to the effects of climate change (Wu, 2016), which makes their conservation a top priority. Protecting these species and their habitats is crucial, not only for their survival, but also for the overall health of the ecosystem.

The real or potential geographic distribution of a species can be established by identifying their suitable environmental conditions, these are then modeled within an

ecological space using its occurrence data. Subsequently, the locations where these suitable environments are spread across a geographical space can be identified. This procedure is formally referred to as Ecological Niche Modeling (ENM). (Soberón, 2010). The presence of a species in the geographical space can be explained by the interaction between the three factors (Biotic-Abiotic-Mobility) in the BAM model proposed by (Soberón & Peterson, 2008). Nevertheless, there exist various factors that can prevent a species from inhabiting environmentally suitable areas within the ecological space (A). These factors encompass geographic barriers (M) that constrain dispersal across biogeographically accessible regions, as well as biological interactions (B) such as competition for resources (Pearson, 2010). Within this context, owing to the extensive spatial scale employed for ecological niche modeling in this study, variables derived from the Environmental(A) component prove more suitable than those from the Biological(B) component in elucidating the areas of suitability for a given species. (Barve et al., 2011).

Predictive models for potential species distribution serve as pivotal tools within the realm of conservation biogeography. They provide the means to strategically channel our conservation, planning, and management endeavors toward safeguarding biodiversity (Urbina & Flores, 2010). Biogeographical estimates of snake diversity would contribute to global and regional strategies for conservation. However, detailed data have not yet been compiled for the Neotropics, even though it comprises one of the richest herpetofauna in the world (Needleman et al., 2018; Guedes et al., 2018; Rautsaw et al., 2022).

Although a broad scientific consensus has been established on the presence of anthropogenic climate change, and its effects on wildlife, this is the first study to evaluate the biogeographic patterns for the conservation of Ecuadorian vipers under future climate change scenarios. This research aims to (a) Identify the natural regions of Ecuador where significant shifts occur (expansions/contractions) in the environmental suitability areas (ecological niches) for Ecuadorian vipers under future climate change scenarios. , (b) Estimate the degree of conservation (%) of the areas of environmental suitability of the Ecuadorian vipers in the National System of protected Areas (SNAP), and (c) identify priority natural regions of Ecuador for the conservation of vipers, given the concentration of richness, endangered species, and endemism in climate change scenarios.

2. MATERIALS AND METHODS

2.1 Bioclimatic Layers

The bioclimatic layers necessary for the modeling environmental suitability areas and their projections for future climate change scenarios were obtained from the Worldclim2 database (Hijmans et al., 2005; Fick & Hijmans, 2017) (<http://www.worldclim.org>). The 19 bioclimatic layers of the present (Average for the years 1970-2000) and two future climate change scenarios (RCP 4.5 and RCP 8.5) were downloaded in raster format with a spatial resolution of 30 arc seconds (~1 Km²) for year 2050. We avoided using the four bioclimatic layers combining temperature and precipitation information (mean temperature of wettest quarter, mean temperature of driest quarter, precipitation of warmest quarter and precipitation of coldest quarter), as these show unusual spatial abnormalities in the form of odd discontinuities between adjacent pixels (Escobar et al., 2014). The climate change scenarios are based on HadGEM2-ES data (a fully coupled atmosphere-ocean climate model) which interactively represents terrestrial and oceanic carbon cycles and dynamic vegetation with the option to prescribe atmospheric CO₂ concentrations or to prescribe anthropogenic CO₂ emissions and simulate CO₂ concentrations (Jones et al., 2011). The RCP 8.5 model represents an extreme scenario in terms of greenhouse gas emissions, while the RCP 4.5 scenario assumes lower greenhouse gas emissions (Riahi et al., 2011).

2.2 Species occurrence database

Species records were obtained based on a systematic bibliographic review of viperids recorded in continental Ecuador for 17 species: *B. schlegelii*, *B. campbelli*, *B. hyoprora*, *B. lojanus*, *B. microphthalmos*, *B. asper*, *B. atrox*, *B. bilineatus*, *B. brazili*, *B. osbornei*, *B. pulcher*, *B. punctatus*, *B. taeniatus*, *L. acrochorda*, *L. muta*, *P. arcossae*, *P. nasutum* (<https://bioweb.bio/faunaweb/reptiliaweb/>). Records and georeferenced localities were obtained for the entire distribution range of the species, from the following open-access digital repositories: GBIF (<https://www.gbif.org/>), Vertnet (<http://vertnet.org>), Bioweb (<https://bioweb.bio/>), Naturalist (<https://www.inaturalist.org/>), QCAZ (<https://bioweb.puce.edu.ec/>), FHGO, (<http://www.biovirtual.unal.edu.co/es/colecciones/detail/364574/>) (<https://vivarium.org.ec/fhgo/>), and scientific collections from the National Institute of Biodiversity of Ecuador (INABIO) (<https://bndb.sisbioecuador.bio/>).

We then generated a taxonomically and geographically curated database. To achieve this, we (a) checked for atypical records, (b) checked for taxonomic names with possible errors (c) eliminated duplicate data and records without spatial data in order to avoid biased data (Elith et al., 2011).

2.3 Delimitation of accessibility areas

The accessibility area (M) in the BAM model (Barve et al., 2011), refers to the geographic area that has been accessible to the species through dispersal during relevant periods (Soberón, 2010). It was delimited based on the geographic distribution of the validated records of each species based on biogeographical regions for the Neotropics (Morrone, 2014), additionally, the delimitation considered physical barriers such as watersheds and mountain ranges, facilitated by a digital elevation model. (Mota et al., 2019; Zurell et al., 2020).

2.4 Modeling of areas of environmental suitability and their projections in future climate change scenarios.

We followed the protocol proposed by (Mota et al., 2019) to model the areas of environmental suitability (ecological niche) and generate projections for each species (Appendix I). The selection of variables was based on: (a) extracting the values of the 15 bioclimatic layers associated with the record points of the viper species to be modeled, with the tool "extract multi values to points" from ARCMAP 10.5 (www.esri.com/es-es/arcgis/); (b) a Jackknife analysis to determine which are the most important variables for the model in the Maxent software (Phillips et al., 2006); (c) a Pearson correlation analysis between the variables and the climatic data associated with the record points with the Past software (Hammer et al., 2001). The model was generated with the records and the non-correlated bioclimatic variables prioritized by Jackknife test (Elith et al., 2011). (Mota et al., 2019)

Model validation is based on randomly selecting 20% of the records as test data to estimate omission rates over 5 replications, 5000 iterations, and with the threshold "10 percentile training presence" in order to exclude outlier records (Zurell et al., 2020). Finally, the best model was selected based on the low omission rates of the test points, AIC, and the values of the partial ROC statistic (Cobos et al., 2019). The area under the partial ROC quantile is currently considered the standard method for assessing the

accuracy of predictive distribution models(Mota et al., 2019). It avoids the alleged subjectivity in the threshold selection process, when scores derived from the continuous probability are converted into a binary presence-absence variable(Lobo et al., 2008).

The modeling processes was automated with a script in R studio (<https://www.r-project.org/>) by using the Kuenm package(Cobos et al., 2019). Kuenm is an R package designed to process the calibration, creation and evaluation of ENMs making collaborative use of the machine learning software for species distribution models maxent (Phillips et al., 2006).

The calibration of the models was done by creating a series of candidate models with the combination of the different parameters (regularization multiplier, combinations of feature classes, and distinct sets of environmental predictors) offered by Maxent software. For each setting, two models are created, one with the full data set and the other just with model training data (Cobos et al., 2019). The best model was then chosen based on statistical significance, predictability and complexity, in that order of importance. First, the models were filtered by statistical importance based on partial ROC as it was established that is a more appropriate measurement than a full ROC (Jiménez-Valverde, 2012;Lobo et al., 2008).

The set of generated models were then evaluated by their omission rate ($10\% <$) of the testing data, in order to measure model performance (Anderson et al., 2003). Finally, the best final model was chosen based on their complexity based on AICc values ($2 <$) from Partial ROC, a measure that explains how well the model fits the data while favoring simpler models (Warren, 2011).

