



# Potential Distribution and Connectivity for Two Plethodontid Salamanders: Conservation Areas and Landscape Corridors for Two Endemic Species of México and Guatemala

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## Abstract

Habitat loss is one of the most important threats to biodiversity; it alters the habitat connectivity of species and is among the main causes of the global amphibian extinction crisis. Identifying the potential areas of distribution and connectivity of species is of the utmost importance so that informed decisions can be made for the conservation of vulnerable amphibian populations. In this study, we performed species distribution models and used circuit theory to model omnidirectional connectivity for two plethodontid salamanders of conservation concern distributed in the forests of Chiapas, Mexico, and Guatemala (*Bolitoglossa franklini* and *Bolitoglossa lincolni*). Potential distribution maps show an affinity for well-preserved montane forests for both species. Likewise, we found that the niches of the species are not similar. The connectivity models show that the main areas of connectivity are in the Meseta Central de Chiapas, Sierra Madre de Chiapas, and the Cordillera Volcánica Guatemalense, in this last range, important areas of connectivity were located, as well as least-cost paths and barriers to the movement of both species. We identified that important areas of climatic suitability and connectivity are not within the protected natural areas and may be threatened by the increasing influence of anthropogenic activities. The results of our study show the importance of preserving the regional forests to ensure the persistence of species with arboreal habits and high sensitivity to habitat transformation, as well as to recognize and prioritize potential areas for management and protection in both southern Mexico and Guatemala.

**Keywords** Plethodontidae · *Bolitoglossa franklini* · *Bolitoglossa lincolni* · Connectivity · Sierra Madre de Chiapas · Guatemala Mountain Range

## Introduction

The world's forests are highly diverse in terms of species, but it is estimated that at least 46% of them have disappeared due to human activities (Crowther et al. 2015),

and only 40% remain free of modification (Grantham et al. 2020). The forests in tropical regions have a third of the global biodiversity (Giam 2017), however, there is a great loss of vertebrates, mainly due to habitat loss and land change use, affecting the diversity, distribution, and species interaction, and, hence, the ecosystem functioning (Jetz et al. 2007; Thompson et al. 2017). Currently, amphibians are facing an environmental crisis due to their population reduction and the extinction of different species in several regions of the planet (Stuart et al. 2004). For instance, in Mesoamerica, threats to amphibians are much higher than in all the rest of the American continents (Alroy 2015; Scheele et al. 2019) due to habitat modification (Whitfield et al. 2016). In the south of Mexico, a collapse and reduction of amphibian populations, particularly of amphibian species that can be found in cloud forests and within mountain ranges has been occurring for years (Lips 2008). In Guatemala, local extirpations of plethodontid salamanders have

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been happening even in protected natural areas (Rovito et al. 2009). Among the plethodontid salamanders, the genus *Bolitoglossa* is widely distributed from southwestern North America to northern Brazil and the central mountains of Bolivia; the greatest diversity and endemism of the genus is found in the geological complex known as Nuclear Central America (Wake and Lynch 1976; Rovito and Parra-Olea 2016). *Bolitoglossa franklini* and *B. lincolni* are phylogenetically closely related and considered sister species (Wake and Lynch 1982; Parra-Olea et al. 2004; Vásquez-Almazán and Rovito 2014). They have an allopatric distribution and are found in pine, pine-oak, and cloud forest areas within Chiapas and Guatemala's occidental Central Mountains (Wake et al. 1980).

*Bolitoglossa franklini* is a complex species, regarded as vulnerable (IUCN SSC Amphibian Specialist Group 2020a) and distributed in the Sierra Madre de Chiapas until the southwest Pacific slopes in western Guatemala (Wake et al. 1980), within pine forests and pine-oak forest between 1500 and 3200 m a.s.l. They are mainly arboreal and use bromeliads as their main microhabitat in mature and conserved forests (Wake and Lynch 1976). *Bolitoglossa lincolni*, however, is a near-threatened species (IUCN SSC Amphibian Specialist Group 2020b) distributed mainly in the pine and pine-oak forests in the Central Plateau of Chiapas (CCP), the mountain range of Cuchumatanes, Cuilco Sierra, and the San Marcos region in the Cordillera Volcánica Guatemalense (GVC) (Wake and Lynch 1976; Wake et al. 1980), and it is found in disturbed areas, exhibiting a generalist habit (Wake and Lynch 1976; Rovito et al. 2009). Despite the differences observed in both species, the populations share threats to their conservation such as the loss and transformation of habitat due to forest exploitation, agricultural activities, and the growth of human settlements in their distribution areas (IUCN SSC Amphibian Specialist Group 2020a, 2020b).

