

## Impact of climate and land cover changes on the potential distribution of four endemic salamanders in Mexico

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### ABSTRACT

Anthropogenic changes, such as land use and climate change, are the greatest threats to biodiversity, especially for amphibians, which are the most endangered vertebrate class worldwide. Species distribution modelling was applied to assess how expected future climate and land cover change scenarios might influence the geographic distribution and habitat connectivity of four salamanders endemic to Mexico: (*Aquiloerycea cephalica* (Cope, 1865), *Isthmura bellii* (Gray, 1850), *Pseudoeurycea robertsi* (Taylor, 1939), and *Pseudoeurycea leprosa* (Cope, 1869)). For this, the Community Climate System Model (CCSM4) with two Representative Concentration Pathways (RCP 45 and RCP 85) and two modelling methods (Maxent in ENMeval and an ensemble model in biomod2) were used. The most important environmental variables explaining the distribution of the target species, as well as the environmental niche overlap between them, were also determined. *Abies* forest cover was one of the most important variables explaining the current distribution of *P. robertsi* (contribution of 39%), *P. leprosa* (contribution of 18%), and *A. cephalica* (contribution of 22%) with a positive effect. The distribution of these three species was also limited by maximum temperatures, whereas the *I. bellii* distribution was more limited by minimum temperatures. The environmental niches of *P. leprosa* and *A. cephalica* were significantly similar ( $D = 0.637$ ,  $I = 0.801$ ,  $p\text{-value} = 0.02$ ), as well as the environmental niches of *P. robertsi* and *P. leprosa* ( $D = 0.640$ ,  $I = 0.797$ ,  $p\text{-value} = 0.01$ ). As expected, all salamander species were predicted to face a reduction in their potential distribution (reductions between 2.64 and 32.16%) and landscape connectivity (reductions between 4.93 and 73.92%) under future scenarios of climate and land cover change. Different models and scenarios were inconsistent in determining which species' distribution would suffer the biggest reduction in the future. However, *P. robertsi* suffered the largest reduction in connectivity under both scenarios of climate change. Similarly, our results suggest that Sierra de las Cruces and Corredor Biológico Chichinautzin are very important areas in terms of connectivity. Unfortunately, great losses of *Abies* and *Pinus* forests were also predicted to occur in these areas between 2011 and 2014. According to these findings, the preservation of *Abies* forests of the Trans-Mexican Volcanic Belt is essential to preserve *P. robertsi*, *P. leprosa*, and *A. cephalica* salamanders, whereas the preservation of Corredor Biológico Chichinautzin and Sierra de las Cruces is essential to maintain landscape connectivity for *P. leprosa*, *A. cephalica*, and *I. bellii*. Thus, these areas should be prioritized in conservation programs.

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## 1. Introduction

In recent decades, anthropogenic alterations have increased exponentially; land use and climate change have caused a decline in population sizes, geographic range, and plant and animal diversity (Steffen et al., 2015), as well as mass species extinction worldwide (Ceballos et al., 2015). The situation is critical because approximately 32% of all land vertebrate species are experiencing declines and local population losses (Ceballos et al., 2017). In addition, it has been documented that almost 200 species of vertebrates have become extinct in the last 100 years, representing approximately 2 species per year (Ceballos et al., 2017). The situation is especially worrisome for amphibians under climatic change scenarios; 35% of the species around the world are classified as threatened with extinction according to the International Union for the Conservation of Nature (IUCN) Red List (IUCN, 2021; Stuart et al., 2004). Thus, amphibian populations occurring near major urban areas, such as the center of Mexico, are expected to suffer range contractions, population declines, and even extinction due to climate change and the lack of suitable habitats and connectivity between them (Ochoa-Ochoa et al., 2012). Landscape connectivity is considered a pivotal element of landscape structure, and it is defined as the degree to which the landscape facilitates the movement of organisms between resource patches (Taylor et al., 1993). Connectivity can be viewed from two different perspectives: at a landscape level, implying the connectivity between the different elements present in an area, such as land cover vegetation, land use, mountains, and rivers; and at an organism level, considering the organism's ability to move through the different covers (resistance surfaces) (Garrido-Garduño et al., 2016).

Plethodontidae is one of the most diverse families of salamanders in the world, including around 492 species (AmphibiaWeb, 2021) distributed predominantly in America from southern Canada to the Amazon basin in Brazil (Min et al., 2005). In Mexico, 139 plethodontid species have been described, of which more than 81% are endemic to this country (AmphibiaWeb, 2021; Frost, 2019). Moreover, 69% of the Mexican plethodontid salamander species are in the endangered or critically endangered categories according to the IUCN (AmphibiaWeb, 2021; IUCN, 2021). Most plethodontid species have small ranges and thus a low dispersal ability, as well as very specific micro-habitat requirements (Wake & Lynch, 1976; Wake, 1987), such as a narrow thermal tolerance (Markle & Kozak, 2018), which make them particularly susceptible to climate and landscape changes (Chen et al., 2011; La Sorte & Jetz, 2010). Therefore, understanding how endemic species will respond to current and future land use and climate change would shed light on the direction and magnitude of the climate and land use change effect on salamanders in Mexico.

