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Contraction or expansion? Modeling the response of South American *Hedeoma* (Lamiaceae) species to future climate shifts

¿Contracción o Expansión? Modelización de la respuesta de las especies sudamericanas de *Hedeoma* (Lamiaceae) a los futuros cambios climáticos

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Abstract

Climate change is driving significant shifts in the geographic distribution of plant species, particularly affecting those with medicinal and cultural value. In this study, we modeled the current and future (2070) potential distributions of four South American *Hedeoma* species (*H. mandoniana*, *H. medium*, *H. polygalifolia*, and the micro-endemic *H. teyucuarensis*) using MaxEnt and three climate scenarios (RCP 2.6, 4.5, and 8.5). Our results reveal heterogeneous responses: *H. mandoniana* is projected to undergo a significant range contraction (up to 38%) and an upslope displacement in the Andes, driven by elevation and clay content. In contrast, *H. medium* showed a robust expansion potential (42-59%) toward Uruguay, likely favored by greater climate stability and its edaphic generalist nature. The micro-endemic *H. teyucuarensis* species exhibited high vulnerability due to its extremely narrow thermal tolerance and dependence on specific sandy soils in Misiones, Argentina. The present study emphasizes that niche breadth and soil specificity are critical determinants of climate change resilience.

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The Misiones Province Law XVI–No. 185 declares *Hedeoma teyucuaensis* a “Natural Monument and of Public Interest” for the purposes of preservation, conservation, and reproduction. We propose urgent *in situ* conservation priority for *H. teyucuaensis*, currently under IUCN assessment, to mitigate the risks posed by environmental shifts and overexploitation.

Keywords: Climate; endemism; MaxEnt; soil.

Resumen

El cambio climático está impulsando alteraciones significativas en la distribución geográfica de las plantas, afectando particularmente a aquellas con valor medicinal y cultural. En este estudio, se modelaron las distribuciones potenciales actuales y futuras (2070) de cuatro especies sudamericanas de *Hedeoma* (*H. mandoniana*, *H. medium*, *H. polygalifolia* y la microendémica *H. teyucuaensis*) utilizando MaxEnt y tres escenarios climáticos (RCP 2.6, 4.5 y 8.5). Nuestros resultados revelan respuestas heterogéneas: se proyecta que *H. mandoniana* experimentará una contracción significativa de su área (hasta un 38%) y un desplazamiento altitudinal en los Andes, impulsado por la elevación y el contenido de arcilla. Por el contrario, *H. medium* mostró un robusto potencial de expansión (42–59%) hacia Uruguay, favorecido probablemente por una mayor estabilidad climática y su carácter de generalista edáfica. La especie microendémica *H. teyucuaensis* exhibió una alta vulnerabilidad debido a su tolerancia térmica extremadamente estrecha y su dependencia de suelos arenosos específicos en Misiones, Argentina. Estos hallazgos enfatizan que la amplitud de nicho y la especificidad edáfica son determinantes críticos de la resiliencia ante el cambio climático. La Ley XVI N° 185 de la provincia de Misiones declara a *Hedeoma teyucuaensis* como “Monumento Natural y de Interés Público” para su preservación, conservación y reproducción. Proponemos otorgar prioridad urgente a la conservación *in situ* de *H. teyucuaensis*, actualmente en proceso de evaluación por la UICN, a fin de mitigar los riesgos derivados de los cambios ambientales y la sobreexplotación.

Palabras clave: Clima; endemismo; MaxEnt; suelo.

INTRODUCTION

The genus *Hedeoma* Pers. (Lamiaceae) comprises approximately 43 species distributed from the United States of America to Uruguay and central Argentina. In South America, notable species include *Hedeoma multiflora* Benth., *H. medium* Epling, *H. mandoniana* Wedd., *H. polygalifolia* Benth., and *H. teyucuaensis* (Fig. 1) (Slanis & Bulacio, 2005; Keller & Tressens, 2016; Peralta *et al.*, 2020). This genus is recognized for its medicinal, cultural, and economic importance due to the phytochemical properties and their traditional uses in various communities.

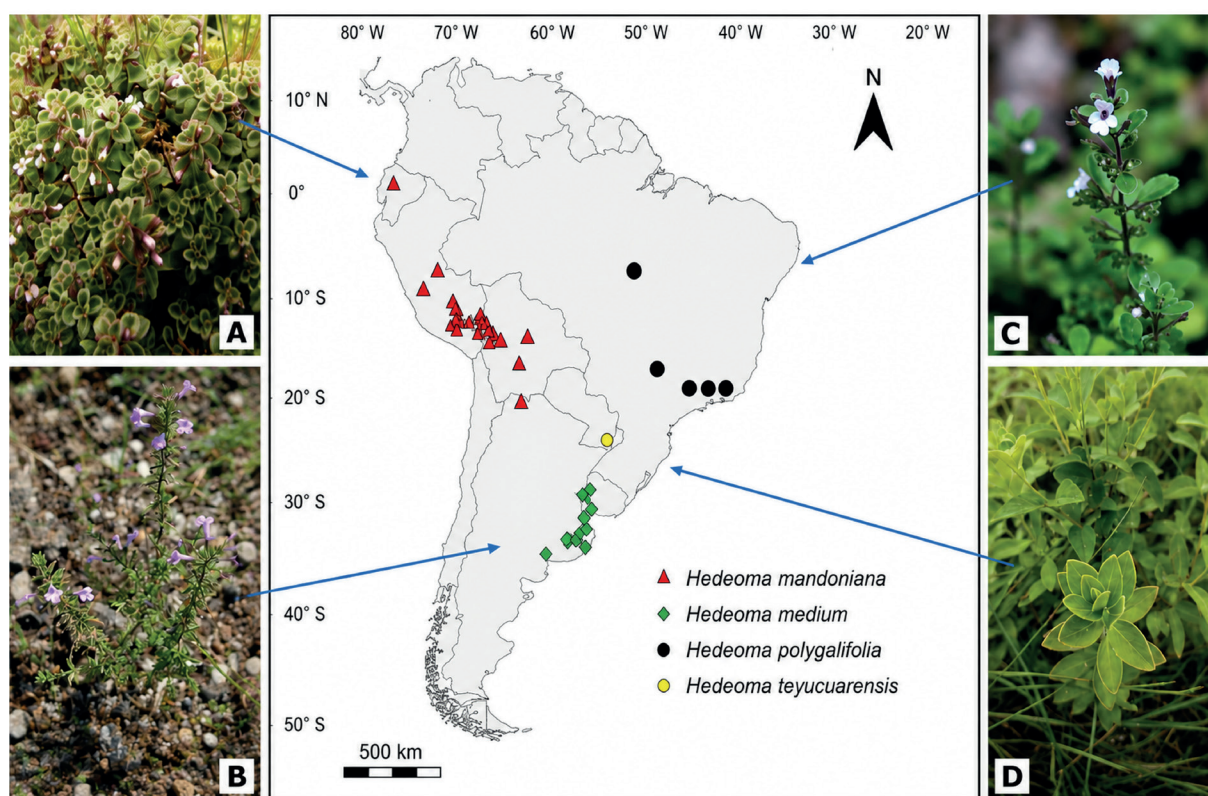


Fig. 1. Study area and distribution of occurrence records for the analyzed *Hedeoma* species.

Fig. 1. Área de estudio y distribución de los registros de ocurrencia de las especies de *Hedeoma* analizadas.

Studies conducted on methanolic extracts of their aerial parts have revealed high antioxidant capacity, mainly associated with the presence of phenolic compounds such as rosmarinic, chlorogenic, and caffeic acids (Viveros-Valdez *et al.*, 2008; Cárdenas-Valdovinos *et al.*, 2025).

Hedeoma mandoniana is widely used in both traditional medicine and agriculture across various Andean regions and cultures. In traditional medicine, it is highly valued for alleviating diverse digestive ailments—including stomachaches, diarrhea, colic, flatulence, and vomiting—as well as for treating respiratory conditions such as colds, flu, and coughs (Laupa Roman & Vengoa Valdiglesias, 2013). In the region of Iruya (Salta, Argentina), for instance, it is specifically consumed as an infusion to treat coughs. Furthermore, the species is reported to have antiasthmatic, expectorant, antispasmodic, antiseptic, analgesic, anti-inflammatory, and febrifuge effects; it is employed in the treatment of tumors, fractures, halitosis, altitude sickness, and headaches (Huaman Espinoza & Zurita Valdez, 2020), with specific medicinal applications against migraines documented in Bolivia (Girault, 1984). Beyond its medicinal qualities, the plant's essential oil, extracted from fresh leaves, exhibits significant insecticidal properties. This has led to its traditional use as a repellent by Quechua Indians (Bastien, 1983; Fournet *et al.*, 1996; Vilaseca *et al.*,

2004) and its application as an organic fumigant to protect crops, such as potatoes, against insects and fungi (Huaman Espinoza & Zurita Valdez, 2020). Additionally, the plant holds culinary and cultural significance; its dried leaves, known for their flavoring properties, are used as a condiment by the Aymara indigenous people in the Eastern Cordillera of the Bolivian Andes (Pestalozzi & Torrez, 1998), while in Iruya, it is sometimes cultivated by locals to smudge environments during Holy Week festivities.