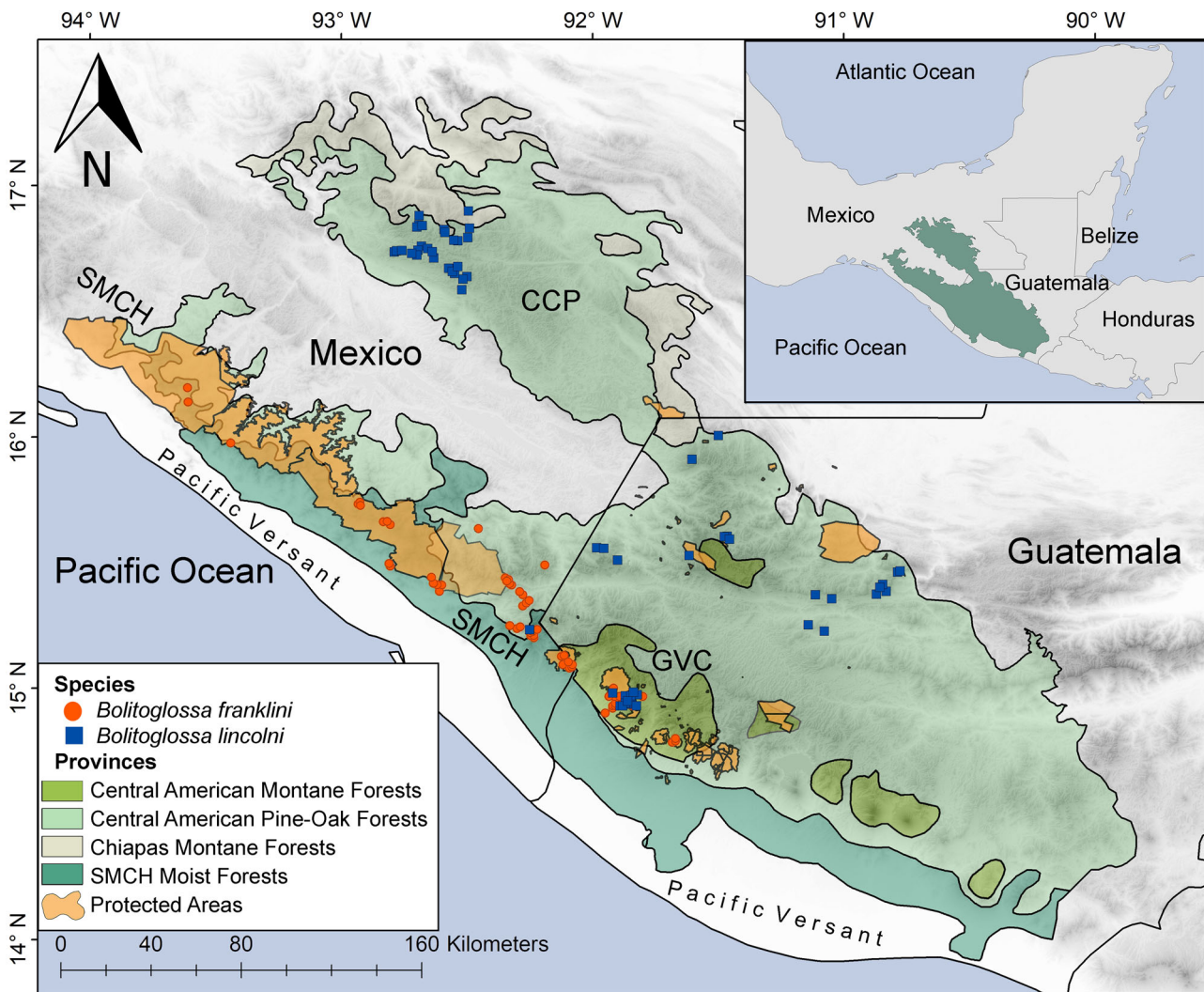
It is crucial to delineate the species distribution area to establish conservation areas for preserving these species and habitat conservation. The species distribution models (SDM) estimate the environmental suitability and potential distribution areas using the species presence records and the geographic and environmental conditions (Peterson 2006; Elith and Leathwick 2009; Warren 2012). These predictions are valuable for assessing the potential distribution and, therefore, the conservation status of rare, endemic, or poorly studied species (Guisan et al. 2013). Such SDMs are also useful in determining suitable habitats for populations of undiscovered species, detecting climatic barriers to dispersal, and for exploring ecological divergence between closely related taxa when species share distribution ranges (Cunningham et al. 2009; Glor and Warren 2011; Hu and Jiang 2018).

Landscape connectivity is the degree to which the environment simplifies or prevents an organism's movement between different locations (Taylor et al. 1993; Tischendorf and Fahrig 2000). Habitat fragmentation can modify connectivity, imposing barriers to organism movement and affecting the individuals' ability to disperse and reach habitable places (Wiens et al. 2009). Amphibians are very susceptible to habitat transformation due to their limited vagility and high sensitivity to microclimatic variation (Nowakowski et al. 2015). The habitat fragmentation and land change use can modify the migration paths or affect their general movement (Ray et al. 2002), in salamanders, it has been observed that reduced connectivity is mainly due to poor habitat quality and increased anthropogenic activities (Ashrafzadeh et al. 2019). Thus, for species with limited dispersal capacity, their habitats are expected to offer suitable conditions for their maintenance and reproduction as well to preserve their dispersion paths, and the evolutionary process at different spatial and temporal scales (Pelletier et al. 2014; Hilty et al. 2019).

A practice that can guarantee biodiversity conservation, along with the functioning and stability of the ecosystem, is the identification and design of corridors, which will facilitate the appropriate dispersion of the species in the landscape (Thompson et al. 2017). The connectivity between habitats can be modeled as a cost measure where the landscape elements are allocated resistance values according to the degree to which they allow or hinder the movement of individuals (Adriaensen et al. 2003). One of the most used methodologies for this purpose is the circuit theory; this analysis uses resistance and flow values of the movement and, therefore, can be applied to predict the movement and the probability of dispersal of organisms while generating measures of connectivity or isolation between populations, patches of habitats, or protected natural areas (McRae et al. 2008).