For this study, four threatened salamanders endemic to Mexico (i.e., *Aquiloerycea cephalica* (Cope, 1865), *Isthmura bellii* (Gray, 1850), *Pseudoeurycea robertsi* (Taylor, 1939), and *Pseudoeurycea leprosa* (Cope, 1869) that inhabit different topographic reliefs were selected. *A. cephalica* occurs in the Trans-Mexican Volcanic Belt (TMVB) and the Sierra Madre Oriental (SMO) (Parra-Olea et al., 2005) between 1100–3000 m a.s.l. and inhabits *Pinus*, *Pinus-Quercus*, and cloud forests. *I. bellii*, occurs in the TMVB and along the western and southern margins of the Mexican plateau, and it has been found in different habitats, such as *Pinus-Quercus*, cloud, and mixed forests and in human-altered habitats, such as coffee and banana plantations (Parra-Olea et al., 2016; Ramírez-Bautista et al., 2014). Its altitudinal range is 750–3300 m a.s.l. *P. leprosa*, is a montane species that occurs in the TMVB, the Mexican Plateau, and the SMO (Frost, 2019). It mainly inhabits areas covered by *Pinus* and *Pinus-Quercus* forests (IUCN, 2021), as well as *Abies* forests (Sunny et al., 2021), and has been recorded at 2500–3200 m a.s.l. The geographic distribution of *P. robertsi* is very restricted; it only occurs in the Nevado de Toluca Volcano (NTV) in the TMVB (Sunny et al., 2021), and it inhabits *Abies-Pinus* forests at high elevations of 2900–3600 m a.s.l.

The TMVB is one of the most diverse biogeographic provinces

(<http://www.conabio.gob.mx/>) of Mexico in terms of terrestrial fauna, hosting the largest number of endemic amphibian and reptile species (Flores-Villela & Canseco-Márquez, 2007). However, the TMVB is also one of the most urbanized areas of the country, with 3.4% of the area highly fragmented by urban settlements and 44.7% by agricultural areas (Sunny et al., 2017), which disrupts forest connectivity, reducing gene flow and increasing the extinction risk of these threatened species. In the present study, environmental niche modeling (ENM) was used to identify the current and future potential distribution and landscape connectivity of these four endemic salamanders. We hypothesized that climate and land use change would reduce the suitable habitats of the species in the future. In particular, the following research questions were answered: 1) Which climatic, topographic, and land use variables determine the current distribution of each salamander species? 2) How similar are the environmental niches of the four species? 3) What are the current and future potential distributions of the four salamanders? and 3) Will the potential distribution and landscape connectivity of the four salamander species experience an expansion or a reduction and to what degree?

## 2. Materials and methods

### 2.1. Species occurrence and environmental variables

ENM analysis was performed on four plethodontid species found in the TMVB (*P. robertsi*, *P. leprosa*, *A. cephalica*, and *I. bellii*). Occurrence records, with geographical coordinates, were obtained from fieldwork and online databases, namely REMIB (<http://www.conabio.gob.mx/remib>), UNIBIO (<http://unibio.unam.mx/>), Global Biodiversity Information Facility (GBIF; <https://www.gbif.org>), HERPNET (<http://www.herpnet.net/>), the Vertebrate Network (VerNet, <http://vertnet.org/index.html>), IREKANI (<http://unibio.unam.mx/irekani/>), and iNaturalist ([www.iNaturalist.com.mx](http://www.iNaturalist.com.mx)). Only records from 2000 to 2021 were considered for the analysis, as land use and vegetation covers were used to create the ENM, and land use changes occurred in Mexico in the last two decades. For example, 594 kha of humid primary forest were lost in this country 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). Cleaning of the occurrence data was carried out with the ntbox package (Osorio-Olvera et al., 2020) in R 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 as this method has been shown to substantially reduce the degree of overfitting in the model (Boria et al., 2014; Segurado et al., 2009). After filtering the data, 78 records were obtained for *P. robertsi* (Fig. 1A), 115 for *P. leprosa* (Fig. 1B), 107 for *A. cephalica* (Fig. 1C), and 141 for *I. bellii* (Fig. 1D). Finally, the accessibility area considered for each species was the biogeographic regions with records of the species or records near their borders; see Fig. 1 (Barve et al., 2011).