Hedeoma medium is mainly known for its use in treating digestive disorders (Vercelli *et al.*, 2013), and to date, no scientific reports have been found regarding the ethnobotanical use of *H. polygalifolia*. Whereas *H. mandoniana* and *H. medium* are relatively well documented regarding their traditional uses, *H. polygalifolia* remains one of the least studied South American representatives of the genus, with very limited information available on its ecology, phytochemistry, and ethnobotanical relevance (Flora e Funga do Brasil, 2025).

Hedeoma teyucuaensis is valued in local culture for its use as a flavoring agent in yerba mate (*Ilex paraguariensis* A.St.-Hil.) and tereré infusions, using both vegetative and reproductive branches. In addition, the decoction of its roots is traditionally used to combat intestinal parasites. In general, whole-plant extraction is performed, generating a significant impact on natural populations (Keller & Tressens, 2016). Notably, *H. teyucuaensis* is currently undergoing a formal extinction risk assessment by the IUCN, following its inclusion in technical workshops in 2024 due to its extreme endemism and habitat vulnerability. This species is endemic to Misiones province (Argentina). It grows in a wooded grassland on a sandy edaphic substrate, in a relict of the Brazilian Cerrado. The particular habitat specificity of *H. teyucuaensis*, combined with the general cultural and economic reliance on wild *Hedeoma* populations, renders it particularly vulnerable to the climatic alterations affecting its natural habitats.

The accumulation of greenhouse gases and subsequent climate change profoundly affect the geographic distribution of plant species (Román-Palacios & Wiens, 2020; Intergovernmental Panel on Climate Change (IPCC), 2023; Kang *et al.*, 2025). These climatic shifts can manifest as either an expansion or a contraction of the areas occupied by these species, heavily depending on environmental pressures and the plants' adaptive capacities (Bedair *et al.*, 2025; Kang *et al.*, 2025; De Diego *et al.*, 2026) and depending on their physiological or phenological traits (Zhao *et al.*, 2018). Furthermore, species with broader ecological niche ranges exhibit a greater ability to utilize resources and adapt to changing environmental conditions compared to those with narrow ecological niches, which face higher risks of habitat loss and displacement (Huang *et al.*, 2024).

Medicinal plants may be particularly susceptible to climate change due to overexploitation (Peralta *et al.*, 2020) and changes in land use (Vercelli *et al.*, 2013; Rohde *et al.*, 2019; Nagahama & Bonino, 2020).

However, the few studies that have addressed the impact of climate change on medicinal species in southern South America have revealed heterogeneous patterns in their distributional changes (Nagahama & Bonino, 2020; Peralta *et al.*, 2024; García *et al.*, 2025). In this context, understanding how the geographic distribution of selected *Hedeoma* species may shift under future climate scenarios is of critical importance.

Based on this evidence, we hypothesize that South American *Hedeoma* species will respond differently to future climate scenarios according to their ecological niche breadth and edaphic specialization, with habitat specialists showing stronger range contractions than ecological generalists. Specifically, this study aims (i) to characterize the current ecological niches of these species using bioclimatic and occurrence data; (ii) to model their current and future potential distributions under three different climate change scenarios (RCPs 2.6, 4.5 and 8.5) using MaxEnt; and (iii) to compare ecological niche breadth among species to identify those most vulnerable to climate shifts.

MATERIALS AND METHODS

Study area

The studied *Hedeoma* species are distributed across different habitats in South America. Among them, *H. mandoniana* is a perennial species that extends along the Andean corridor from southern Peru and Bolivia to northern Argentina (Slanis & Bulacio, 2005). In contrast, the remaining three subshrub species occupy lower altitudinal zones characterized by different ecological frameworks: *Hedeoma medium* features a broader distribution extending from northeastern and central Argentina to southern Uruguay, preferentially colonizing high-luminosity environments and well-drained, dry soils within the subtropical biome (Xifreda, 1999; Barboza *et al.*, 2006). *Hedeoma teyucuaensis* is a micro-endemic species from northeastern Argentina, where it thrives strictly associated with isolated sandstone rocky outcrops within the seasonally dry tropical forest biome. *Hedeoma polygalifolia* is restricted to subtropical highland grasslands of southern Brazil, where it inhabits montane environments characterized by shallow, well-drained soils and high environmental heterogeneity (Flora e Funga do Brasil, 2025) (Table 1).

Table 1. Geographic distribution, ecological characteristics, and occurrence records of the four South American *Hedeoma* species included in the ecological niche modelling analyses.

Tabla 1. Distribución geográfica, características ecológicas y registros de ocurrencia de las cuatro especies sudamericanas de *Hedeoma* incluidas en los análisis de modelado de nicho ecológico.

Taxa	Biogeographic provinces (Cabrera & Willink, 1980)	Soils	Elevation (m a.s.l.)
<i>H. mandoniana</i>	Pastures and mist scrublands under thickets, and among rocky outcrops in somewhat damp places in Southern Peru, Bolivia, and northwestern Argentina (Salta and Jujuy province).	Sandy and rocky	2500 - 3900
<i>H. medium</i>	Pampean Steppe (eastern Argentina, provinces of Entre Ríos and Buenos Aires, and the departments of Paysandú and Soriano, Uruguay).	Sandy	0 - 500
<i>H. polygalifolia</i>	Grasslands in the state of Rio Grande do Sul, Brazil.	Not reported	700 - 800
<i>H. teyucuarensis</i>	Grasslands in Misiones, Argentina.	Sandy	0 - 200

Occurrence records

Occurrence records were obtained from field collection, herbarium specimens (BAB, BAF, CORD, SI) (Thiers, continuously updated), from the Documenta Florae Australis database (www.darwin.edu.ar/iris), Flora Argentina y del Conosur website (www.floraargentina.edu.ar), and specialized literature. Specimens lacking geographic coordinates were georeferenced using Google Earth Pro. The correct identification of each specimen was verified, excluding those whose identity could not be confirmed or that lacked information on the collection site. Records were meticulously reviewed to ensure the accuracy of geographic coordinates, and duplicate points were removed. To reduce the effect of spatial autocorrelation in Species Distribution Models (SDMs), records located less than 1 km apart were eliminated. This procedure was performed using the package Wallace v.1.0.6.1 (Kass *et al.*, 2018) implemented in R 3.6.1 (R Core Team, 2024). A total of five occurrence records were obtained for *H. teyucuarensis*, 10 for *H. polygalifolia*, 20 for *H. medium*, and 30 for *H. mandoniana* (Fig. S1).

Environmental variables and predictor selection

Nineteen bioclimatic variables and elevation data were obtained from the WorldClim2 database (<http://www.worldclim.org>) at a spatial resolution of 30 arc-seconds (approximately 1 km²) (Fick & Hijmans, 2017). Additionally, eight soil variables were incorporated, obtained from the SOILGRIDSTM database (<https://www.isric.org>) (Hengl *et al.*, 2017), adjusted to the same spatial resolution as the bioclimatic variables. All layers were clipped to the calibration area, defined according to the Biotic-Abiotic-Mobility (BAM) theoretical framework (Soberón & Peterson, 2005; Peterson *et al.*, 2008). For *H. medium*, *H. mandoniana*, and *H. polygalifolia*, the calibration

area consisted of polygons buffered by 200 km² around their recorded distribution points. Given the micro-endemic nature of *H. teyucuaensis*, whose global distribution is restricted to a specialized rocky outcrop habitat (approx. 2 km²), the small sample size (n=5) represents the near-total known occurrence of the species. Consequently, model results for this taxon were interpreted as indicative of habitat suitability rather than broad geographic potential, following recommendations for rare species with narrow ecological niches (Shcheglovitova & Anderson, 2013).

To minimize model overfitting caused by covariance among variables, which could lead to misleading results, a Pearson correlation analysis was applied to identify highly correlated variable pairs ($r > 0.80$), removing redundant variables (Fig. S2) (Herrando-Moraira *et al.*, 2020; Scrivanti & Anton, 2020). Pearson correlation tests were conducted using INFOSTAT v.2.0 (Di Rienzo *et al.*, 2020). The final selected variables were: Elevation, Bio1 (annual mean temperature), Bio2 (mean diurnal range), Bio3 (isothermality), Bio7 (annual temperature range), Bio12 (annual precipitation), Bio15 (precipitation seasonality), Bio18 (precipitation of the warmest quarter), BLDFIE (bulk density), CLYPPT (clay content), CRVFOL (coarse fragments volumetric content), ORCDRC (soil organic carbon content), and PHIHOX (soil pH) (Table 2). The selection of bioclimatic and edaphic variables was based on their biological relevance and direct relation to the ecological requirements of *Hedeoma* species (Peralta *et al.*, 2024).