The previously described approaches are rarely used among Mexican amphibians; however, their application in the study of plethodontid salamanders in central Mexico has been useful in identifying priority areas and corridors (Vargas-Jaimes et al. 2021; Sunny et al. 2022), along with the identification of barriers and their effect on the population isolation (Velo-Antón et al. 2013; Sunny et al. 2022).

In this study, we utilized SDMs to describe the potential distribution and evaluate the similarity of the climatic niches of two sister species of the genus *Bolitoglossa*, (*B. lincolni* and *B. franklini*). Additionally, we applied a circuit theory approach to find the corridors between core areas, least-cost path corridors, and bottlenecks for the movement of plethodontid salamanders in the mountains of southern Mexico and Guatemala. Therefore, this study aimed to determine the potential distribution of the two salamander species, identify corridors and pinch points (bottlenecks) in



**Fig. 1** Study area and salamander species presence points. The green areas are the M used for each salamander studied. CCP Chiapas Central Plateau, SMCH Sierra Madre de Chiapas, GVM Guatemala Volcanic Mountain Range

the study area, and analyze the corridor network to identify important core areas and corridors to keep the network connection and, consequently, to enhance information within the conservation actions for the salamanders of southern Mexico and Central America.

## Methods

### Study Area

The study area is located between southern Mexico and western Guatemala, in the area known as Nuclear Central America, and comprises 169,501 km<sup>2</sup>. Specifically, this area includes the Sierra Madre de Chiapas (SMCH), Central Chiapas Plateau (CCP), and the highlands of Guatemala (Cordillera de Los Cuchumatanes (CC), the relief of this area forms a mountainous landscape with an abrupt topography

that allows the presence of different climates and ecosystems that have evolved many species and endemics (INE/ SEMARNAT 1999). In the SMCH, there is the largest proportion of conserved forest areas under protection, like the Sepultura, El Triunfo, Tacaná Volcano, and Fraileskana, one of the most important cloud forests in the region. In Guatemala, several protected natural areas occur in the study area, like Volcán Tacaná, Tajumulco, and Volcán Lacandón, as well as the Visis-Cabá (CONAP 2021) (Fig. 1). In the study area, the predominant vegetation is cloud forests, pine forests, pine-oak forests, and agricultural areas, mainly coffee plantations, corn crops, and pastures for cattle.

### Species Occurrence and Environmental Variables

Occurrence records of *Bolitoglossa franklini* and *B. lincolni* were obtained from online sources, GBIF (<https://www.gbif.org>), Consejo Nacional de la Biodiversidad (CONABIO;

<https://www.gob.mx/conabio>); data from regional collections; Colección Herpetológica de El Colegio de la Frontera Sur (ECOSUR-SC) and Colección Zoológica Regional Secretaría de Medio Ambiente e Historia Natural (SEMAHN) and field surveys in the Sierra Madre de Chiapas to detect the presence of *B. franklini*. Seven field trips were conducted between October and March 2020–2022, during the dry season, two-three persons conducted free transect walks during the day between the hours of 10:00–16:00, and at night 20:00–24:00 h, in the habitat of the species between 1800 and 2200 m asl, the sampling involved an active search within bromeliads, the main microhabitat of the species, as well in bark, fallen trunks, and leaf litter (Wake and Lynch 1976). Cleaning of the occurrence data was carried out with the *thin* command of the library *spThin* (Aiello-Lammens et al. 2015) for R software (4.00; R Development Core Team 2019) as follows: 1) occurrence data was previsualized to remove erroneous records or records outside the potential geographic range, 2) duplicate records were eliminated, and 3) to avoid pseudoreplication, the species' distribution data were subsampled considering only records that were spaced at least 1 km from each other, according to the range of dispersal abilities observed in Plethodontidae salamanders (Smith and Green 2005; Lowe et al. 2008). This method substantially reduces the overfitting in the model (Segurado et al. 2006; Boria et al. 2014). We obtained 228 records for *B. franklini* and 92 for *B. lincolni*. (Supplementary Information 1, SI1). After applying spatial filtering, we retained 69 and 63 records, respectively.

### Species Distribution Models

To delimit the distribution of a species, it is necessary to determine a calibration space for the models, or M according to the BAM diagram, which represents the accessible area for a species and is compatible with the biogeographic history of the species (Soberon and Peterson 2005). For this purpose, we selected and grouped the Central American pine-oak forests (CAPOF), Central American montane forests (CAMF), Chiapas montane forests (CMF), and Sierra Madre de Chiapas moist forests (SMF) ecoregions according to Olson et al. 2001 (Fig. 1). For the environmental niche modeling, we use the bioclimatic layers available in Worldclim Project 2 (Fick and Hijmans 2017) and the ENVIREM climate layers (Title and Bemmels 2017). To prevent the models from having an effect caused by the over-parameterization and collinearity between the layers, we discarded some bioclimatic layers based on the variance inflation factor (VIF), which quantifies the multicollinearity between the layers, indicating the degree that a variable increases the standard error of the regression. The VIF was calculated with the package *usdm* 1.1.18 for R, with a threshold of 10, where higher values