2.5 Natural regions of Ecuador where the major changes occur in the ecological niche of Ecuadorian vipers, in future climate change scenarios

To determine the natural region where the most significant changes occur we computed the Relative Ecological Importance (REI), which is determined by the ratio of suitability to availability $REI = (\text{Suitability of a habitat} / \text{Total availability of that habitat})$ (<https://bioweb.bio/faunaweb/amphibiaweb/RegionesNaturales>). This index serves as a valuable tool for assessing the relative significance of ecosystem availability in the context of biodiversity conservation (Ortega et al., 2015). This index was calculated for all viper species in every natural region of Ecuador, and contrast it with the future niche

projections in climate change scenarios RCP 4.5 and RCP 8.5. A REI value of 1 signifies that the habitat is perfectly suitable and is of maximum importance for the species' conservation (Ortega et al., 2015)

2.6 Degree of conservation of environmental suitability areas of Viperidae in the National System of Protected Areas (SNAP)

To determine the degree of conservation of the areas of environmental suitability of Viperidae species in the SNAP, we proceed to spatially estimate the percentage (%) of the suitability model area included in each protected area. A shapefile with the SNAP were downloaded from Sistema Único de Información Ambiental (<http://suia.ambiente.gob.ec/>)

2.7 Priority natural regions of Ecuador for Viperidae conservation in climate change scenarios based on richness, endemism, and threat status.

Climate contraction is defined as the reduction of the areas of environmental suitability (A) within the area of accessibility (M) in a defined period of time for the species (Scheele et al., 2017), while expansion is the increase of environmentally suitable areas for the species within its geographic area of accessibility for a given time period (Sjödin et al., 2018; Pulliam, 1986).

Models of environmental suitability for Ecuadorian viperid species were overlapped to determine which natural region has greater accumulation of ecological niche through the sum of raster layers with map algebra tool of ARCMAP 10.5 (www.esri.com/es-es/arcgis/). We conducted an analysis of the spatial ecological patterns related to species richness, endemism, threatened species, REI and determined priority natural regions. Subsequently, we duplicated this procedure using future projections. These models and their projections were then be compared against the shape file of natural regions, employing multicriteria assessment, to determine the foremost conservation priority region for vipers.

3. RESULTS

3.1 Current and future distribution of the ecological suitable areas of Ecuadorian vipers

In this study, we undertook an investigation on the biogeography of Viperidae species in continental Ecuador using ecological niche modeling under current and future climate scenarios. Our analysis revealed that the ecological niche of these species is widely distributed across most tropical areas, spanning from southern Mexico to the southeastern part of Brazil. With the exception of higher altitudes regions associated with colder and drier ecosystems, nearly all of Ecuador includes suitability areas for vipers. Notably, the montane and Amazon region located to the east of Ecuador exhibited the highest species richness and overlap of vipers, while the western coastal lowlands displayed the lowest species richness (Figure 1).

In terms of future climate change scenarios, namely RCP 4.5 and 8.5 (Figure 1), we observed similar patterns in the distribution of the vipers' ecological niche. Both scenarios predict a significant contraction of the ecological niche, with 65.04% reduction in RCP 4.5 and 67.32% reduction in RCP 8.5 (Figure 1). This contraction results in the near-total loss of ecological niche coverage in the western lowlands of Ecuador, while the eastern part experiences comparatively less change in niche coverage. However, it is important to note that some species' ecological niches may expand to higher altitudes, indicating the emergence of new suitability areas in the future (Figure 2).

Among the 17 viper species studied, 10 (58.82%) lost all of their environmentally suitable habitats in both climate change scenarios, including *Bothrocophias campbelli* (Vulnerable) and *Porthidium arcossae* (Endangered) (Table 1.). Additionally, five species experienced a high reduction (>50%) in their niche coverage, including *B. bilineata*, *B. pulchra*, *B. taeniata*, *B. campbelli*, *B. hyoprora*, *B. microphthalmus*, *B. asper*, *B. atrox*, *B. brazili*, *B. lojanus*, and *B. osbornei*. *P. nasutum*. Most species lose from 50 to 100% of its niche (Figure 3, Table 1). Notably, only two species showed considerable ecological niche expansion (>10%): *B. lojanus* (>40%) and *P. nasutum* (>200%) (Table 1)

Table 1 Ecological niche area (Km²) for Ecuadorian vipers in current and future scenarios.

Species (UICN Threat category) /model in Km ²	Current	RCP45	Ecological niche modeling		RCP4.5 Expansion Km ² /(%)	RCP8.5 Contraction Km ² /(%)	RCP85 Expansion Km ² /(%)
			RCP85	RCP4.5 Contraction Km ² /(%)			
<i>Bothriechis schlegelii</i> (LC)	509062	0	0	509062 (100%)	0 (0%)	509062 (100%)	0 (0%)
<i>Bothriopsis bilineata</i> (LC)	3644111	1534414	1432748	2113948 (58.%)	0 (0%)	2211246 (60.68%)	0 (0%)
<i>Bothriopsis pulchra</i> (LC)	38168	0	0	38168 (100%)	0 (0%)	38168 (100%)	0 (0%)
<i>Bothriopsis taeniata</i> (LC)	5406104	0	0	5406104 (100%)	0 (0%)	5406104 (100%)	0 (0%)
<i>Bothrocophias campbelli</i> (VU)	69638	0	0	69638 (100%)	0 (0%)	69638 (100%)	0 (0%)
<i>Bothrocophias hyoprora</i> (LC)	4679710	2570797	2406787	2552313 (54.54%)	0 (0%)	2403031 (51.35%)	0 (0%)
<i>Bothrocophias microphthalmus</i> (LC)	1324065	1109734	912545	345580 (26.1%)	131082 (9.9%)	491625 (37.13%)	79444 (6%)
<i>Bothrops asper</i> (LC)	1482271	325281	313148	1162100 (78.4%)	0 (0%)	1173958 (79.2%)	0 (0%)
<i>Bothrops atrox</i> (LC)	5440764	0	0	5440764 (100%)	0 (0%)	5440764 (100%)	0 (0%)
<i>Bothrops brazili</i> (LC)	3456731	0	0	3456731 (100%)	0 (0%)	3456731 (100%)	0 (0%)
<i>Bothrops lojanus</i> (VU)	6656	3788	5090	6057 (91%)	3035 (45.6%)	5764 (86.6%)	6656 (61.4%)
<i>Bothrops osbornei</i> (VU)	37224	8072	14737	29630 (79.6%)	540 (1.5%)	24902 (66.9%)	2427 (6.5%)
<i>Bothrops punctatus</i> (LC)	115171	0	0	115171(100%)	0 (0%)	115171(100%)	0 (0%)
<i>Lachesis acrochorda</i> (LC)	270797	0	0	270797 (100%)	0 (0%)	270797 (100%)	0 (0%)
<i>Lachesis muta</i> (LC)	7325120	0	0	7325120 (100%)	0 (0%)	7325120 (100%)	0 (0%)
<i>Porthidium arcossae</i> (EN)	5087	0	0	5087 (100%)	0 (0%)	5087 (100%)	0 (0%)
<i>Porthidium nasutum</i> (LC)	326966	1141172	1070365	0(0%)	810875 (248%)	0(0%)	742212 (227%)

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Table 2 Relative importance of ecosystem availability decline (%) in future climate change scenarios . *Amazon (A), Andean shrub (A.S), Choco Andean forest (C.T.R), deciduous forest (D.F), Dry shrub (DS), Eastern Foothill (E.F), Eastern Montane (E.M), Paramo (P) Western Foothill (W.F), and for western montane(W.M).*

Natural Regions	CU	RCP 4.5	RCP 8.5	Decline in REI RCP 4.5 (%)	Decline in REI RCP 8.5 (%)
A.S	0.20	0.05	0.01	75%	95%
A	0.41	0.18	0.18	56%	56%
W.M	0.15	0.06	0.01	60%	93%
W.F	0.30	0.07	0.04	77%	87%
P	0.32	0.07	0.03	78%	91%
E.F	0.45	0.17	0.17	62%	62%
E.M	0.38	0.13	0.07	66%	82%
D.S	0.11	0.01	0.01	91%	91%
D.F	0.10	0.01	0.01	90%	90%
C.T.R	0.22	0.03	0.02	86%	91%