For future projections (period 2070), three Atmosphere-Ocean General Circulation Models (AOGCMs) were used: CCSM4 (Community Climate System Model version 4), CGCM3 (Coupled General Circulation Model version 3), and HadGEM2 (Hadley Centre Global Environment Model version 2). For each model, three greenhouse gas concentration scenarios established by the Intergovernmental Panel on Climate Change (IPCC) were applied: Representative Concentration Pathways (RCP) 2.6 (low), 4.5 (intermediate), and 8.5 (high). These three RCPs (2.6, 4.5, and 8.5 W m⁻²) differ in their radiative forcing projections through the year 2100 (Meinshausen *et al.*, 2011; van Vuuren *et al.*, 2011). Depending on greenhouse gas concentrations, each RCP describes a climate scenario with a specific threat level: mild mitigation (RCP 2.6), intermediate (RCP 4.5), and catastrophic with very high emissions (RCP 8.5) (Meinshausen *et al.*, 2011; van Vuuren *et al.*, 2011). This framework was selected to ensure comparability with previous phytogeographic and conservation studies in the region, providing a consistent baseline for evaluating long-term distributional trends (Nagahama & Bonino, 2020; Peralta *et al.*, 2024). Elevation and soil variables were set as static factors for projecting future models, assuming no significant changes in soil properties within the modeled timeframe (Gilani *et al.*, 2020).

Table 2. Environmental variables selected after Pearson correlation analysis ($r < 0.8$) for each *Hedeoma* species.

Tabla 2. Variables ambientales seleccionadas para cada especie de *Hedeoma* tras el análisis de correlación de Pearson ($r < 0,8$).

Species / Layers	Edaphic	Bioclimatic
<i>H. medium</i>	BLDFIE (bulk density) CLYPPT (clay content) CRFVOL (volumetric coarse fragments) ORCDRC (soil organic carbon content) PHIHOX (soil pH)	Bio1 (annual mean temperature) Bio3 (isothermality) Bio7 (temperature annual range) Bio12 (annual precipitation) Bio15 (precipitation seasonality) Bio18 (precipitation of warmest quarter)
<i>H. mandoniana</i>	BLDFIE (bulk density) CLYPPT (clay content) CRFVOL (volumetric coarse fragments) ORCDRC (soil organic carbon content) PHIHOX (soil pH)	Bio1 (annual mean temperature) Bio2 (mean diurnal range) Bio3 (isothermality) Bio7 (temperature annual range) Bio12 (annual precipitation) Bio15 (precipitation seasonality)
<i>H. teyucuarensis</i>	BLDFIE (bulk density) CLYPPT (clay content) CRFVOL (volumetric coarse fragments) PHIHOX (soil pH) SND (sand content)	Bio1 (annual mean temperature) Bio3 (isothermality) Bio7 (temperature annual range) Bio12 (annual precipitation) Bio15 (precipitation seasonality) Bio18 (precipitation of warmest quarter)
<i>H. polygalifolia</i>	BLDFIE (bulk density) CLYPPT (clay content) CRFVOL (volumetric coarse fragments) ORCDRC (soil organic carbon content) PHIHOX (soil pH)	Bio1 (annual mean temperature) Bio2 (mean diurnal range) Bio3 (isothermality) Bio7 (temperature annual range) Bio12 (annual precipitation) Bio15 (precipitation seasonality) Bio18 (precipitation of warmest quarter)

Species distribution modeling

Models were run in MaxEnt v.3.4.3 using the standard parameter configuration (autofeatures enabled, regularization multiplier = 1, maximum iterations = 500, 10,000 background points, convergence threshold = 10^{-5}). For model calibration, 75% of the recorded localities were randomly selected, reserving the remaining 25% for validation through a bootstrap resampling procedure with 10 replicates, to reduce dependence on a single partition of occurrence records. Model performance was evaluated using the area under the receiver operating characteristic curve (AUC), because it remains the most widely used discrimination metric in MaxEnt-based ecological niche modelling (Peterson, 2007; Lobo *et al.*, 2008; Elith & Leathwick, 2009). Variable importance in the SDMs was assessed via permutation values, Jackknife tests, and response curves calculated by MaxEnt (Phillips *et al.*, 2017). Model projections were saved in ASCII raster format and imported into QGIS (QGIS Development Team, 2021). To determine total potential area in km² for current and future predictions, MaxEnt outputs were reclassified to convert continuous outputs into binary presence/absence maps (0–1), using the logistic threshold based on the 10th percentile training

presence localities. This threshold assumes a 10% error rate in presence records, thus excluding the 10% of values with the lowest probability. The 10th percentile criterion is commonly used in conservation studies (Scrivanti & Anton, 2021). However, due to the limited number of occurrence records available for *Hedeoma teyucuaensis* and *H. polygalifolia*, their distributions were analyzed directly using continuous probability maps. Applying thresholds to models based on small sample sizes can introduce significant bias, as minor variations in training data may lead to substantial changes in binary classifications, potentially underestimating or overestimating the species' potential distribution (Bean *et al.*, 2012).

Furthermore, given the restricted distribution and potentially specialized ecological niches of these species, the use of continuous outputs allows for a more realistic representation of environmental suitability gradients, avoiding the loss of information associated with binarization. This approach is particularly appropriate for rare or endemic species, where uncertainty in occurrence records and limited spatial representation can compromise the robustness of threshold-based methods (Hernández *et al.*, 2006; Wisz *et al.*, 2008).

RESULTS

Model performance variable importance

The AUC values for the current and future scenarios ranged from 0.844 to 0.997 (Fig. S3), indicating that the models had good to excellent predictive capacity across all taxa. The environmental variables included in each model are shown in Table 2. For *H. mandoniana*, the variables that contributed most were elevation and clay content. For a probability between 0.8 and 1, the elevation range is between 3500- 6000 masl, and the clay content range is between 27.5%- 45%. For *H. medium*, significant contributions came from precipitation seasonality and isothermality. In this case, the optimal precipitation seasonality range was 0–25%, while isothermality values between 39%- 44.5% were associated with high occurrence probability (0.8–1). Despite the limited number of occurrence records for *H. teyucuaensis* and *H. polygalifolia*, their models exhibited the highest predictive accuracy. *Hedeoma teyucuaensis* reached an AUC of 0.992 for the current period and up to 0.997 in future scenarios (CCSM4, RCP 4.5). The primary bioclimatic drivers for this species were annual temperature range (21.3-21.8 °C) and high sand content. For *H. polygalifolia* (current AUC = 0.959), the distribution was mainly delimited by soil bulk density and soil organic carbon content.

Current and future predicted distribution

The projections generated through species distribution models indicated that the current potential distribution of *H. mandoniana* covers approximately 1507870 km². This area is mainly concentrated in Ecuador, along the Andes mountain range in Peru, Bolivia, and northwestern Argentina. *Hedeoma medium* had a current potential distribution of 157111 km², primarily distributed in southern Uruguay and the east and south of Buenos Aires (Fig. 2). *Hedeoma polygalifolia* is distributed in southern Brazil in the states of Rio Grande do Sul, covering 21101 km², and for *H. teyucuaensis*, its current potential distribution covered 1561 km² in Misiones, Argentina (Fig. 3). In the intermediate RCP 4.5 scenario, most of the current distribution is maintained, slightly decreasing by 11%, retracting in northern Peru. In the mild RCP 2.6 scenario, the distribution area contracts by 25% and shifts toward the coast of Peru and Ecuador. In the RCP 8.5 scenario, the distribution area contracts by 45% and shifts toward the coast of Peru and Ecuador.