indicate collinearity (Dormann et al. 2013; Naimi et al. 2014). The final set of variables was: annual mean diurnal range (Bio 2), temperature seasonality (Bio 4), mean temperature of the wettest quarter (Bio 9), precipitation seasonality (Bio 15), precipitation of the wettest quarter (Bio 16), precipitation of the warmest quarter (Bio 18), precipitation of the coldest quarter (Bio 19), climatic moisture index, potential evapotranspiration (PET) of the driest quarter, and PET seasonality (Supplementary Information 2, SI2; Supplementary Table S1). For the environmental niche modeling, we used the maximum entropy analysis implemented in Maxent 3.4.1 (Phillips and Dudík 2008). Before the elaboration of the SDM, using independent evaluation metrics of the threshold, we looked for the optimal set of parameters to obtain the most parsimonious model with the ENMeval package (Muscarella et al. 2014). One test considered for the evaluation of the model was the AUC test, which measures the discriminatory capacity, where the highest values indicate that the model has a reliable capacity to distinguish between the test locations and the background points (Peterson 2011). The difference in the AUC (AUC DIFF) is the difference between the AUC calculated from the training locations and the AUC test. This parameter quantifies the overfitting of the models, high values indicate excessive overfitting of the model (Warren and Seifert 2011), and the Akaike information criterion corrected for small samples (AICc) shows the goodness of fit and the complexity of the model. The models with the lowest AICc value are considered the best of the set of models obtained (Warren and Seifert 2011). To obtain the evaluation metrics, we generated 10,000 random points that were used as background points. We partitioned the number of records by the “Checkerboard1” method with an aggregation factor of 5; this method generates a grid over the study area as a Chessboard, which partitions the localities into cells (bins), although it does not offer a balanced number of presences in each cell, and it performs an equal sampling of the geographical and environmental space (Muscarella et al. 2014). Subsequently, the complexity of the models was estimated based on the regularization multiplier (RM) and the Maxent features classes. The RM determines how concentrated or adjusted the distribution is; values less than 1.0 will give rise to a more localized distribution and adjusted to the presence registers, which can lead to overfitting in the models. High values of the RM will give a more dispersed and less localized prediction. For our study, we obtained the most parsimonious model by testing all possible combinations between the RMs and Maxent's feature classes; we tested 10 RMs in a range from 1 to 5, with increments of 0.5 and six feature classes: linear (L), quadratic (Q), product (P), threshold (T), and hinge (H). With the information obtained, we built the model in Maxent, implemented in Dismo 1.1–4 (Hijmans et al. 2017) for R. To quantify the

area of climatic suitability, we converted the continuous potential map to a binary map according to a cut-off threshold of the 10-percentile training presence. Additionally, to evaluate the precision of the Maxent model, we transformed the area under the curve (AUC) by calculating the partial ROC (partial receiver operating characteristic curve graphics, Peterson et al. 2008), which was obtained by evaluating the statistical significance through null distributions; we calculated the Partial ROC in the package `ntbox` (Osorio-Olvera et al. 2020) in R, applying 1000 iterations and an error of 5%. The significance of the AUC was estimated with a bootstrapping of 1000 and using 50% of the presences as training locations.

### Similarity, Equivalence, and Niche Overlap

In species with shared ancestry such as *Bolitoglossa franklini* and *B. lincolni*, niche similarity may be more likely but rarely identical (Warren et al. 2008). To identify environmental differences, we compare the ecological niches of the species and determine if they are significantly different from each other, we contrasted the niches of both species according to the method of Broennimann et al. (2012). The bioclimatic variables used in the modeling were reduced using an ordering technique with a principal component analysis (PCA), and then we delimited the environmental space using the first two axes of the PCA. Species presence records were plotted within the environmental space using a Kernel density function, which corrects the potential bias of sampling errors (Broenniman et al. 2012) (Fig. 2d). The niche overlap was calculated with the Schoener's D metric (Schoener 1970; Rödder and Engler 2011), which calculates the habitable space based on its abundance of the species and the Hellinger distance I, which quantifies the probability of distribution of the species to inhabit a given area, calculating the overlap of the niches (Warren et al. 2008). Both metrics have ranges from 0 to 1, where 1 indicates that the niches are identical. The estimates of presence density and the similarity of the niche between species in the environmental space were repeated 100 times to generate a null distribution comparable with the observed D value; non-significant results indicate that the niches are not identical. The analyses were carried out with the `ecospat` 3.1 package (Di Cola et al. 2017), and the presence density for the two species were plotted with `ggplot2` (Wickham 2016) for R.