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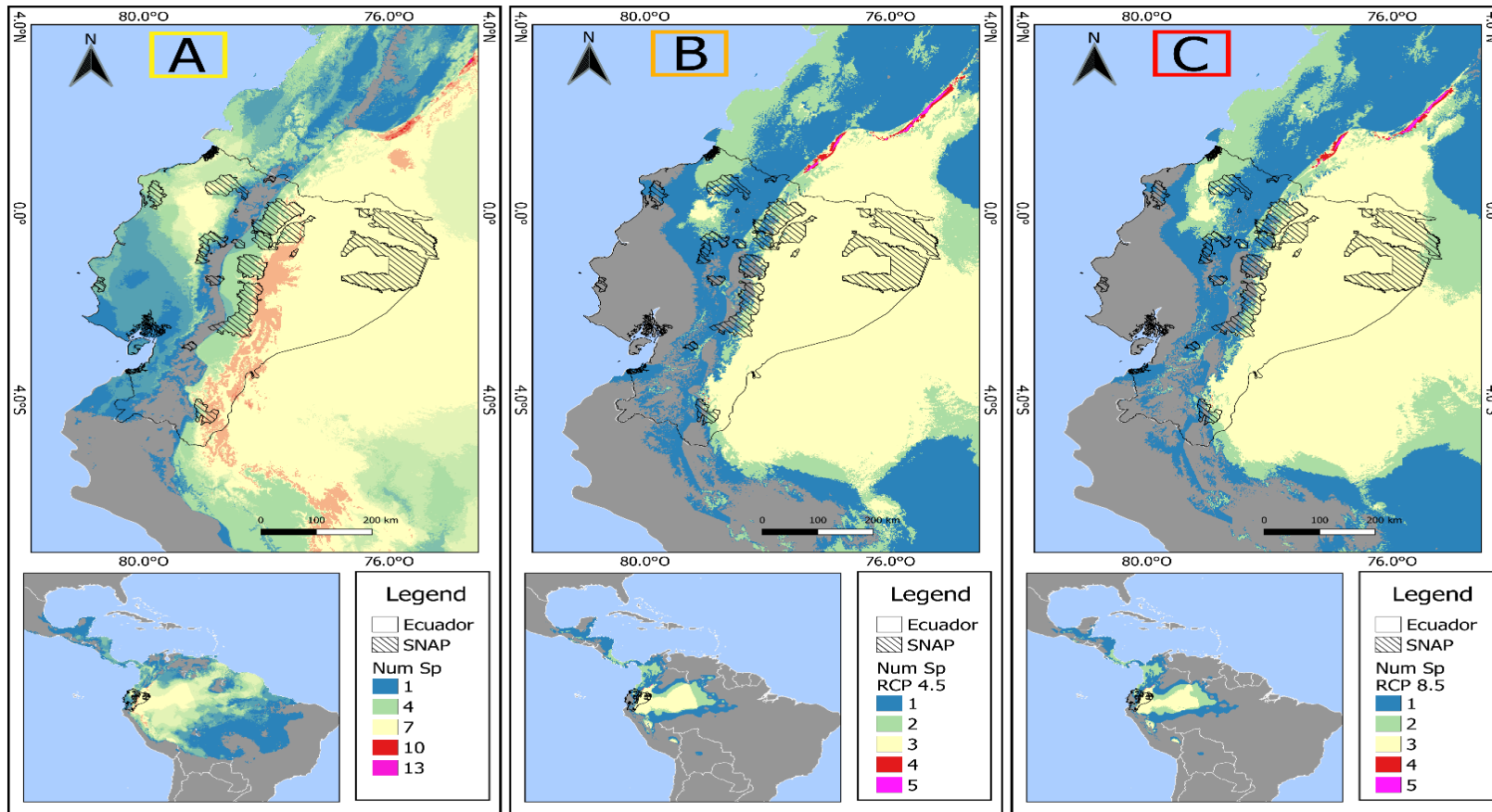


Figure 1 Biogeography of Viperidae species in continental Ecuador based on ecological niche modeling to represent the richness of 17 species in current and future climate scenarios: (A) current climate Scenario; (B) RCP 4.5 scenario and (C) RCP 8.5 scenario

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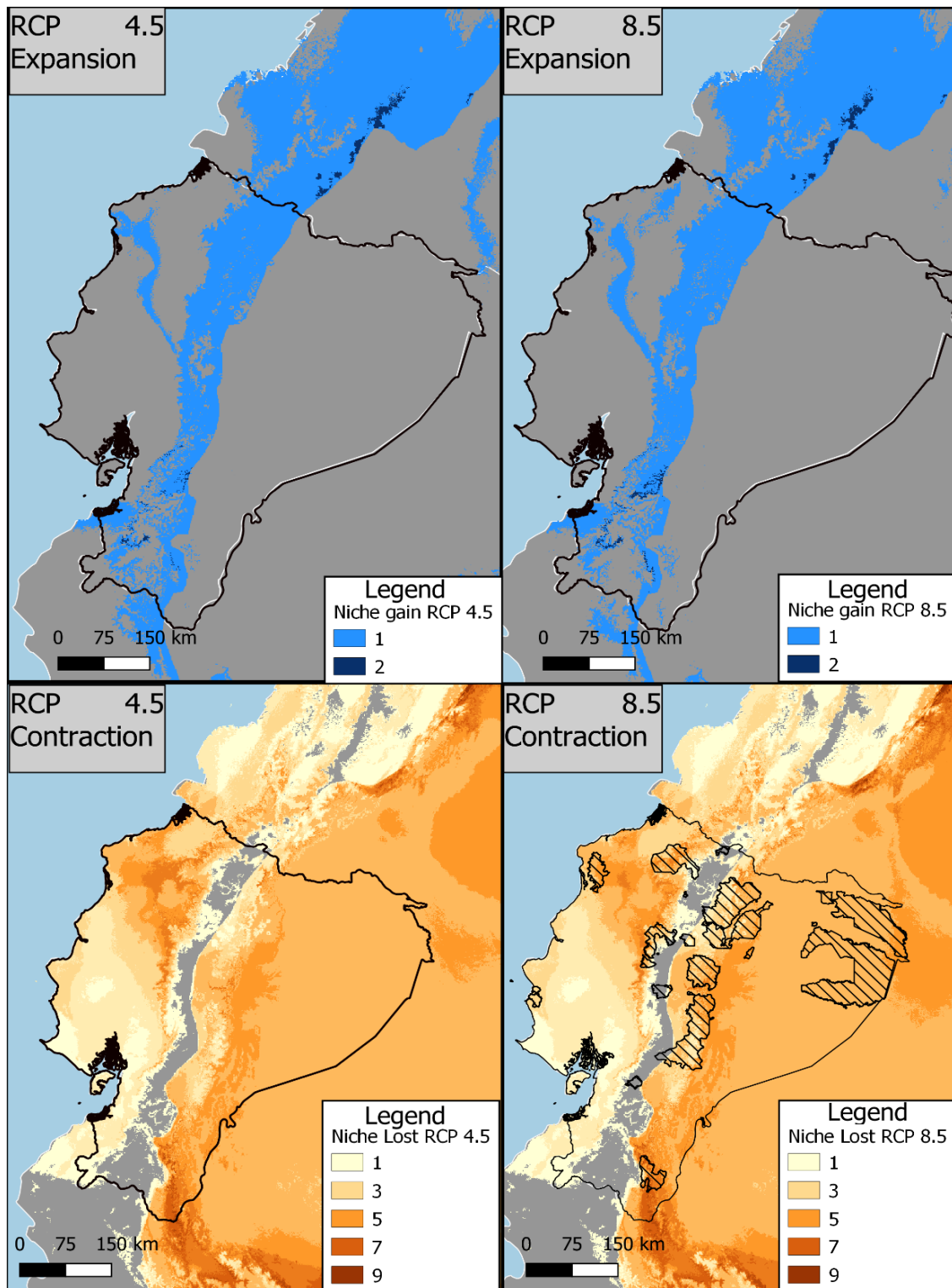