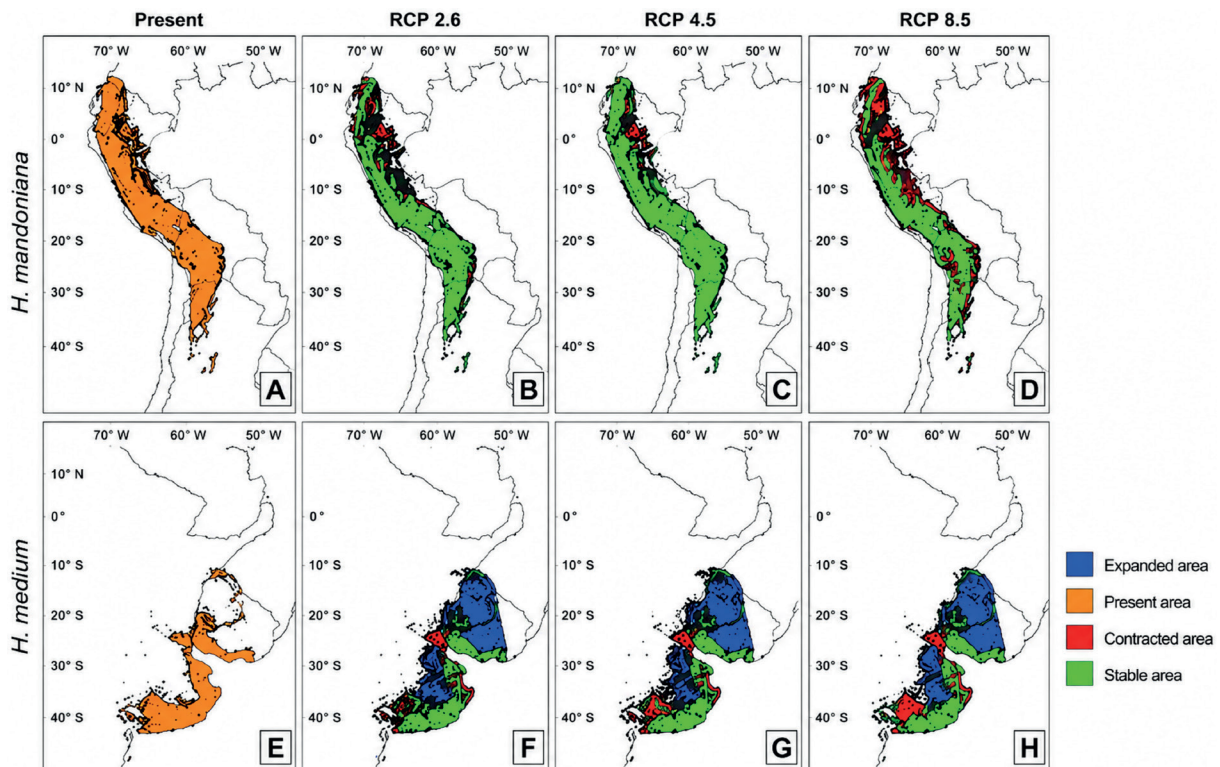


Fig. 2. Potential distribution maps of *Hedeoma mandoniana* and *Hedeoma medium* generated using Species Distribution Models (SDMs). Current climatic conditions and future projections for the year 2070 under the RCP 2.6, RCP 4.5, and RCP 8.5 climate scenarios are shown.

Fig. 2. Mapas de distribución potencial de *Hedeoma mandoniana* y *Hedeoma medium* obtenidos mediante modelos de distribución de especies (SDM). Se muestran las condiciones climáticas actuales y las proyecciones futuras para el año 2070 bajo los escenarios climáticos RCP 2.6, RCP 4.5 y RCP 8.5.

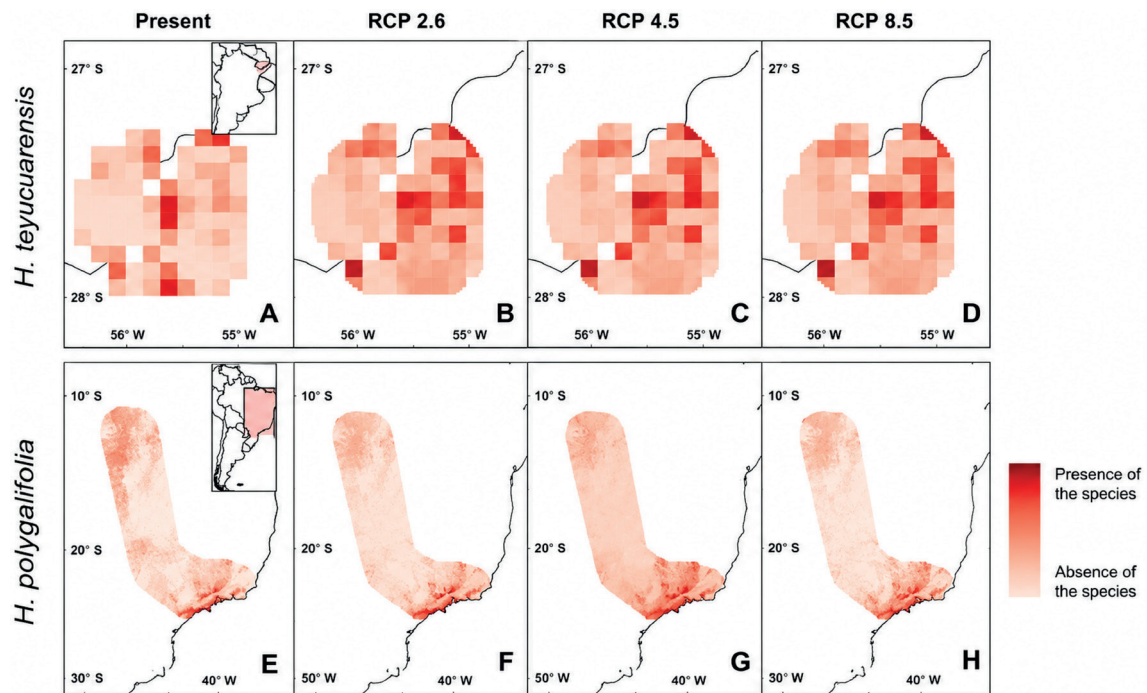


Fig. 3. Habitat suitability maps (presence/absence) for *Hedeoma polygalifolia* and *Hedeoma teyucuarensis* generated using Species Distribution Models (SDMs). Current conditions and projected distributions for the year 2070 under the RCP 2.6, RCP 4.5, and RCP 8.5 climate scenarios are presented.

Fig. 3. Mapas de idoneidad del hábitat (presencia/ausencia) para *Hedeoma polygalifolia* y *Hedeoma teyucuarensis*, obtenidos mediante modelos de distribución de especies (SDM). Se presentan las condiciones actuales y las proyecciones para el año 2070 bajo los escenarios climáticos RCP 2.6, RCP 4.5 y RCP 8.5.

In the catastrophic RCP 8.5 scenario, the distribution contracts by 38%, mainly in Bolivia. *Hedeoma medium* expanded under all climate scenarios, with projected increases ranging from 42% under the intermediate RCP 4.5 scenario to 59% under the mild RCP 2.6 scenario, while the catastrophic RCP 8.5 scenario predicted an intermediate expansion of 45%. Under all scenarios, the potential distribution shifted toward Uruguay, with a slight reduction in southern and central Buenos Aires. For *H. teyucuarensis*, the potential area showed under RCP 8.5, maintaining its core suitability in the Teyú Cuaré region but with no potential for expansion due to soil specificity (Table 3).

Table 3. Current and projected potential distribution of *Hedeoma mandoniana*, *H. medium*, *H. teyucuarensis*, and *H. polygalifolia* based on predictions from Species Distribution Models (SDMs) under current and future climate scenarios (2070; RCP 2.6, 4.5, and 8.5). Values correspond to the mean projections of three AOGCMs using the 10th percentile training threshold. Total area gain or loss is expressed in km² and percentage.

Tabla 3. Distribución potencial actual y proyectada de *Hedeoma mandoniana*, *H. medium*, *H. teyucuarensis* y *H. polygalifolia* basada en las predicciones de los Modelos de Distribución de Especies (MDE) bajo escenarios climáticos actuales y futuros (2070; RCP 2.6, 4.5 y 8.5). Los valores corresponden a las proyecciones promedio de tres modelos de circulación general de la atmósfera y el océano (AOGCM), utilizando el umbral de entrenamiento correspondiente al percentil 10. La ganancia o pérdida total de área se expresa en km² y porcentaje.

Species	RCP scenario	Current area (km ²)	Future area (km ²)	Total loss (L)/gain (G) (km ²)	Percentage (%)
<i>H. mandoniana</i>	Current	1507870	-	-	-
	2.6		1123880	383990 (L)	-25
	4.5		1341410	166460 (L)	-11
	8.5		942090	565780 (L)	-38
<i>H. medium</i>	Current	157111	-	-	-
	2.6		249149	92038 (G)	59
	4.5		222479	65368 (G)	42
	8.5		227309	70198 (G)	45
<i>H. teyucuarensis</i>	Current	1561	-	-	-
	2.6		1513	48 (L)	-3
	4.5		1512	49 (L)	-3
	8.5		1512	49 (L)	-3
<i>H. polygalifolia</i>	Current	21101	-	-	-
	2.6		16900	4201 (L)	-20
	4.5		22236	1135 (G)	5
	8.5		21687	586 (G)	3

DISCUSSION

The projections derived from the ecological niche models revealed heterogeneous responses among the four *Hedeoma* species studied, illustrating how climatic and edaphic factors interact to shape their future potential distributions. Overall, these results support the hypothesis that species with narrow ecological amplitudes and strong environmental specialization will experience more pronounced range contractions under climate change, while generalists may benefit from the shifting climatic envelope.

Ecological drivers of distributional patterns

For *H. mandoniana*, the contraction and westward shift of its suitable area across the Andes can be attributed primarily to the two major contributing variables, elevation and clay content. Both variables reflect the orographic and edaphic characteristics of the Andes, where the species currently occupies high-altitude environments between 3500–6000 masl. The contraction pattern is consistent with the phenomenon known as “upslope displacement,” in which species migrate from low, warmer areas toward

higher, cooler, and more humid zones in response to rising temperatures (Larsen *et al.*, 2012; Rodríguez-Craverro *et al.*, 2017). Similar upward shifts have been documented in high mountain floras worldwide, such as the increase in alpine plant diversity in Swiss peaks over the last century (Thuiller, 2007) and the predicted upward movement of *Podocarpus oleifolius* in the tropical Andes (Villamonte Cuneo, 2018).