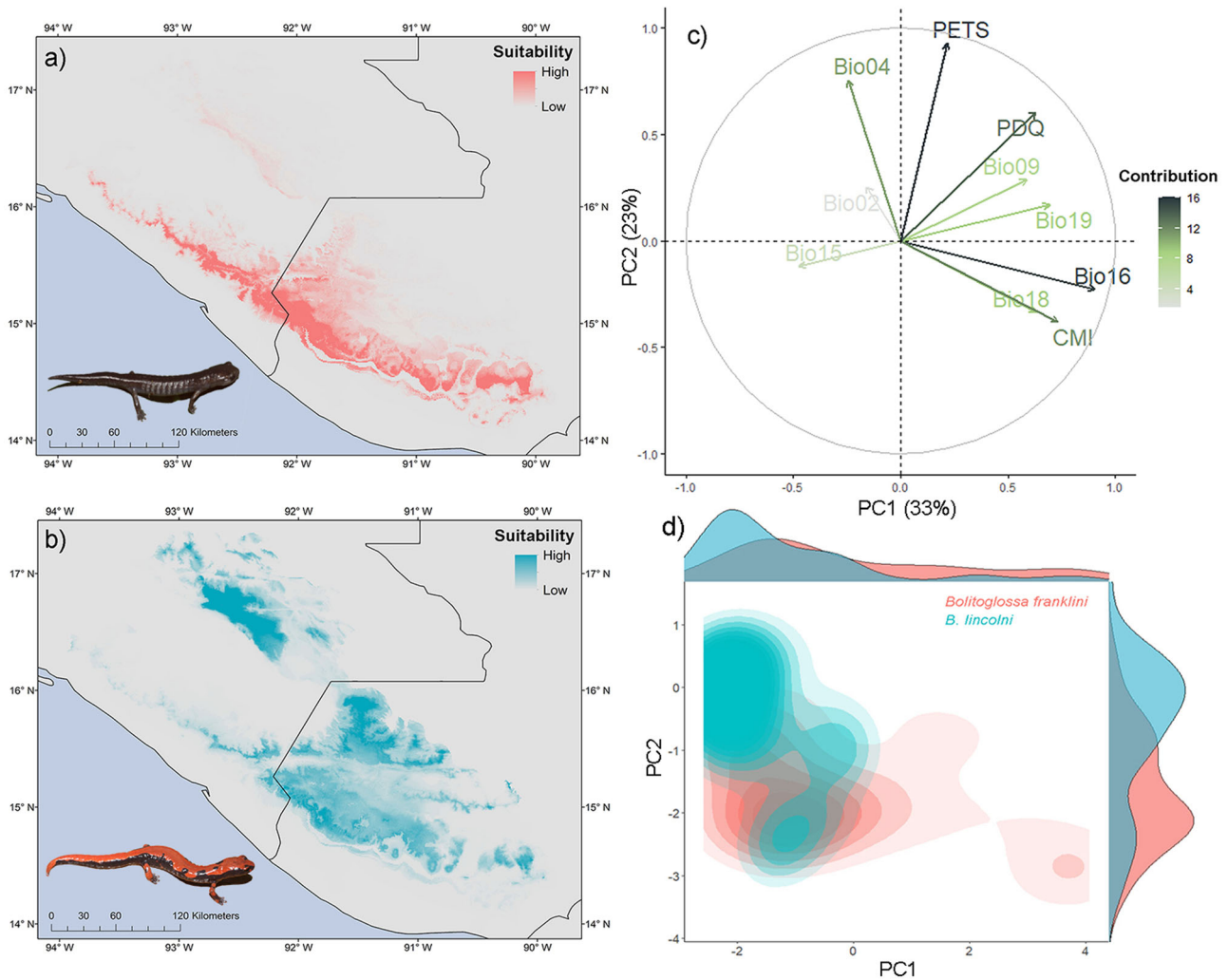
### Connectivity Models

To evaluate the connectivity patterns between the *B. franklini* and *B. lincolni* localities, we calculated landscape resistance using circuit theory, which models the movement patterns of species in a complex landscape

(McRae et al. 2008). The geographic area used to model connectivity was delimited by a minimum convex polygon made from the sample points, with a buffer of 20 km to minimize the increase in resistance values (Koen et al. 2010). The models were elaborated with the presence of localities and a resistance surface layer, which was elaborated from the information obtained from the land cover of Copernicus Global Land Service for the year 2019 at a resolution of 100 m (Buchhorn et al. 2020). The layers contain spatial information about the different types of coverage and the influence that humans have on them, and have continuous field values expressed as percentages (Buchhorn et al. 2020). We resampled the layers and assigned low resistance values to pixels that represented high coverage percentages, and we included a layer of roads, infrastructure, and cities obtained from OpenStreetMap (2020) contributors (<http://www.openstreetmap.org/>). The layer was rasterized and rescaled using the Mosaic to Raster tool of ArcMap 10.8. Finally, the resistance values of the landscape were scaled to 5–100 (Supplementary SI2, Supplementary Fig. S1).

The connectivity patterns were obtained with the CIRCUITSCAPE 4.0.5 software, which calculates the effective resistance to movement and all possible paths between pairs of locations or focal nodes, where a node is arbitrarily connected to a 1-amp current source, while the other node is connected to ground (McRae 2006). The process is carried out through iterations between pairs of occurrence points used as focal nodes, and they are expressed in current values on a current map (Supplementary SI2, Supplementary Fig. S2). Additionally, the least cost path (LCP) was determined with the Linkage Mapper 3.0.0 extension for ArcMap (McRae and Kavanagh 2011). The software calculates all possible routes and their cost in the landscape, showing the lowest cost routes based on the Cost Distance algorithm. This is a calculation of the minimum accumulated cost distance between two nodes. The result is a raster layer with cell values that represent the accumulated cost from a nearby source cell. From this raster, the LCPs are calculated in a vector layer of lines that establish the optimal routes for the establishment of corridors (Adriaensen et al. 2003). To assess the relative importance of core areas, we use current flow centrality analysis. In this approach, core areas are treated as nodes and the current flow through the network is calculated, thus determining the importance of each node and corridor in maintaining connectivity between habitat patches (Carroll et al. 2012; Dutta et al. 2016).