Figure 2 Ecological expansion and contraction for Ecuadorian vipers in climate change scenarios RCP 4.5 and RCP 8.5
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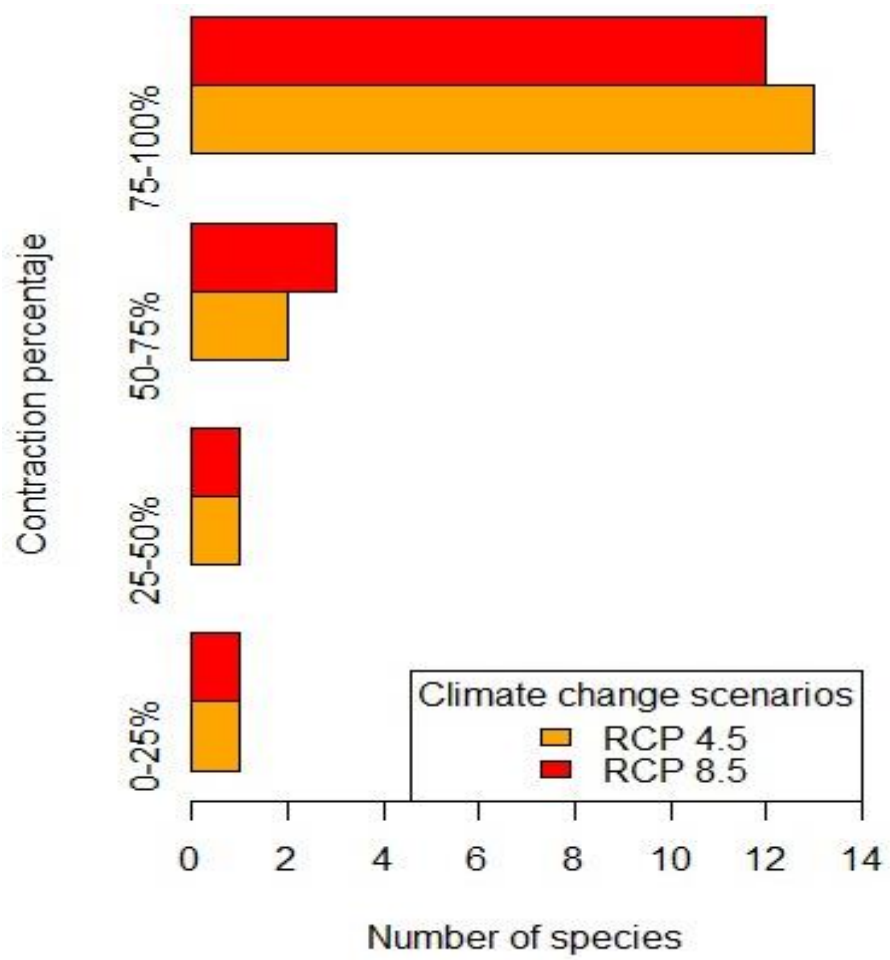


Figure 3. Ecological niche contraction and vipers' species in climate change scenarios RCP 4.5 and RCP 8.5 in Ecuador.
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3.2 Natural regions of Ecuador and environmental suitability of Ecuadorian vipers in current and future climate change scenarios.

In both RCP 4.5 and 8.5 climate change scenarios for year 2050, there are patterns of niche contractions occurring mostly in the lowlands, particularly in the eastern part of Ecuador (Figure 2). Conversely, climate niche expansions are notably shift from foothill and lowland environmental conditions towards higher regions in both scenarios (Figure 2).

Among the natural regions in the current scenario, the Amazon (A; REI=0.41) and Eastern Foothill (E.F; REI=0.45) are regions with the highest Relative Ecological Importance index. In both future climate the amazon and eastern foothill remain the natural Regions with the highest REI. Under the RCP 4.5 scenario, the Dry shrub (D.S) and Deciduous Forest (D.F) experiencing the greatest REI decline, with 91% and 90%, respectively. On the other hand, the Andean Shrub (A.S) and Western Montane (W.M) have the highest decline in REI under the RCP 8.5 scenario, with 95% and 93%, respectively (Table 2).

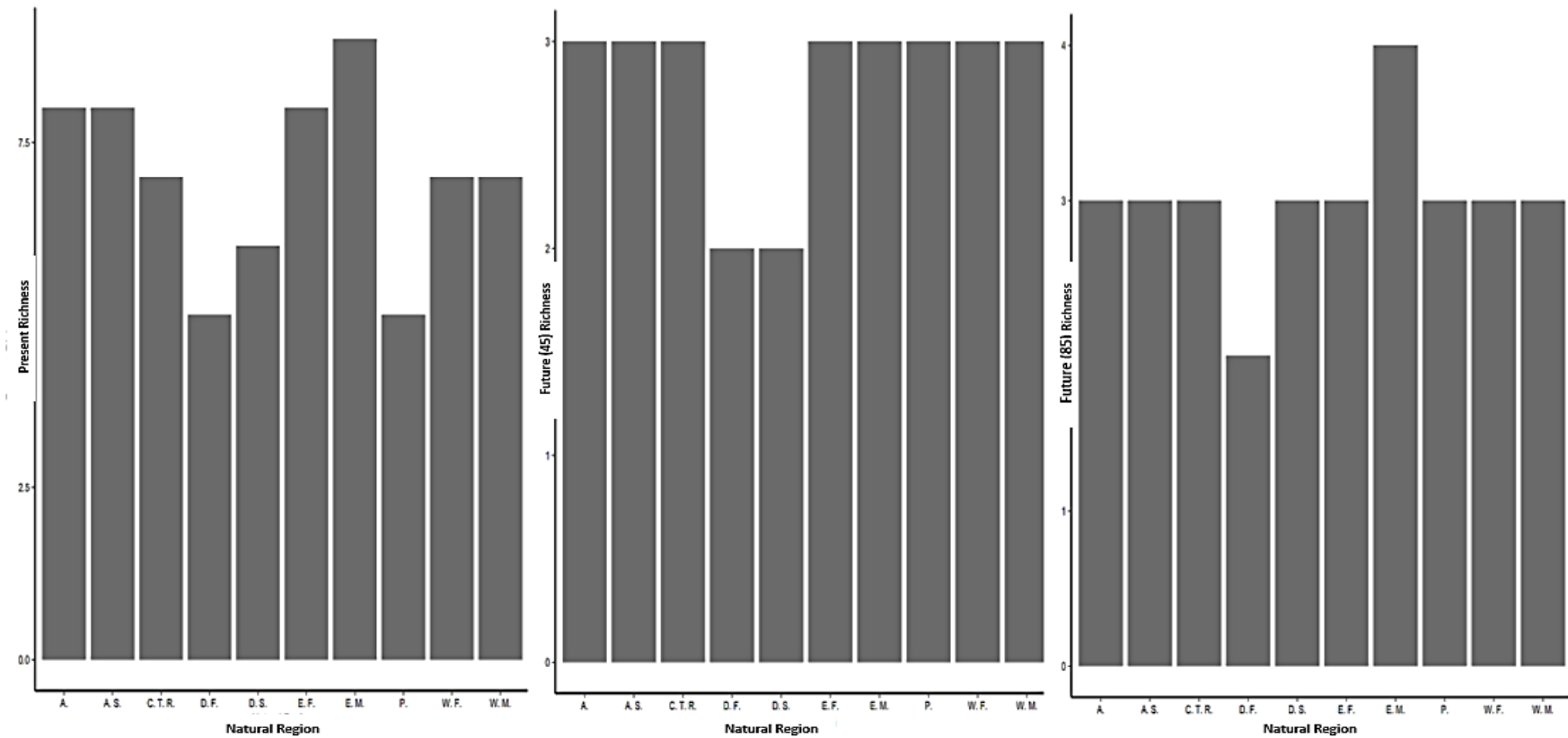


Figure 4 Cumulative species Richness in Ecuador's natural regions in current (A), RCP 4.5 (B) and (C) RCP 8.5 scenarios

Amazon (A), Andean shrub (A.S) Choco Andean forest (C.T.R), deciduous forest (D.F), Dry shrub (D.S), Eastern Foothill (E.F), Eastern Montane (E.M), paramo (P), Western Foothill (W.F), and for western montane (W.M).

3.2.1 Current Climate scenario

Cumulative richness reveals that the highest number of viper species is located in the Eastern Montane (E.M) with nine species, followed by Amazon (A), Andean Shrub (A.S), and Eastern Foothill (E.F) with 8 species each (Figure 4A). The natural regions with the lowest species richness, with a total of five species each, are the Dry Forest (D.F) and Paramo (P) regions. For more information see (Figure 4). In the current climate change scenario, identifying priority natural regions for conservation is crucial for threatened species. Among them, *Bothrocophias campbelli* (VU) has a high priority in the Western Foothill region (REI 0.6). *Bothrops lojanus* (VU) prioritizes the Eastern Montane region (REI 0.15). *Bothrops osbornei* (VU) shows the highest priority in the Western Foothill region (REI 0.53). *Porthidium arcossae* (EN), an endemic and endangered species, has a priority in the Dry Shrub region (REI 0.2) (Table 3).

Table 3 Relative importance of ecosystem availability (REI = suitability/availability) per natural region in current and future climate scenario for threatened viperid species in Ecuador.