In contrast, *H. medium* demonstrated a robust expansion potential under all RCP scenarios (ranging from 42% to 59%), extending its range westward and northward into central Uruguay while retracting slightly from southern Buenos Aires and Entre Ríos in Argentina. The two variables with the highest present contribution, precipitation seasonality (31.6%) and isothermality (28%), highlight the species' sensitivity to climatic stability and hydric availability. The South American monsoon system, and particularly the South Atlantic Convergence Zone (SACZ), largely determines rainfall variability in this region (Grimm, 2011), and future projections indicate increased precipitation over Uruguay (Uribe Botero, 2015). This may explain the predicted shift of *H. medium* toward wetter zones, maintaining its hydric requirements under changing climates.

The influence of isothermality, which reflects the ratio of diurnal to annual temperature oscillations, provides additional insight into the thermal behavior of *H. medium*. The present range (39-44.5%) indicates relatively low temperature variability within months, implying a preference for stable thermal regimes. As global warming reduces frost occurrence, *H. medium*, which is sensitive to freezing events, could find expanded suitable habitats in regions that become thermally more favorable. According to Rodríguez-Craverro *et al.* (2017), such range expansions may occur when populations currently inhabit climates cooler than their physiological optimum; thus, moderate warming could improve their growth and reproductive performance. This mechanism likely explains why *H. medium* was the most positively affected species in all future scenarios. Furthermore, the predicted expansion into Uruguay suggests that *H. medium* may act as an edaphic generalist compared to its congeners; while the climatic envelope becomes favorable in these new areas, the species' ability to colonize them would depend on its tolerance to the diverse soil mosaics of the Río de la Plata grasslands, which differ from the specific rocky or sandy substrates required by *H. teyucuarensis* or *H. mandoniana*.

Hedeoma teyucuarensis displayed only a minor contraction (3%) in projected distribution; however, given its microendemic status, even small reductions represent severe threats. The principal variable influencing its distribution was annual temperature range (33.4% contribution), with an extremely narrow tolerance window (21.3–21.8 °C) that likely governs key phenological processes such as flowering and growth onset (Robbiati *et al.*, 2017). This limited thermal amplitude leaves little adaptive margin under scenarios of increased temperature variability.

The secondary variable, sand content (30.1%), reflects the species' dependence on well-drained soils typical of the humid subtropical environment of Misiones. These edaphic conditions, acidic, nutrient-poor, and highly permeable, are found primarily around San Ignacio, Argentina (Torresin, 2023). Such soil specificity may restrict potential colonization of new habitats, constraining its resilience to environmental change. Consequently, *H. teyucuaensis* should be prioritized for *in situ* conservation and habitat protection in Misiones. Our results reinforce the preliminary findings of the 2024 IUCN assessment workshops, providing quantitative evidence of the species' climatic fragility and justifying its proposed high-threat category.

For *H. polygalifolia*, the dominant predictors—soil bulk density (54.2%) and soil organic carbon content (11.4%)—indicate that edaphic properties play a critical role in determining its current and future potential range. Although its modeled expansion under future scenarios is modest (+3–5%), the predicted shift toward southeastern Brazil aligns with the elevated landscapes of the Mantiqueira and Espinhaço mountain ranges, within the Atlantic Plateau. These areas, characterized by rounded hills (“mares de morros”) and humid montane climates, are known to become increasingly favorable for forest species under warming scenarios (Siqueira *et al.*, 2019; Neto dos Santos *et al.*, 2023). The association between *H. polygalifolia* and higher-altitude, organic-rich soils supports the idea that elevation will act as a buffering factor against climatic stress, as previously observed for other endemic South American taxa (Grossi *et al.*, 2017). Nonetheless, the same dependency on specific soil structures may restrict its adaptive capacity if land-use changes degrade these habitats.

Together, these results suggest that *Hedeoma* species respond to climate change through a combination of altitudinal migration, latitudinal displacement, and edaphic filtering. The patterns observed are consistent with broader Neotropical trends in which Andean and Atlantic taxa either shift upward or migrate toward regions of climatic stability (Galindo *et al.*, 2010). Yet, the magnitude of these responses varies according to niche breadth: *H. mandoniana* exemplifies a specialized montane species vulnerable to warming, *H. medium* represents a generalist capable of expansion, and *H. teyucuaensis* and *H. polygalifolia* illustrate microendemic and edaphically constrained taxa with high conservation concern.

Despite the strong predictive accuracy of our models (AUC 0.84–0.99), their reliability for microendemic species remains limited by the small number of occurrence points (Shcheglovitova & Anderson, 2013). Expanding field surveys to remote or under-sampled areas is essential to refine model calibration and to detect potential refugia. Furthermore, while our approach assumed static soil and elevation layers, dynamic feedbacks between climate, erosion, and vegetation could alter edaphic conditions in the long term.

Incorporating mechanistic and dispersal-based modeling frameworks in future studies would enhance the predictive realism of these projections (Thuiller, 2007).

CONCLUSION

Our findings demonstrate that climate change will exert complex and species-specific effects on *Hedeoma* distributions in southern South America. The upward displacement of *H. mandoniana* in the Andes, the expansion of *H. medium* in temperate lowlands, and the restricted persistence of *H. teyucuarensis* and *H. polygalifolia* collectively underscore the necessity of integrating climatic, edaphic, and biogeographical data in conservation planning. Specifically, the high vulnerability of the micro-endemic *H. teyucuarensis* provides critical quantitative evidence to support its ongoing extinction risk assessment by the IUCN. Considering their medicinal and cultural significance, proactive strategies, including habitat protection, sustainable harvesting, and *ex situ* propagation, should be implemented to safeguard these taxa. Ultimately, the resilience of *Hedeoma* species to climate change will depend not only on their ecological plasticity but also on timely conservation actions that bridge ecological modeling with traditional knowledge and robust policy frameworks.

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CONFLICTS OF INTEREST

We declare that there are no conflicts of interest between the authors or with others.

REFERENCES

- Barboza, G. E., Cantero, J. J., Núñez, C. O., Pacciaroni, A. & Ariza Espinar, L. (2006). Flora Medicinal de la Provincia de Córdoba (Argentina). Museo Botánico, Universidad Nacional de Córdoba.
- Bastien, J. W. (1983). Pharmacopeia of Qollahuaya Andeans. *Journal of Ethnopharmacology* 8 (1): 97-111.

- Bean, W. T., Stafford, R. & Brashares, J. S. (2012). The effects of small sample size and sample bias on threshold selection and accuracy assessment of species distribution models. *Ecography* 35 (3): 250-258. <https://doi.org/10.1111/j.1600-0587.2011.06545.x>
- Bedair, H., Hazzazi, Y., Abo Hatab, A., Halmy, M. W. A., Dakhil, M. A., Alghariani, M. S., Sumayli, M., El-Shabasy, A. & El-Khalafy, M. M. (2025). Predicting climate-driven shift of the East Mediterranean endemic *Cynara cornigera* Lindl. *Frontiers in Plant Science* 16. <https://doi.org/10.3389/fpls.2025.1461639>
- Cabrera, A. L. & Willink, A. (1980). Biogeografía de América Latina. (2.^a ed. corregida). Secretaría General de la Organización de los Estados Americanos.
- Cárdenas-Valdovinos J. G., Mena-Violante H. G., Rosas-Cárdenas F. F., Angoa-Pérez M. V. & Luna-Suárez S. (2025). Phytochemistry and Biological Activities of *Hedeoma piperita* Benth. (Quiensabe). *International Journal of Molecular Sciences* 26 (4): 1640. <https://doi.org/10.3390/ijms26041640>
- Di Rienzo, J. A., Casanoves, F., Balzarini, M., González, L., Tablada, M. & Robledo, C. (2020). *InfoStat* (Version 2020) [Software]. Universidad Nacional de Córdoba. <https://www.infostat.com.ar/>
- De Diego, F. C., Nores, M. J., Anton, A. M., Fortunato, R. H. & Robbiati, F. O. (2026). Climate change could negatively affect the distribution of xerophytic legume shrubs (*Senna* series *Aphyllae*, Caesalpinioideae) in southern South America drylands. *New Zealand Journal of Botany* 64 (1): e70062
- Elith, J. & Leathwick, J. R. (2009). Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* 40: 677-697. <https://doi.org/10.1146/annurev.ecolsys.110308.120159>
- Fick, S. E. & Hijmans, R. J. (2017). WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37: 4302-4315. <https://doi.org/10.1002/joc.5086>
- Flora e Funga do Brasil (2025). Jardim Botânico do Rio de Janeiro. Retrieved from <http://floradobrasil.jbrj.gov.br/>
- Fournet, A., Ferreira, M. E., Arias, A. R., Ortiz, S. T., Fuentes, S., Nakayama, H., Schinini, A. & Hocquemiller, R. (1996). Insecticidal activity of medicinal plants of the Paraguayan Chaco against *Triatoma infestans*. *Journal of Ethnopharmacology* 52: 145-149.
- Galindo, G., Armenteras, D. & Alamaraz, J. S. (2010). Modelamiento de la distribución de especies: estado del arte e implicaciones en la conservación de la biodiversidad. *Gestión y Ambiente* 13: 69-80.
- García, S. A., Nores, M. J., De Diego, F., Bach, H. G., Peralta, P. A. & Robbiati, F. O. (2025). Climate change and shifting distributions of medicinal and aromatic *Lippia* and *Salimena* species (Verbenaceae) in southern South America: a species distribution modelling approach.