Finally, we calculated the bottlenecks or constriction zones for the movement of the species (pinch points) in the study area. These are used to identify important areas for connectivity due to a high flow of individuals, where high values indicate that corridors are vulnerable to unfavorable conditions (McRae et al. 2008).



**Fig. 2** Potential distribution of **a** *Bolitoglossa franklini* and **b** *B. lincolni*; **c** PCA and contribution of environmental variables in the niche overlap of both species; **d** overlap of the niche for both *Bolitoglossa* species, the shaded areas indicate the density of occurrences for each species

## Results

### Species Distribution Models

For *B. franklini*, we obtained 61 models, of which the least complex model ( $AICc = 1296.5$ ) had the following parameters: LQH with a regularization multiplier ( $rm$ ) of 2.5 and an  $AUC = 0.94$ . For *B. lincolni*, we obtained 61 models, two of them being equally parsimonious ( $\Delta AICc \leq 2$ ). For this species, niche modeling was performed with the following parameters:  $AICc = 1219.0$ , LQH with a  $rm = 3.5$ , and an  $AUC = 0.93$ . The performance of the models was adequate; according to the calculation of the partial ROC bootstrap tests, 100% of the models were statistically significant with AUC ratio values of 1.89 for *B. franklini* and 1.86 for *B. lincolni*, ( $p < 0.001$ ). The potential distribution of both species shows an area of climatic suitability in the mountains of Chiapas and Guatemala. For *B. franklini*, a

potential distribution area of  $8121.8 \text{ km}^2$  was achieved (Fig. 2a), and for *B. lincolni*, a distribution area of  $9411.9 \text{ km}^2$  was determined (Fig. 2b); these areas are approximately 13.7 and 15.9% of the study area, respectively. For *B. franklini*, the areas of greatest suitability were located mainly in the Cordillera Volcánica Guatemalense (GVC) and in the Sierra Madre de Chiapas (SMCH) in the Istmo de Tehuantepec. Its distribution is reduced, and only the tops of the mountains of the region have suitability. In this area, there are at least three important protected natural areas, the Biosphere Reserves of El Triunfo, La Sepultura, and Volcán Tacaná in México. *Bolitoglossa lincolni*, in México, is distributed mainly in the Meseta Central de Chiapas (CCP); the analysis showed a region of low probability of presence for the species located in lowlands located between the CCP and the Sierra de los Cuchumatanes. In the GVC area, both species overlap in their distribution. In México, the distribution of *B. lincolni* is not

documented within federally protected areas, and in Guatemala, its distribution occurs in at least four important ANPs: Visis Cabá, Covirey, Volcán Tajumulco, and Volcán Lacandón. According to the jackknife analysis carried out in Maxent, the variable with the greatest relative contribution to the distribution models was the mean temperature of the driest quarter for *B. franklini* (Bio9 = 24.1%) and *B. lincolni* (Bio9 = 72.8%) (Supplementary SI2, Supplementary Table S2).

### Similarity, Equivalence, and Niche Overlap

Niche overlap analysis by PCA (Fig. 2c, d) showed that the contributions of the first two axes to PCA were 33.3 and 23%, respectively, and the precipitation of the wettest quarter (Bio16 = 24.5%) was the variable that explains the greater variation in the PC1 component, while the variation in the PC2 component indicated that the niche overlap was mainly explained by the seasonality of PET (37.5%). Schoener's D and Warren's I tests indicated non-significant values for the equivalence and similarity of the niches between *B. franklini* and *B. lincolni* ( $D = 0.40$ ,  $P > 0.001$ ,  $I = 0.58$ , and  $P > 0.001$ ).

### Connectivity Analysis

According to connectivity models based on circuit theory, for *B. franklini*, we identified a potential corridor that extends between the "La Sepultura" Biosphere Reserve in the SMCH, Mexico, to the Chicabal volcano in the GVC (Fig. 3a). The connectivity of the populations of *B. franklini* (Fig. 3a) is lower in the western extension of the SMCH, near the Isthmus of Tehuantepec, especially in the La Sepultura and La Frailescana. The SMCH shows important areas for connectivity and LCPs within El Triunfo Biosphere Reserve (ETBR); however, two larger areas of connectivity were also observed outside of these protected areas. These are mainly found in Mexico in the Motozintla mountains, adjacent to the Pico El Loro-Paxtal state reserve, and in Guatemala in the area between the Tajumulco Volcano reserve and the Esquipulas and Astillero San Marcos Municipal reserves (Fig. 3a). The least cost routes for *B. franklini* are found mainly in the extreme east of the SMCH and the GVC. In Mexico, the routes with medium to high costs for the movement of the species are within the El Triunfo Biosphere Reserve, CPL and Tacaná Volcano. In Guatemala, LCPs with low to moderate values are found between the Tajumulco Volcano and Chicabal Volcano. In Mexico, the western extension of the SMCH offers the most costly and resistant routes for the movement of *B. franklini*, within the protected areas of La Frailescana and La Sepultura, covering a length of 109.2 km, from the area corresponding to Cerro Quetzal (CQ) in the ETBR, to Cerro Tres

Picos in La Sepultura (Fig. 3a). For *B. lincolni*, the lowest to moderate cost LCPs are in the Central Chiapas Plateau, while the high to higher cost routes for the species are in the Cuchumatanes region and Sierra de Cuilco.