Natural Regions	<i>Bothrocophias campbelli</i> (VU)			<i>Bothrops lojanus</i> (VU)			<i>Bothrops osbornei</i> (VU)			<i>Porthidium arcossae</i> (EN)		
	C	RCP 4.5	RCP 8.5	C	RCP 4.5	RCP 8.5	C	RCP 4.5	RCP 8.5	C	RCP 4.5	RCP 8.5
Andean Shrub	0.01	-	-	0.11	0.04	0.07	0.11	0.01	0.01	0.00	-	-
Amazon	0	-	-	0	0.00	0	0	0.00	0	0	-	-
Western Montane	0.40	-	-	0.03	0.01	0.02	0.47	0.13	0.13	0.02	-	-
Western Foothill	0.60	-	-	0.01	0.00	0	0.53	0.29	0.36	0.07	-	-
Paramo	0.01	-	-	0.05	0.01	0.03	0.07	0.00	0	0.00	-	-
Easter Foothill	0.00	-	-	0.00	0.00	0.02	0.00	0.00	0	0.00	-	-
Easter Montane	0.07	-	-	0.15	0.02	0.01	0.00	0.00	0	0.00	-	-
Dry Shrub	0.01	-	-	0.00	0.09	0.1	0.02	0.01	0.02	0.2	-	-
Deciduous Forest	0.00	-	-	0.01	0.05	0.04	0.02	0.03	0	0.07	-	-
Choco Tropical Rainforest	0.26	-	-	0.00	0.00	0	0.18	0.02	0.15	0.02	-	-

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3.2.2 Climate change scenario RCP 4.5

In the RCP 4.5 climate change scenario, eight natural regions have an equal conservation priority based on their species richness as they host three species each (Figure 3B). These regions are Amazon (A), Andean Shrub (A.S), Choco Andean Forest (C.T.R), Eastern Foothill (E.F), Eastern Montane (E.M), Paramo (P), Western Foothill (W.F), and Western Montane (W.M). However, the Dry Forest (D.F) and Dry Shrub (D.S) regions have the lowest species richness, with only two species each.

Priority natural regions for conservation, based on threatened species, are as follows. For the vulnerable species *Bothrops lojanus*, the priority natural region is the Dry Shrub, with an REI of 0.09. Additionally, for *Bothrops osbornei*, the Western Foothill is the priority natural region by a significant margin, with an REI of 0.29. However, for the other two species, no priority region for conservation exists as their ecological niche is disappearing. Consequently, there is no priority natural region for conservation due to the complete disappearance of the ecological niche of the endemic species *Porthidium arcoae* in Ecuador (Table 3).

3.2.3 Climate change scenario RCP 8.5

In the context of climate change scenario RCP 8.5, the natural region with the highest priority for viper conservation is the eastern montane (E.M) (Figure 3). This region exhibits the highest species richness, with a total of four species. On the other hand, the dry forest (D.F) region contains the lowest species richness, with only two species in its area. The remaining natural regions all contain three viper species niches (Figure 4). Therefore, conservation efforts should focus on protecting the eastern montane region as a high priority.

The conservation priorities for the vulnerable species *Bothrops lojanus* and *Bothrops osbornei* in the RCP 8.5 scenario are similar to those in RCP 4.5. For *Bothrops lojanus*, the Dry Shrub region remains the priority natural area, while the Western Foothill continues to be the priority region for *Bothrops osbornei*. However, just like in RCP 4.5, the other two species have no priority conservation regions as their ecological niches are disappearing. This leads to the absence of a priority natural region for the conservation of the endemic species *Porthidium Arcoae* in Ecuador. (Table 3).

3.3 Conservation of environmental suitability areas from Ecuadorian vipers in the National System of protected Areas (SNAP)

The total area encompassing the ecological niche models for the 17 viper species recorded in continental Ecuador is 266,126 Km² with 45,117 Km²(16.95%) falling within the SNAP (Figures 1 and 5). Suitability areas for all species have modeled with less of 25% of its niche inside the SNAP. Out of the 17 viper species analyzed, a total of 8 species have less than 15% of their ecological niche coverage, accounting for approximately 58.82% of the studied viper species. *Bothriopsis bilineata* and *Bothriopsis*

taeniata show the highest coverage percentages, with 24.6% and 24.5%, respectively. In contrast, *Bothrops asper* and *Bothriechis schlegelii* have the lowest coverage percentages of 6.27% and 6.97%, respectively. Notably, the Vulnerable (VU) species, *Bothrops lojanus* and *Bothrops osbornei*, exhibit coverage percentages of 20.1% and 14.76%, respectively. Additionally, the endemic species *Porthidium arcossae*, classified as Endangered (EN), demonstrates relatively low niche coverage of 9.11% (Table 4).

The number of niche species covered by the SNAP ranges from 8 to 1. Among the protected areas there are notable variations in the ecological niche coverage. The highest species ecological niche coverage, with a total of 8 species, is found in protected areas such as P.N.L., P.N.P., P.N.San., P.N.Sum., and R.E.Cay. These areas are primarily located in the eastern mountainous region of Ecuador, which exhibits the highest level of ecological niche overlap. On the other hand, there are protected areas that show comparatively lower niche coverage, with only 1 species present. These areas include P.N.Caj. and R.E.Man., located in the western part of Ecuador (Figure 5). It is important to note that these areas also have relatively smaller coverage within the SNAP.

Table 4 Ecological niche area (Km²) for Ecuadorian vipers in current climate scenario inside the SNAP (%)

Species (UICN Threat category)	Ecological niche (Km ²)	Área covered by SNAP (%)
<i>Bothriechis schlegelii</i> (LC)	509062	6.97
<i>Bothriopsis bilineata</i> (LC)	3644111	24.6
<i>Bothriopsis pulchra</i> (LC)	38168	22.06
<i>Bothriopsis taeniata</i> (LC)	5406104	24.59
<i>Bothrocophias campbelli</i> (VU)	69638	14.23
<i>Bothrocophias hyoprora</i> (LC)	4679710	24.68
<i>Bothrocophias microphthalmus</i> (LC)	1324065	24.41
<i>Bothrops asper</i> (LC)	1482271	6.27
<i>Bothrops atrox</i> (LC)	5440764	22
<i>Bothrops brazili</i> (LC)	3456731	19.36
<i>Bothrops lojanus</i> (VU)	6656	20.1
<i>Bothrops osbornei</i> (VU)	37224	14.76
<i>Bothrops punctatus</i> (LC)	115171	13.95
<i>Lachesis acrochorda</i> (LC)	270797	9.2
<i>Lachesis muta</i> (LC)	7325120	21.35

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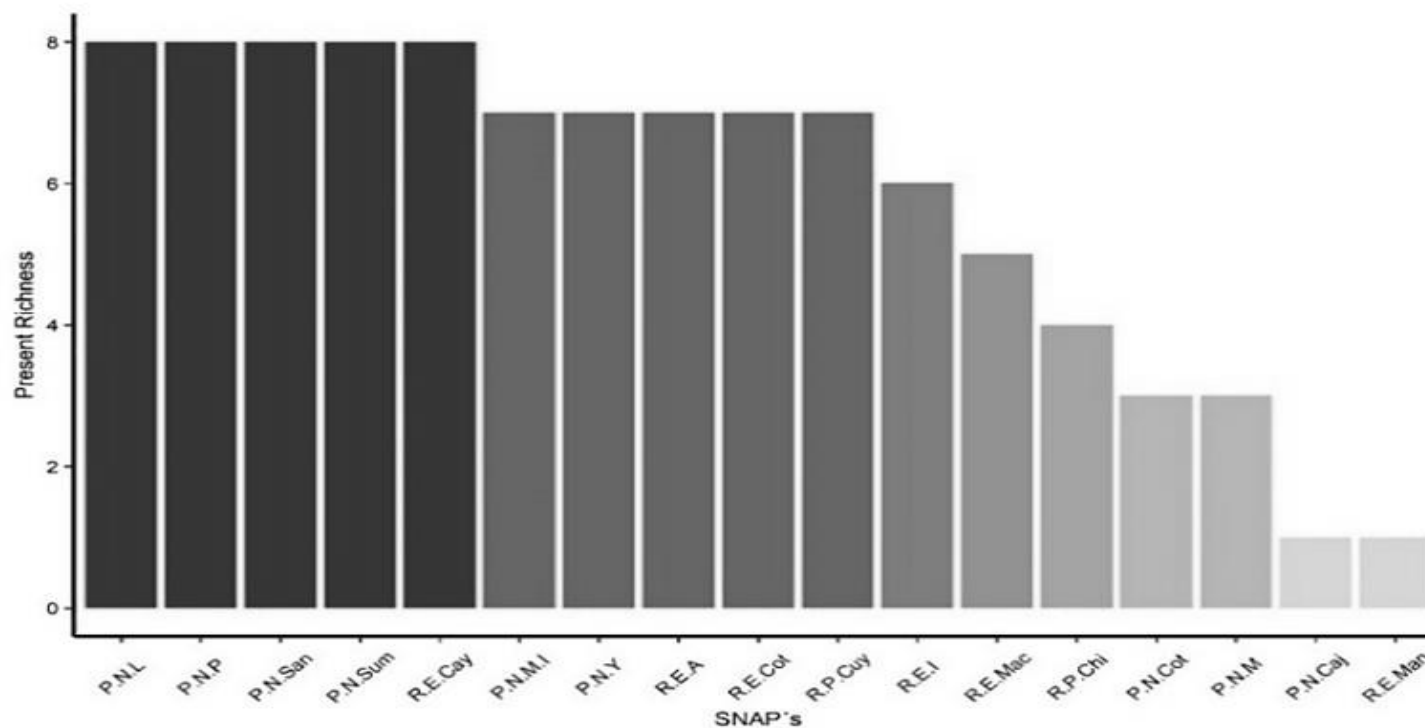