- Plant Ecology and Evolution* 158: 403-417. <https://doi.org/10.5091/plecevo.157560>
- Gilani, H., Goheer, M. A., Ahmad, H. & Hussain, K. (2020). Under predicted climate change: distribution and ecological niche modelling of six native tree species in Gilgit-Baltistan, Pakistan. *Ecological Indicators* 111: 106049. <https://doi.org/10.1016/j.ecolind.2019.106049>
- Girault, L. (1984). Kallawaya: Guérisseurs itinérants des Andes. Recherches sur les pratiques médicinales et magiques (Collection Mémoires, 107). Institut Français de Recherche Scientifique pour le Développement en Coopération (ORSTOM).
- Grimm, A. M. (2011). Interannual climate variability in South America: Impacts on seasonal precipitation, extreme events, and possible effects of climate change. *Stochastic Environmental Research and Risk Assessment* 25: 537-554.
- Grossi, M. A., Draper, D., Apodaca, M. A., Katinas, L. & Gutiérrez, D. G. (2017). The road to 2020 targets and the learnings from the emblematic South American plant genus *Nassauvia* (Asteraceae). *Biodiversity and Conservation* 26: 329-351.
- Hengl, T., Mendes de Jesus, J., Heuvelink, G. B., Ruiperez Gonzalez, M., Kilibarda, M., Blagotić, A., Shangguan, W., Wright, M. N., Geng, X., Bauer-Marschallinger, B., Guevara, M. O., Vargas, R., MacMillan, R. A., Batjes, N. H., Leenaars, J. G. B., Ribeiro, E., Wheeler, I., Mante, S. & Kempen, B. (2017). SoilGrids250m: global gridded soil information based on machine learning. *PLoS ONE* 12: e0169748. <https://doi.org/10.1371/journal.pone.0169748>
- Hernández, P. A., Graham, C. H., Master, L. L. & Albert, D. L. (2006). The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29 (5): 773-785. <https://doi.org/10.1111/j.0906-7590.2006.04700.x>
- Herrando-Moraira, S., Vitales, D., Nualart, N., Gómez-Bellver, C., Ibáñez, N., Massó, S., Cachón-Ferrero, P., González-Gutiérrez, P. A., Guillot, D., Herrera, I., Shaw, D., Stinca, A., Wang, Z. & López-Pujol, J. (2020). Global distribution patterns and niche modelling of the invasive *Kalanchoe × houghtonii* (Crassulaceae). *Scientific Reports* 10: 3143. <https://doi.org/10.1038/s41598-020-60079-2>
- Huaman Espinoza, W. W. & Zurita Valdez, E. Y. (2020). Evaluación bioconservante del aceite esencial de Pacha Muña (*Hedeoma* Wedd), en la vida útil de la lechuga (*Lactuca sativa* L.) mínimamente procesada, Palcamayo-Tarma. (Bachelor thesis), Universidad Nacional del Centro del Perú, Perú. Retrieved from <http://www.uncp.edu.pe>
- Huang, Q., Liu, H., Li, C., Zhu, X., Yuan, Z., Lai, J., Cao, M., Huang, Z., Yang, Y., Zhuo, S., Lü, Z. & Zhang, G. (2024). Predicting the geographical distribution and niche characteristics of *Cotoneaster multiflorus* based on future climate change. *Frontiers in Plant Science* 15. <https://doi.org/10.3389/fpls.2024.1360190>

- Intergovernmental Panel on Climate Change (IPCC). (2023). Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, H. Lee & J. Romero, eds.]. IPCC, Geneva, Switzerland. <https://doi.org/10.59327/IPCC/AR6-9789291691647>
- Kang, Y., Lin, F., Yin, J., Han, Y., Zhu, M., Guo, Y., Tang, F. & Li, Y. (2025). Projected distribution patterns of *Alpinia officinarum* in China under future climate scenarios: insights from optimized Maxent and Biomod2 models. *Frontiers in Plant Science* 16. <https://doi.org/10.3389/fpls.2025.1517060>
- Kass, J. M., Vilela, B., Aiello-Lammens, M. E., Muscarella, R., Merow, C., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P. & Kessler, M. (2018). Wallace: a flexible platform for reproducible modeling of species niches and distributions built for community expansion. *Methods in Ecology and Evolution* 9: 1151-1156. <https://doi.org/10.1111/2041-210X.12945>
- Keller, H. A. & Tressens, S. G. (2016). *Hedeoma teyucuaensis* (Lamiaceae), una especie nueva de Misiones, Argentina. *Darwiniana, nueva serie* 4: 5-11. <https://doi.org/10.14522/darwiniana.2016.41.692>
- Larsen, T. H., Brehm, G., Navarrete, H., Franco, P., Gómez, H., Mena, J. L., Morales, V., Argollo, J., Blacutt, L. & Canhos, V. (2012). Desplazamientos de los rangos de distribución y extinciones impulsados por el cambio climático en los Andes tropicales: síntesis y orientaciones. In: S. K. Herzog, R. Martínez, P. M. Jørgensen, H. Tiessen (Eds.), *Cambio climático y biodiversidad en los Andes tropicales* (pp. 57-78). Instituto Interamericano para la Investigación del Cambio Global (IAI) & Scientific Committee on Problems of the Environment (SCOPE).
- Laupa Roman, J. & Vengoa Valdiglesias, B. (2013). Efecto de tres especies de lamiáceas y tubérculos verdeados de papa sobre *Symmetrischema tangolias* (Gyen) en condiciones de laboratorio. *Cantua* 15: 41-47.
- Lobo, J. M., Jiménez-Valverde, A. & Real, R. (2008). AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography* 17: 145-151. <https://doi.org/10.1111/j.1466-8238.2007.00358.x>
- Meinshausen, M., Smith, S. J., Calvin, K., Daniel, J. S., Kainuma, M.L., Lamarque, J. F., Matsumoto, K., Montzka, S. A., Raper, S. C. B., Riahi, K., Thomson, A., Velders, G. J. M. & van Vuuren, D. P. (2011). The RCP greenhouse gas concentrations and their extensions from 1765 to 2300. *Climatic Change* 109: 213-241. <https://doi.org/10.1007/s10584-011-0156-z>
- Nagahama, N. & Bonino, E. E. (2020). Modeling the potential distribution of *Valeriana carnososa* Sm. in Argentinean Patagonia: a proposal for conservation and in situ cultivation considering climate change