Within the distribution area of the species, the connectivity analysis detected 29 areas of relative importance for *B. franklini*, among them, the areas of higher current-flow centrality are located in the area bordering Mexico and Guatemala, of which the most extensive habitat is located in the mountains of Motozintla (between the protected areas CPL and VTBR) and has an extension of 169.4 km<sup>2</sup>, the second most central core area is located in the VTBR and has an extension of 44.7 km<sup>2</sup>. In the ETBR, La Frailescana, and La Sepultura natural areas, the core area extensions are mainly isolated on the mountain tops.

The areas of greatest current-flow centrality are found for *B. lincolni* in the mountains of the CCP, in the region, there are areas of greatest centrality located on the summits of the Central American pine-oak Forest, the largest central area is in Mexico and has an extension of 172 km<sup>2</sup>, the second largest area (100.2 km<sup>2</sup>) is in the area of the Tajumulco Volcano in Guatemala (Fig. 3b).

According to the Pinch points analysis, constriction zones or unfavorable conditions that could break the corridors of both species are found at several points along the corridors, potentially due to the topography of the terrain and climatic conditions of the low-elevation lands (Fig. 3c, d).

### Discussion

Our results show a significant area of environmental suitability for *B. franklini* and *B. lincolni* in the mountains of southern Mexico and western Guatemala. The species distribution model shows that suitable climatic conditions for *B. franklini* distribution are found mainly in the GVC, the pine-oak forests of Central America, and the montane forests of Central America. In Mexico, its distribution occurs in the humid forests of the SMCH but can be restricted to the top of the mountains, as the surroundings are characterized by suboptimal habitats that may be uninhabitable due to their poor climatic suitability. Therefore, migration may be impossible even at short geographical distances (Sexton et al. 2009). Within our results, the distribution of *B. lincolni* is listed mainly in the pine-oak forests of Central America in the CCP, the Central American montane forests of the Cuchumatanes, and the GVC. Its distribution overlaps with that of *B. franklini* in the same areas, where it has been previously proposed as a zone of secondary contact, in which the hybridization of both species is promoted (Wake et al. 1980). Furthermore, our SDM confirms the affinity of both





regions with plethodontid species. The advantage that the niches are not equivalent is that it reduces physiological pressures and species interactions (Baken et al. 2020).

Connectivity analysis indicates that the SMCH and the GVC have important corridors for *B. franklini*, yet the areas with greater connectivity and less resistance to movement are particularly found between the territorial limits of Mexico and Guatemala (Fig. 3). Our centrality analysis shows that, in the GVC and between the Pico de Loro, El Paxtal, and Volcán Tacaná reserves (VTBR) in Mexico, and between the VTBR and Volcán Tajumulco in Guatemala are significant habitat areas for focal species, there are conserved forests with canopy cover > 70% (Buchhorn et al. 2020) where significant communities of salamanders are found (Wake and Lynch 1976). In the case of *B. lincolni*, a wide-ranging corridor is observed in the region of the Chiapas montane forests, which includes the CCP, the Sierra de los Cuchumatanes, Cuilco and the GVC. These areas present a complex matrix composed of the presence of pine and pine-oak forests under different stages of succession and agricultural areas (INEGI 2016; Buchhorn et al. 2020).

Despite the coverage of the species' potential corridors, favorable conditions for their movement are not found all over their extent. According to our circuit analyses, the routes with the lowest cost and the greatest connectivity for the dispersal of *B. franklini* are found in the GVC in western Guatemala, between the Volcán Tacaná and Volcán Tajumulco reserves. This area has mixed forests and conserved mature forests, with canopy cover greater than 70% (Buchhorn et al. 2020), and is surrounded by forest areas with integrity rates of less than 50% (Grantham et al. 2020). The areas with lower connectivity are found in the SMCH between the protected natural areas of El Triunfo and La Sepultura. In contrast to the GVC, this area corresponds to a mountain chain that descends in altitude from 3000 to 1500 m a.s.l., and it is characterized by having a rugged relief in the Isthmus of Tehuantepec (Wake and Lynch 1976). The cloud forest habitats within these areas are restricted to the top of mountains, above 1800 m a.s.l.; therefore, the habitable areas for *B. franklini* and other plethodontid species are reduced to isolated habitat patches (sky islands), causing allopatric distributions because of historical climatic fluctuations (Wake and Lynch 1982).

According to the bottlenecks (pinch points) for *B. franklini*, the corridors most susceptible to losing connectivity are in Guatemala, within the Tacaná and Tajumulco volcanos. There are potential dispersal routes between these protected natural areas and the surrounding local reserves; nonetheless, these areas are immersed in a matrix with low rates of landscape connectivity (Grantham et al. 2020) since these areas are between the cities of the central region of Guatemala and the Pacific coastal region.