Figure 5 Cumulative richness of species per Protected area

Parque Nacional Llanganates (P.N.L.), Parque Nacional Podocarpus (P.N.P), Parque Nacional Sangay(P.N.San) , P.N.Sum Parque Nacional Sumaco Napo-Galeras(P.N.Sum), Reserva Ecológica Cayambe-Coca (R.E.Cay), Parque Nacional Machalilla, Isla de la Plata(P.N.M.I), Parque Nacional Yasuní (P.N.Y), Reserva Ecológica Antisana (R. E. A.), Reserva Ecológica Cotacachi-Cayapas (R.E.Cot) ,Reserva de Producción Faunística Cuyabeno (R.P. Cuy), Reserva Ecológica Los Illinizas (R.E.I),Reserva Ecológica Mache – Chindul (R.E.Mac), Reserva de Producción Faunística Chimborazo (R.P.Chi), Parque Nacional Cotopaxi (P.N.Cot), Parque Nacional Machalilla (P.N.M), for Parque Nacional Cajas (P.N.Caj) , Reserva Ecológica Manglares – Churute (R.E.Man).

4 DISCUSSION

Herein we evaluate the biogeographical patterns of Ecuadorian vipers under future climate change scenarios and identify priority regions for their conservation. The results revealed significant implications for the ecological suitability and conservation of these vipers. One of the key findings is the potential disappearance of the ecological niche of 10 out of the 17 viper species studied under both RCP 4.5 and RCP 8.5 climate change scenarios. This alarming outcome highlights the vulnerability of these species to the projected changes in climate for the year 2050.

The loss of their environmentally suitable habitats could have severe consequences for their survival and population dynamics (Diele et al., 2020). Furthermore, both climate change scenarios predict a substantial contraction of the ecological niche for Ecuadorian vipers. In RCP 4.5, a reduction of 65.04% in niche coverage is projected, while RCP 8.5 anticipates a reduction of 67.32%. These reductions indicate a significant decline in suitable habitats for vipers, particularly in the western lowlands of Ecuador. The shrinking ecological niche coverage in these areas could lead to population fragmentation, reduced gene flow, and increased competition for limited resources among vipers (Needleman et al., 2018).

The distribution and richness of viper species across the different natural regions in Ecuador is a key factor to consider in the development of conservation strategies for these important reptiles, particularly in the face of climate change as one of the main drivers of the current biodiversity crisis (Weiskopf et al., 2020). The disappearance and contraction of the ecological niche have several implications for the conservation of Ecuadorian vipers. Firstly, it emphasizes the urgent need for proactive conservation measures to mitigate the negative effects of climate change on these species. Efforts should focus on identifying and protecting the remaining suitable habitats.

The identification of priority regions for conservation, based on species richness, endangered species, and endemism, provides a valuable framework for guiding conservation planning and management strategies. The different natural regions in Ecuador that host viper populations are characterized by unique environmental conditions that influence the diversity and distribution of these species.

The Eastern Montane region, which includes the forest at highlands in the Andes Mountains, has a high species richness of vipers (Figure 1) due to the diverse habitats it provides, including cloud forests, montane forests, and high-elevation grasslands (Pepin et al., 2022), which highlight this region as an important area for biodiversity of vipers's conservation.

The Amazon region, on the other hand, is characterized by the humid and tropical rainforest ecosystems that support a diverse range of flora and fauna, including eight species of vipers (Figure 1 and 4). The Andean Shrub region, located in the inter-Andean valleys, has a semi-arid climate and supports a variety of vegetation types such as dry forests, scrublands, and cactus groves (Hazzi et al., 2018).

The Paramo region, located in the high-elevation grasslands of the Andes Mountains, is characterized by harsh environmental conditions, including low temperatures, scarce precipitation and strong winds (Tovar et al., 2013), which biogeographically limit the diversity of species. The lower species richness in the natural regions of the lowlands of the coast in Ecuador (D.S and D.F) could be due to the extremely dry and hot climatic conditions, human impact through deforestation and habitat conversion (<https://bioweb.bio/faunaweb/amphibiaweb/RegionesNaturales>).

The identification of priority regions for viper conservation becomes crucial in light of the projected to climate change scenarios. The natural regions where significant declines in ecological suitability are expected, such as the Dry Shrub and Deciduous Forest in RCP 4.5, and Andean Shrub and Western Montane in RCP 8.5, should receive special attention and conservation efforts. These regions are likely to experience the most pronounced impacts on viper populations and require targeted conservation strategies to safeguard their ecological functionality. Efforts should focus in the Eastern montane and Amazon Region which have the highest REI in current and future climate change scenarios. Moreover, the conservation of Ecuadorian vipers within the National System of Protected Areas (SNAP) is inadequate, as none of the studied species have at least 25% of their niche coverage inside the SNAP. This highlights the need for expanding the protected area network to encompass a greater proportion of the vipers' ecological niche. Priority should be given to protected areas with high ecological niche overlap.

The results of our study provide valuable insights into the distribution patterns of vipers and highlight the regions that are of particular importance for conservation. By considering species richness, endangered species, and endemism, we can identify areas that harbor high biodiversity and support unique and vulnerable viper populations.

The identification of priority natural regions for conservation based on species richness and threatened species is crucial in the face of climate change. In the current climate scenario, the Eastern Montane region stands out as a hotspot of viper diversity, along with the Amazon and Eastern Foothill regions, emphasizing their significance for conservation. These regions should be prioritized for protection to ensure the long-term survival of vipers in Ecuador and to safeguard biodiversity. Additionally, priority regions for conservation have been identified for threatened viper species in both scenarios. However, the possible disappearance of endemic and threatened viper species in future climate scenarios can have profound impacts on biodiversity and ecosystem dynamics (Eguiguren et al., 2016). Urgent and targeted conservation efforts are essential to protect these vulnerable species and their habitats, ensuring the preservation of biodiversity and ecosystem integrity in Ecuador. Moreover, conserving areas with threatened species safeguards broader biodiversity, supports local communities by providing essential ecosystem services, aligns with international conservation targets, and enhances ecosystem resilience in the face of environmental challenges (Weiskopf et al., 2020). Directing efforts to protect these areas can significantly contribute to preserving vulnerable species and the ecosystems they inhabit, promoting a more sustainable and resilient future for our planet.

Although some regions may have a lower conservation priority in terms of species richness (dry Shrub, deciduous forest and paramo), they should not be overlooked as they still contribute to the overall viper biodiversity and may play important ecological roles. Therefore, conservation efforts should consider the unique characteristics and ecological significance of each natural region to ensure the comprehensive protection and preservation of viper species in the face of climate change, such as REI.

In light of these findings, the identification of priority natural regions for viper conservation becomes even more crucial. It is essential to focus conservation efforts on protecting and restoring the habitats within these priority regions to mitigate the potential negative impacts of climate change on viper populations. Conservation actions should include the establishment and expansion of protected areas, habitat restoration initiatives, and the

implementation of sustainable land-use practices to ensure the long-term survival of vipers and maintain the ecological integrity of their habitats. Furthermore, allocating resources and implementing targeted conservation measures in these priority regions, we can maximize the effectiveness of conservation efforts and contribute to the long-term persistence of Ecuadorian vipers.