- projections. *Journal of Applied Research on Medicinal and Aromatic Plants* 16: 100240. <https://doi.org/10.1016/j.jarmap.2020.100240>
- Neto dos Santos, G., Silva, A. & Higuchi, P. (2023). Subtropical high-montane forest climate refuges in Brazil. *Scientia Agricola* 80. <https://doi.org/10.1590/1678-992X-2022-0044>
- Peralta, P. A., Guariniello, J. & Escandón, A. S. (2020). Revisión de la situación de *Hedeoma multiflora* Benth. (Peperina de las Lomas): especie aromática medicinal argentina en riesgo. *Boletín Latinoamericano y del Caribe de Plantas Medicinales y Aromáticas* 19: 1-14.
- Peralta, P. A., Nores, M. J., Bach, H. G. & Robbiati, F. O. (2024). Facing climate change: Range dynamics and chromosome diversity in *Hedeoma multiflora* Benth., a South American aromatic-medicinal plant at risk. *Flora* 315: 152519. <https://doi.org/10.1016/j.flora.2024.152519>
- Pestalozzi, H. U. & Torrez, M. A. (1998). *Flora ilustrada altoandina: La relación entre hombre, planta y medio ambiente en el Ayllu Majasaya Mujlli (Prov. Tapacarí, Depto. Cochabamba, Bolivia)*. Editorial Herbario Nacional de Bolivia - Herbario Forestal Nacional "Martín Cárdenas".
- Peterson, A. T. (2007). Why not WhyWhere: the need for more complex models of simpler environmental spaces. *Ecological Modelling* 203: 527-530. <https://doi.org/10.1016/j.ecolmodel.2006.12.023>
- Peterson, A. T., Papes, M. & Soberón, J. (2008). Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecological Modelling* 213: 63-72. <https://doi.org/10.1016/j.ecolmodel.2007.11.008>
- Phillips, S. J., Anderson, R. P., Dudík, M., Schapire, R. E. & Blair, M. E. (2017). Opening the black box: an open source release of Maxent. *Ecography*, 40: 887-893. <https://doi.org/10.1111/ecog.03049>
- QGIS Development Team. (2021). *QGIS Geographic Information System (Version 3.x)* [Software]. Open Source Geospatial Foundation. <http://qgis.osgeo.org>
- R Core Team. (2024). *R: A language and environment for statistical computing* [Software]. R Foundation for Statistical Computing. <https://www.R-project.org>
- Robbiati, F. O., Amarilla, L. D., Anton, A. M., & Fortunato, R. H. (2017). Phenotypic variation in arid and semi-arid zones of southern South America: the case of *Senna* series *Aphyllae* (Fabaceae, Caesalpinioideae) *Botanical Journal of the Linnean Society* 183 (3): 454-473. <https://doi.org/10.1093/botlinnean/bow012>
- Rodríguez-Craverro, J. F., Grossi, M. A., Fuentes-Castillo, T. & Gutiérrez, D. G. (2017). Cambio climático y modelado de distribución de especies de *Stevia* (Asteraceae) en el noroeste de la Argentina. *Ecología Austral* 27: 462-473. <https://doi.org/10.25260/EA.17.27.3.0.588>
- Rohde, R. F., Hoffman, M. T., Durbach, I., Venter, Z. & Jack, S. (2019). Vegetation and climate change in the Pro-Namib and Namib Desert based on repeat photography: insights into climate trends.

- Journal of Arid Environments* 165: 119-131. <https://doi.org/10.1016/j.jaridenv.2019.01.007>
- Román-Palacios, C. & Wiens, J. J. (2020). Recent responses to climate change reveal the drivers of species extinction and survival. *Proceedings of the National Academy of Sciences* 117: 4211-4217. <https://doi.org/10.1073/pnas.191300711>
- Scrivanti, L. R. & Anton, A. M. (2020). Spatial distribution of *Poa scaberula* (Poaceae) along the Andes. *Heliyon* 6: e05220. <https://doi.org/10.1016/j.heliyon.2020.e05220>
- Scrivanti, L. R. & Anton, A. M. (2021). Impact of climate change on the Andean distribution of *Poa scaberula* (Poaceae). *Flora* 278: 151805. <https://doi.org/10.1016/j.flora.2021.151805>
- Shcheglovitova, M. & Anderson, R. P. (2013). Estimating optimal complexity for ecological niche models: A jackknife approach for species with small sample sizes. *Ecological Modelling* 269: 9-17. <https://doi.org/10.1016/j.ecolmodel.2013.08.011>
- Siqueira, S., Higuchi, P. & Da Silva, A. (2019). Contemporary and future potential geographic distribution of *Cedrela fissilis* Vell. under climate change scenarios. *Revista Árvore* 43: e430303.
- Slanis, A. C. & Bulacio, E. (2005). *Hedeoma mandonianum* (Lamiaceae) en Argentina. *Boletín de la Sociedad Argentina de Botánica* 40: 285-287.
- Soberón, J. & Peterson, A. T. (2005). Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics* 2: 1-10. <https://doi.org/10.17161/bi.v2i0.4>
- Thiers, B. (continuously updated). Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. Retrieved from <http://sweetgum.nybg.org/science/ih/>
- Thuiller, W. (2007). Biodiversity: Climate change and the ecologist. *Nature* 448: 550-552.
- Torresin, J. (2023). Distribución y estado de conservación de especies del género *Hedeoma* en la provincia de Misiones. *Revista Biomas* 14: 83-88.
- Uribe Botero, E. (2015). El cambio climático y sus efectos en la biodiversidad en América Latina. Documentos de Proyectos, LC/W.693. CEPAL, Santiago, Chile. Retrieved from <https://hdl.handle.net/11362/39855>
- van Vuuren, D. P., Edmonds, J. A., Kainuma, M., Riahi, K. & Weyant, J. (2011). A special issue on the RCPs. *Climatic Change* 109: 1-4. <https://doi.org/10.1007/s10584-011-0157-y>
- Vercelli, N., Entraigas, I., Scaramuzzino, R., Migueltoarena, V. & Alfonso, C. D. (2013). Plantas medicinales de los bajos alcalinos de la cuenca del arroyo del Azul (provincia de Buenos Aires, Argentina). *Revista de la Facultad de Ciencias Agrarias Uncuyo* 45: 285-298.
- Vilaseca, A., Guy, I., Charles, B., Guinaudeau, H., de Arias, A. R. & Fournet, A. (2004). Chemical composition and insecticidal activity of *Hedeoma mandoniana* essential oils. *Journal of Essential Oil Research* 16 (4): 380-383. <https://doi.org/10.1080/10412905.2004.9698749>

- Villamonte Cuneo, G. (2018). Modelamiento del efecto del cambio climático en el nicho ecológico fundamental de especies de podocarpáceas peruanas en Sudamérica. (Bachelor thesis), Universidad Ricardo Palma, Perú. Retrieved from <https://hdl.handle.net/20.500.14138/1694>
- Viveros-Valdez, E., Rivas-Morales, C., Carranza-Rosales, A., Mendoza, S. & Schmeda-Hirschmann, G. (2008). Free radical scavengers from the Mexican herbal tea “poleo” (*Hedeoma drummondii*). *Zeitschrift für Naturforschung C* 63 (5-6): 341-346.
- Wisz, M., Hijmans, R., Jin, L., Peterson, A., Graham, C. & Guisan, A. (2008). Effects of sample size on the performance of species distribution models. *Diversity and Distributions* 14: 763-773. <https://doi.org/10.1111/j.1472-4642.2008.00482.x>
- Xifreda, C. C. (1999). Lamiaceae. In F. O. Zuloaga & O. Morrone (Eds.), Catálogo de las plantas vasculares de la República Argentina II. *Monographs in Systematic Botany from the Missouri Botanical Garden* 74: 779-800.
- Zhao, Z., Guo, Y., Wei, H., Zhang, Z., & Wang, J. (2018). Responses of two endemic *Rhodiola* species to climate change on the Tibetan Plateau. *Scientific Reports* 8: 12693. <https://doi.org/10.1038/s41598-018-24360-9>

SUPPLEMENTARY MATERIAL

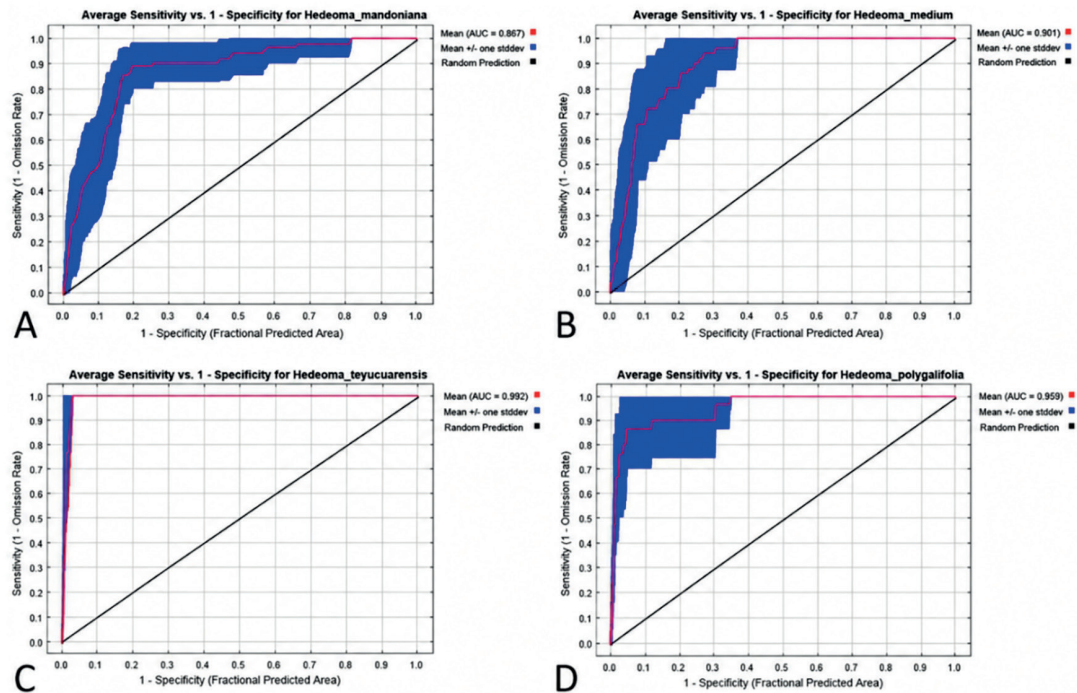


Fig. S1. Area Under the Curve (AUC) values for the potential distribution models of each species. A) *Hedeoma mandoniana*. B) *Hedeoma medium*. C) *Hedeoma teyucarensis*. D) *Hedeoma polygalifolia*.