In Mexico, important low-cost paths are found in the SMCH, between the Tacaná Volcano and the Cordón Pico de Loro Paxtal reserve. This area represents a connection point between the SMCH and the GVC; however, at the same time, it has high anthropogenic disturbances such as high urban areas and mining activity (Godínez-Gómez et al. 2020). For *B. lincolni*, we identified different bottlenecks in the corridors, and the largest ones are found in the CCP. This area is within a matrix of predominantly secondary pine remnants, pine-oak forests, and agricultural areas (INEGI 2016). Herein are the main urbanized areas of the region and the predominance of traditional agriculture, as well as low-intensity forestry practices (González-Espinoza et al. 2007). Even though the region has potential connectivity routes for *B. lincolni*, these areas are not under any federal conservation criteria.

### Implications for Conservation

Our study suggests that the preservation of the region's forests is a conservation priority for the habitat and connectivity areas of the salamander populations found in southern Mexico and Central America, specifically those found in the GVC and SMCH and the CCP, given that in these areas, climatic suitability and potential corridors for the species studied are present. It is essential to know that the areas identified in this study face several challenges for their conservation. The main challenge is to prevent the loss of tropical forests, especially for species with arboreal habits that depend on the vertical structure and microhabitats they provide (McEntire 2016). This is extremely important since, for example in Mexico, 594 Kha of humid primary forest were lost between 2002 and 2019, which places Mexico as the ninth tropical country in primary forest loss according to the Global Forest Watch (Hansen et al. 2013). Ecological studies looking at the importance of forest and habitat structure conservation of plethodontids have examined all the negative consequences and the pressure that changes in land use and climate change exert on the salamander habitats (Díaz-García et al. 2020; Vargas-Jaimes et al. 2021; González-Fernández et al. 2022a) that can drive salamanders to decline in their populations or even to extinction. The SMCH is a valuable corridor for several vertebrate species (Ocampo et al. 2019; Ceballos et al. 2021). In this region, it is estimated that at least 12% of the forest cover was lost between 1970 and 2000 because of agricultural activities and forest extraction (Cortina-Villar et al. 2012). The conversion of forests to agricultural areas can mean additional pressure on the populations and potential corridors of *B. franklini* and other salamanders found in the SMCH, which is also considered one of the most significant coffee-growing areas in Mexico (Schroth et al. 2009).

In Guatemala, the expansion of coffee plantations represents the greatest threat to the populations of several salamander species (IUCN SSC Amphibian Specialist Group 2020a, b). The pine and oak forests of the CCP, the main habitat of *B. lincolni*, lost about 50% of their cover during the last 50 years (Cayueta et al. 2006), although the decline tendency has reduced to 14% of the forest during the last 20 years (Global Forest Watch 2021). For the Guatemalan volcanic mountain range, the corridors in which both species distributions overlap, the greatest threats are erosion and natural and human-caused fires for anthropogenic activities (Bullock et al. 2020). This area is rich in approximately 15 different salamander species (Wake 1987) and we consider that it is necessary to preserve the secondary contact zones to preserve the salamander biodiversity and genetic diversity, since competition events between *B. lincolni* and *B. franklini*, can displace *B. franklini*, which is more sensitive to habitat changes, whereas *B. lincolni* can survive in moderately disturbed areas (Wake et al. 1980; IUCN SSC Amphibian Specialist Group 2020a).

Connectivity preservation is one of the expected benefits of protected natural areas; nevertheless, most of those protected areas are isolated by eroded habitat, which breaks with the connectivity of the landscape (Ward et al. 2020). In the Sierra Madre de Chiapas, most of the forest cover that surrounds the reserve core areas corresponds to traditional shade-grown coffee plantations (Schrot et al. 2009). While in the region agroforestry systems could maintain intermediate levels of connectivity for some vertebrate species (Ocampo et al. 2019), amphibians are most susceptible to habitat change, since they present low species diversity in cultivated areas compared to primary forests (Whitfield et al. 2016). In addition, plethodontid salamanders show little resilience to transformation and loss of forest cover (Díaz-García et al. 2020). Although most of the agriculture takes place in the lowlands, we suppose that with global change these may increase in the highlands of the mountains, reducing or even displacing the areas inhabited by these salamanders (Schrot et al. 2009).

Biodiversity hotspots are often found mainly outside protected areas (Almasieh et al. 2019), currently, the coverage of the protected areas is insufficient on a regional and global scale, as 25% of amphibians are not distributed within the limits of protected natural areas (Nori et al. 2015; González-Fernández et al. 2022b). In Mexico, at least two out of five threatened species of salamanders do not inhabit protected areas (García-Bañuelos et al. 2019). Our results reinforce the above and show that a large portion of the habitat and potential corridors of both species is found outside the protected natural areas, mainly for *B. lincolni*. For this plethodontid the connectivity corridors and current-flow centrality areas in México are found in private natural areas, as there are no nature reserves under federal

protection or large-scale conservation actors (UNEP-WCMC and IUCN 2021), alternative local communities' actions could be effective for protecting their significant habitats (Stachowiak et al. 2021).

This information can be useful for reinforcement and/or conservation protection activities, such as the expansion of protected natural areas, however these actions must be taken carefully to ensure the legitimacy of the processes by the local people and to avoid privileging only certain members of the community and restoration (González-Fernández et al. 2022b), likewise our results can help to carry out activities for amphibian conservation in areas with anthropogenic activities since important areas for conservation were identified, as well as the network of biological corridors and the importance of each one of them as well as the potential distribution areas for the studied species in southern Mexico and Guatemala.

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## Compliance with Ethical Standards

**Conflict of Interest** The authors declare no competing interests.

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