Conclusions

The Eastern Montane region stands out as the key area for conservation based on species richness, harboring the highest species richness in all climate scenarios. Furthermore, specific regions like the Western Foothill and Dry Shrub are crucial for the protection of threatened species, emphasizing their significance in maintaining these species habitat. However, challenges arise as two species face the complete disappearance of their ecological niches, underscoring the urgency for targeted conservation efforts to ensure the survival of these vulnerable species and preserve Ecuadorian viper biodiversity. This study highlights the significant implications of climate change on Ecuadorian vipers. The potential disappearance of their ecological niche and the contraction of suitable habitats underscore their vulnerability. Urgent conservation measures are needed to mitigate these impacts. Identifying priority regions for viper conservation based on species richness and threatened species is crucial. The disappearance of ecological niches poses challenges for threatened species and the endemic species. In summary, proactive conservation efforts, expanded protected areas, and targeted strategies are essential to safeguard Ecuadorian vipers and their habitats. By addressing the identified priority regions using multicriteria, we can enhance the effectiveness of conservation measures in the face of climate change. Future studies could enhance the prioritization process by incorporating additional variables in ecological niche modeling, such as deforestation and land use, and by analyzing beta diversity to better understand species distribution and overlap among natural regions. These data-driven recommendations can contribute to the development of effective conservation strategies to mitigate the impacts of climate change and ensure the long-term survival of these vulnerable reptiles.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

REFERENCES

- Adhikari, D., Reshi, Z., Datta, B. K., Samant, S. S., Chettri, A., Upadhaya, K., Shah, M. A., Singh, P. P., Tiwary, R., Majumdar, K., Pradhan, A., Thakur, M. L., Salam, N., Zahoor, Z., Mir, S. H., Kaloo, Z. A., & Barik, S. K. (2018). Inventory and characterization of new populations through ecological niche modelling improve threat assessment. *Current Science*, 114(3), 519–531. <https://doi.org/10.18520/cs/v114/i03/519-531>
- Anderson, R. P., Lew, D., & Peterson, A. T. (2003). Evaluating predictive models of species' distributions: Criteria for selecting optimal models. *Ecological Modelling*, 162(3), 211–232. [https://doi.org/10.1016/S0304-3800\(02\)00349-6](https://doi.org/10.1016/S0304-3800(02)00349-6)
- Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S. P., Peterson, A. T., Soberón, J., & Villalobos, F. (2011). The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecological Modelling*, 222(11), 1810–1819. <https://doi.org/10.1016/j.ecolmodel.2011.02.011>
- Carrillo, E., Aldás, A., Altamirano, M., Ayala, F., Cisneros-Heredia, D., Endara, A., Márquez, C., Morales, M., Nogales, F., Salvador, P., Torres, M., Valencia, J., Villamarín, F., Yáñez-Muñoz, M., & Zárate, P. (2005). *Lista Roja De Los Reptiles Del Ecuador*.
- Cobos, M. E., Townsend Peterson, A., Barve, N., & Osorio-Olvera, L. (2019). Kuenm: An R package for detailed development of ecological niche models using Maxent. *PeerJ*, 2019(2), 1–15. <https://doi.org/10.7717/peerj.6281>
- Crews, D. (1988). Life History of Snakes Snakes: Ecology and Evolutionary Biology R. A. Siegel J. T. Collins S. S. Novak. *BioScience*, 38(10), 716–717. <https://doi.org/10.2307/1310891>
- Diele, L. M., Figueroa, R. T., Vilela, B., & Rocha, C. F. D. (2020). Are reptiles toast? A worldwide evaluation of Lepidosauria vulnerability to climate change. *Climatic Change*, 159(4), 581–599. <https://doi.org/10.1007/s10584-020-02687-5>
- Ducatez, S., & Shine, R. (2017). Drivers of Extinction Risk in Terrestrial Vertebrates. *Conservation Letters*, 10(2), 186–194. <https://doi.org/10.1111/conl.12258>
- Eguiguren, P. A., Chamba, J. A. M., Aguirre Mendoza, N. A., Ojeda Luna, T. L., Samaniego Rojas, N. S., Furniss, M. J., Howe, C., & Aguirre Mendoza, Z. H. (2016). Tropical ecosystems vulnerability to climate change in southern Ecuador. *Tropical Conservation Science*, 9(4). <https://doi.org/10.1177/1940082916668007>
- Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, 17(1), 43–57. <https://doi.org/10.1111/j.1472-4642.2010.00725.x>
- Escobar, L. E., Lira-Noriega, A., Medina-Vogel, G., & Townsend Peterson, A. (2014). Potential for spread of the white-nose fungus (*Pseudogymnoascus destructans*) in the Americas: Use of Maxent and NicheA to assure strict model transference. *Geospatial Health*, 9(1), 221–229. <https://doi.org/10.4081/gh.2014.19>
- Esquerré, D., Brennan, I. G., Catullo, R. A., Torres-Pérez, F., & Keogh, J. S. (2019). How mountains shape biodiversity: The role of the Andes in biogeography, diversification, and

- reproductive biology in South America's most species-rich lizard radiation (Squamata: Liolaemidae). *Evolution*, 73(2), 214–230. <https://doi.org/10.1111/evo.13657>
- Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37(12), 4302–4315. <https://doi.org/10.1002/joc.5086>
- Guedes, T. B., Sawaya, R. J., Zizka, A., Laffan, S., Faurby, S., Pyron, R. A., Bérnils, R. S., Jansen, M., Passos, P., Prudente, A. L. C., Cisneros-Heredia, D. F., Braz, H. B., Nogueira, C. de C., & Antonelli, A. (2018). Patterns, biases and prospects in the distribution and diversity of Neotropical snakes. *Global Ecology and Biogeography*, 27(1), 14–21. <https://doi.org/10.1111/geb.12679>
- Hammer, Ø., Harper, D. A. T., & Ryan, P. D. (2001). PAST : Paleontological Statistics Software Package for Education and Data Analysis PAST : PALEONTOLOGICAL STATISTICS SOFTWARE PACKAGE FOR EDUCATION AND DATA ANALYSIS Even a cursory glance at the recent paleontological literature should convince anyone tha. *Palaeontologia Electronica*, 4(1), 1–9.
- Hazzi, N. A., Moreno, J. S., Ortiz-Movliav, C., & Palacio, R. D. (2018). Biogeographic regions and events of isolation and diversification of the endemic biota of the tropical Andes. *Proceedings of the National Academy of Sciences of the United States of America*, 115(31), 7985–7990. <https://doi.org/10.1073/pnas.1803908115>
- Herzog, S., Martínez, R., Jorgensen, P. M., & Tiessen, H. (2012). Cambio Climático y Biodiversidad en los Andes Tropicales. In *Cambio Climático y Biodiversidad en los Andes Tropicales*.
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25(15), 1965–1978. <https://doi.org/10.1002/joc.1276>
- Huang, S. P., Chiou, C. R., Lin, T. E., Tu, M. C., Lin, C. C., & Porter, W. P. (2013). Future advantages in energetics, activity time, and habitats predicted in a high-altitude pit viper with climate warming. *Functional Ecology*, 27(2), 446–458. <https://doi.org/10.1111/1365-2435.12040>
- Jiménez-Valverde, A. (2012). Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modelling. *Global Ecology and Biogeography*, 21(4), 498–507. <https://doi.org/10.1111/j.1466-8238.2011.00683.x>
- Jones, C. D., Hughes, J. K., Bellouin, N., Hardiman, S. C., Jones, G. S., Knight, J., Liddicoat, S., O'Connor, F. M., Andres, R. J., Bell, C., Boo, K. O., Bozzo, A., Butchart, N., Cadule, P., Corbin, K. D., Doutriaux-Boucher, M., Friedlingstein, P., Gornall, J., Gray, L., ... Zerroukat, M. (2011). The HadGEM2-ES implementation of CMIP5 centennial simulations. *Geoscientific Model Development*, 4(3), 543–570. <https://doi.org/10.5194/gmd-4-543-2011>
- Lobo, J., Jiménez, A., & Real, R. (2008). AUC: A misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*, 17(2), 145–151. <https://doi.org/10.1111/j.1466-8238.2007.00358.x>