Fig. S1. Curvas AUC (Área Bajo la Curva) de los modelos de distribución potencial para cada especie. A) *Hedeoma mandoniana*. B) *Hedeoma medium*. C) *Hedeoma teyucarensis*. D) *Hedeoma polygalifolia*.

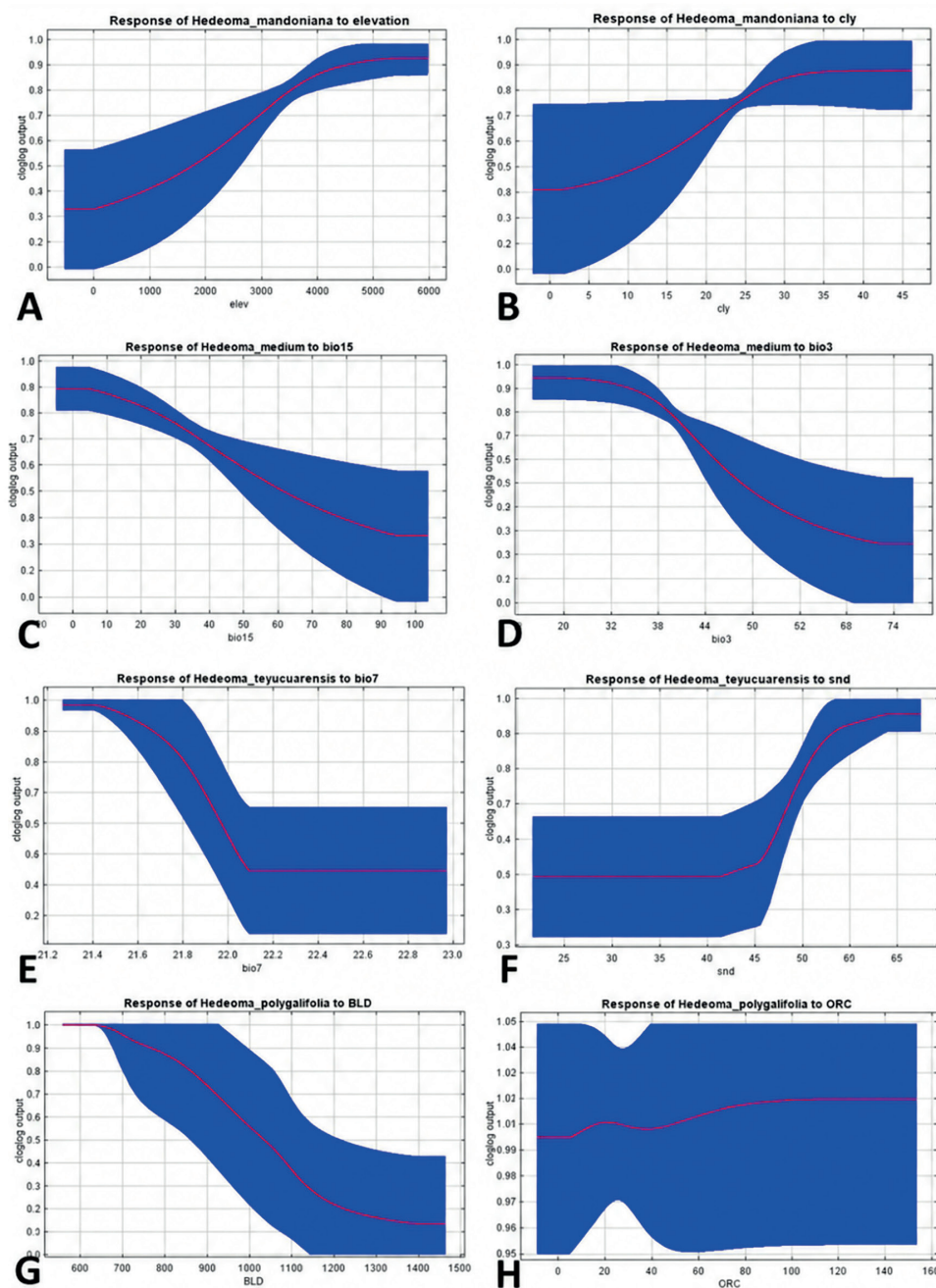


Fig. S2. Response curves for the two environmental variables with the highest contribution to the present potential distribution models. A) Elevation for *Hedeoma mandoniana*. B) Clay content (Cly) for *H. mandoniana*. C) Precipitation seasonality (Bio 15) for *H. medium*. D) Isothermality (Bio 3) for *H. medium*. E) Annual temperature range (Bio 7) for *H. teyucuaensis*. F) Sand content (Snd) for *H. teyucuaensis*. G) Bulk density (Bld) for *H. polygalifolia*. H) Soil organic carbon content (Orc) for *H. polygalifolia*.

Fig. S2. Curvas de respuesta de las dos variables ambientales con mayor contribución a los modelos de distribución potencial actual. A) Elevación para *Hedeoma mandoniana*. B) Contenido de arcilla (Cly) para *H. mandoniana*. C) Estacionalidad de la precipitación (Bio 15) para *H. medium*. D) Isotermalidad (Bio 3) para *H. medium*. E) Rango anual de temperatura (Bio 7) para *H. teyucuaensis*. F) Contenido de arena (Snd) para *H. teyucuaensis*. G) Densidad aparente del suelo (Bld) para *H. polygalifolia*. H) Contenido de carbono orgánico del suelo (Orc) para *H. polygalifolia*.

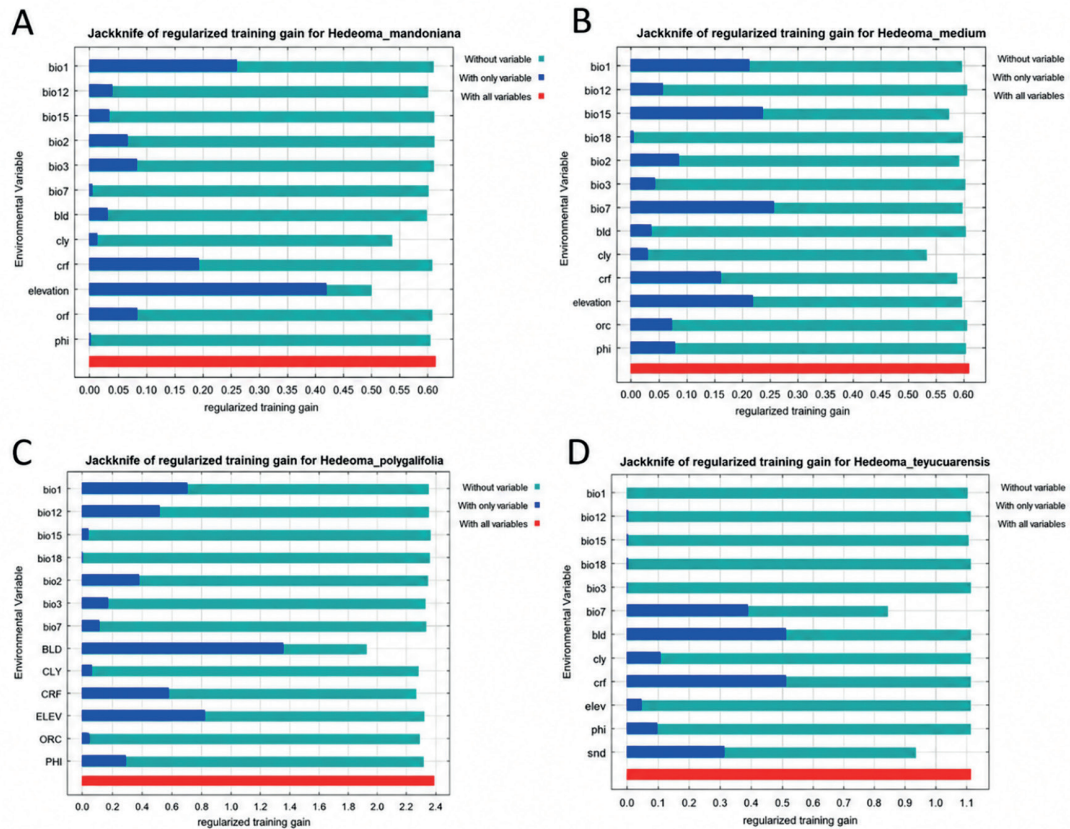


Fig. S3. Jackknife test results showing the relative importance of environmental variables in the species distribution models. A) *Hedeoma mandoniana*. B) *H. medium*. C) *H. polygalifolia*. D) *H. teyucaensis*.

Fig. S3. Resultados de la prueba Jackknife para evaluar la importancia de las variables ambientales en los modelos de distribución de especies. A) *Hedeoma mandoniana*. B) *H. medium*. C) *H. polygalifolia*. D) *H. teyucaensis*.