- Mcpherson, M., Schill, S., Raber, G., John, K., Zenny, N., Thurlow, K., Sutton, A. H., Street, L., Schill, S., José, S., Rica, C., & Pen, M. (2008). GIS-based Modeling of Environmental Risk Surfaces (ERS) for Conservation Planning in Jamaica. *Journal of Conservation Planning*, 4, 60–89.
- Morrone, J. (2014). Biogeographical regionalisation of the neotropical region. In *Zootaxa* (Vol. 3782, Issue 1). <https://doi.org/10.11646/zootaxa.3782.1.1>
- Mota, C., Encarnacion, A., Ortega, M., Prieto, D., Peña, A., & Rojas, O. (2019). Una breve introducción a los modelos de nicho ecológico. *La Biodiversidad En Un Mundo Cambiante: Fundamentos Teóricos y Metodológicos Para Su Estudio*, February 2020, 39–63.
- Needleman, R. K., Neylan, I. P., & Erickson, T. (2018). Potential Environmental and Ecological Effects of Global Climate Change on Venomous Terrestrial Species in the Wilderness. *Wilderness and Environmental Medicine*, 29(2), 226–238. <https://doi.org/10.1016/j.wem.2017.11.004>
- Pandey, D. P., Subedi Pandey, G., Devkota, K., & Goode, M. (2016). Public perceptions of snakes and snakebite management: Implications for conservation and human health in southern Nepal. *Journal of Ethnobiology and Ethnomedicine*, 12(1). <https://doi.org/10.1186/s13002-016-0092-0>
- Pearson, R. G. (2010). Network of Conservation Educators & Practitioners Species' Distribution Modeling for Conservation Educators and Practitioners. In *Conservation*, 3, 54–89. <http://ncep.amnh.org/linc>
- Pepin, N. C., Arnone, E., Gobiet, A., Haslinger, K., Kotlarski, S., Notarnicola, C., Palazzi, E., Seibert, P., Serafin, S., Schöner, W., Terzago, S., Thornton, J. M., Vuille, M., & Adler, C. (2022). Climate Changes and Their Elevational Patterns in the Mountains of the World. *Reviews of Geophysics*, 60(1), 1–40. <https://doi.org/10.1029/2020RG000730>
- Phillips, S. B., Aneja, V. P., Kang, D., & Arya, S. P. (2006). Maximum entropy modeling of species geographic distributions. *International Journal of Global Environmental Issues*, 6(2–3), 231–252. <https://doi.org/10.1016/j.ecolmodel.2005.03.026>
- Pulliam, H. R. (1986). Niche expansion and contraction in a variable environment. *Integrative and Comparative Biology*, 26(1), 71–79. <https://doi.org/10.1093/icb/26.1.71>
- Rautsaw, R. M., Jiménez-Velázquez, G., Hofmann, E. P., Alencar, L. R. V., Grünwald, C. I., Martins, M., Carrasco, P., Doan, T. M., & Parkinson, C. L. (2022). VenomMaps: Updated species distribution maps and models for New World pitvipers (Viperidae: Crotalinae). *Scientific Data*, 9(1), 1–9. <https://doi.org/10.1038/s41597-022-01323-4>
- Riahi, K., Rao, S., Krey, V., Cho, C., Chirkov, V., Fischer, G., Kindermann, G., Nakicenovic, N., & Rafaj, P. (2011). RCP 8.5-A scenario of comparatively high greenhouse gas emissions. *Climatic Change*, 109(1), 33–57. <https://doi.org/10.1007/s10584-011-0149-y>
- Scheele, B. C., Foster, S. C., & Banks, D. B. (2017). Niche contractions in declining species: mechanisms and consequences. *Trends in Ecology & Evolution*, 32, 1–29.
- Shine, R., & Bonnet, X. (2000). Snakes: A new “model organism” in ecological research? *Trends in Ecology and Evolution*, 15(6), 221–222. [https://doi.org/10.1016/S0169-5347\(00\)01853-X](https://doi.org/10.1016/S0169-5347(00)01853-X)

- Sjödin, H., Ripa, J., & Lundberg, P. (2018). Principles of niche expansion. *Proceedings of the Royal Society B: Biological Sciences*, 285(1893). <https://doi.org/10.1098/rspb.2018.2603>
- Soberón, J. (2010). Niche and area of distribution modeling: A population ecology perspective. *Ecography*, 33(1), 159–167. <https://doi.org/10.1111/j.1600-0587.2009.06074.x>
- Soberón, J., & Peterson, A. (2008). INTERPRETATION OF MODELS OF FUNDAMENTAL ECOLOGICAL NICHES AND SPECIES' DISTRIBUTIONAL AREAS. *Biodiversity Informatics*, 5(10), 3392–3396. <https://doi.org/10.1002/pssc.200778935>
- Tovar, C., Arnillas, C. A., Cuesta, F., & Buytaert, W. (2013). Diverging Responses of Tropical Andean Biomes under Future Climate Conditions. *PLoS ONE*, 8(5). <https://doi.org/10.1371/journal.pone.0063634>
- Urbina, N., & Flores, O. (2010). Ecological-niche modeling and prioritization of conservation-area networks for Mexican herpetofauna. *Conservation Biology*, 24(4), 1031–1041. <https://doi.org/10.1111/j.1523-1739.2009.01432.x>
- Warren, S. (2011). Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications*, 21(2), 335–342.
- Weiskopf, S. R., Rubenstein, M. A., Crozier, L. G., Gaichas, S., Griffis, R., Halofsky, J. E., Hyde, K. J. W., Morelli, T. L., Morissette, J. T., Muñoz, R. C., Pershing, A. J., Peterson, D. L., Poudel, R., Staudinger, M. D., Sutton-Grier, A. E., Thompson, L., Vose, J., Weltzin, J. F., & Whyte, K. P. (2020). Climate change effects on biodiversity, ecosystems, ecosystem services, and natural resource management in the United States. *Science of the Total Environment*, 733(xxxx). <https://doi.org/10.1016/j.scitotenv.2020.137782>
- Wu, J. (2016). Detecting and Attributing the Effects of Climate Change on the Distributions of Snake Species Over the Past 50 Years. *Environmental Management*, 57(1), 207–219. <https://doi.org/10.1007/s00267-015-0600-3>
- Yáñez, M., Rangel, C., Murray, K. A., Goldstein, E., Iwamura, T., & Chiappa, X. (2021). Implications of global environmental change for the burden of snakebite. *Toxicon: X*, 9–10. <https://doi.org/10.1016/j.toxcx.2021.100069>
- Zurell, D., Franklin, J., König, C., Bouchet, P. J., Dormann, C. F., Elith, J., Fandos, G., Feng, X., Guillera-Aroita, G., Guisan, A., Lahoz-Monfort, J. J., Leitão, P. J., Park, D. S., Peterson, A. T., Rapacciuolo, G., Schmatz, D. R., Schröder, B., Serra-Diaz, J. M., Thuiller, W., ... Merow, C. (2020). A standard protocol for reporting species distribution models. *Ecography*, 43(9), 1261–1277. <https://doi.org/10.1111/ecog.04960>

APPENDIX I. Selected bioclimatic variables for ecological niche modeling in Ecuadorian vipers.

Bioclimatic Variables																AUC	OR
Species	BIO 1	BIO 2	BIO 3	BIO 4	BIO 5	BIO 6	BIO 7	BIO 10	BIO 11	BIO 12	BIO 13	BIO 14	BIO 15	BIO 16	BIO 17		
<i>Bothriechis schlegelii</i>		X		X	X		X			X		X	X	X		0,892	0,078
<i>Bothriopsis bilineata</i>		X		X	X	X	X					X	X	X		0,871	0,097
<i>Bothriopsis pulchra</i>			X	X		X	X						X	X		0,987	0
<i>Bothriopsis taeniata</i>			X	X	X		X			X			X		X	0,819	0
<i>Bothrocophias campbelli</i>				X	X		X			X			X	X		0,912	0
<i>Bothrocophias hyoprora</i>				X	X	X	X	X		X		X	X	X		0,892	0,059
<i>Bothrocophias microphthalmus</i>	X		X	X			X	X				X	X	X		0,909	0,08
<i>Bothrops asper</i>	X	X		X		X	X	X	X	X			X		X	0,761	0,094
<i>Bothrops atrox</i>		X	X	X	X	X	X			X	X				X	0,808	0,097
<i>Bothrops brazili</i>	X	X	X	X		X	X		X	X	X		X			0,863	0,083
<i>Bothrops lojanus</i>		X	X					X		X	X	X				0,94	0
<i>Bothrops osbornei</i>			X				X	X				X	X		X	0,921	0
<i>Bothrops punctatus</i>			X	X	X		X			X			X		X	0,939	0
<i>Lachesis acrochorda</i>			X	X		X	X	X		X			X		X	0,853	0
<i>Lachesis muta</i>			X	X	X	X	X	X		X		X		X		0,789	0,054
<i>Porthidium arcosae</i>		X	X	X		X	X			X	X	X		X		0,926	0
<i>Porthidium nasutum</i>	X	X		X		X	X	X		X			X		X	0,906	0,055

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