The climatic variables were obtained from WorldClim version 2.1 ([www.worldclim.org](http://www.worldclim.org); Fick & Hijmans, 2017) at a 1 km resolution. Topographic variables ([www.worldclim.org](http://www.worldclim.org)), such as elevation, slope, and aspect (slope and aspect were extracted from elevation using ArcMap 10.5), and land cover variables (Soil use and vegetation series VI, 1:250,000) from the National Institute of Statistics and Geography (<https://www.inegi.org.mx/temas/usosuelo/#Descargas>; INEGI, 2017) were also considered. The land cover layer was generated with satellite images from 2014, and the last update occurred in 2017 (Table A1). From this layer, the different land cover layers were extracted, converted to raster, and transformed from categorical to continuous variables (Table A1) using a resample method that averages the eight surrounding pixel values and the previous pixel value (3 × 3 mean) following Hirzel et al. (2001). With this method, a value between 0 and 1

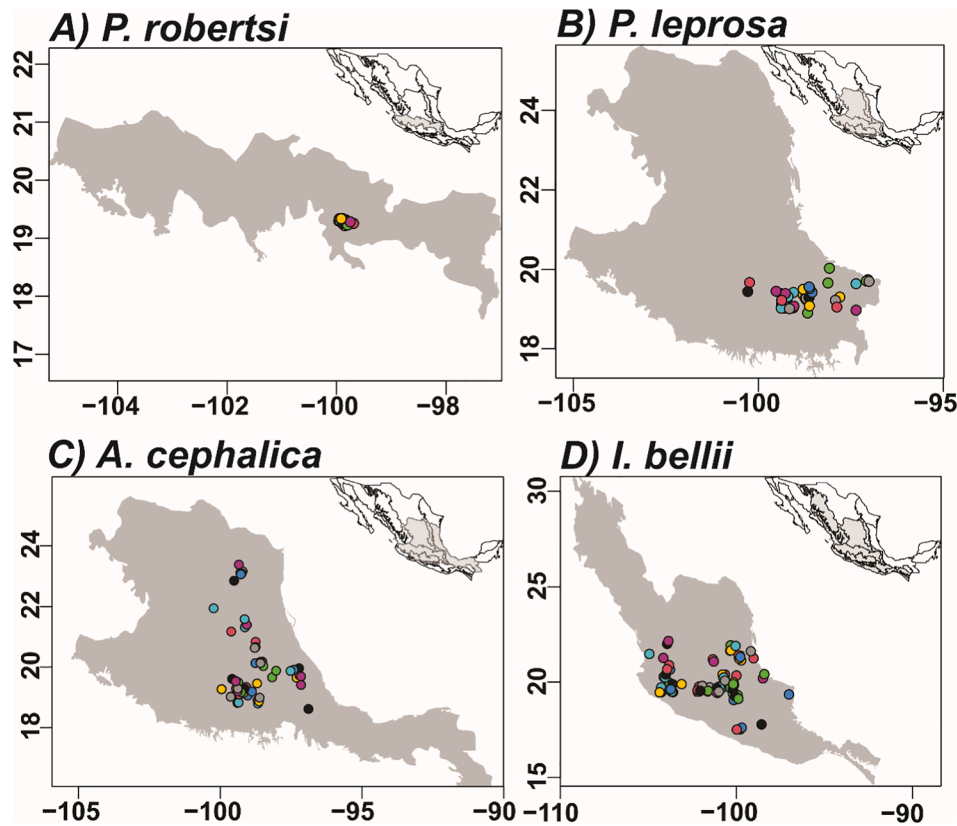


Fig. 1. Occurrence records with the Checkerboard2 method partition, in dark gray the M used.

was obtained for each pixel. This analysis was carried out with IDRISI TerrSet 18.21 software (Clark Labs, 2020) using the Filter module (Gidey et al., 2017). All layers were processed in a raster format, with a 1 km resolution, using the packages raster (Hijmans & van Etten, 2016) and rgdal (Bivand et al., 2015) for R software (version 4.0.0; R Development Core Team, 2019). After a bibliographic review and Pearson's correlation analysis (Fig. A2) carried out with ENMTools (Warren et al., 2010) and usdm (Naimi, 2017) packages for R software to discard highly correlated variables ( $r^2 > 0.7$ , Dormann et al., 2013), the following variables that were considered important for the presence of salamanders were selected (Emel & Storfer, 2015; Emel et al., 2019; Spear & Storfer, 2008; Trumbo et al., 2013): grasslands percentage, arid vegetation percentage, *Pinus* forest percentage, *Quercus* forest percentage, *Abies* forest percentage, agriculture percentage, cloud forest percentage, maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month (BIO6), precipitation of the wettest month (BIO13), and precipitation of the driest month (BIO14). Elevation showed a correlation of  $-0.85$  with BIO6 (Fig. A2). However, since elevation is a very important variable for mountain species, the current and future potential distribution were modeled with and without elevation to determine if there were differences. The distance to urban settlements was not included as a variable in the models because this can generate a bias, as these areas are more easily accessed by observers (Araújo & Guisan, 2006). Instead, present (from the present distribution maps) and future urban areas (from the future distribution maps) were designated as areas of zero habitat suitability (following González-Fernández et al., 2018).

## 2.2. Environmental niche modelling

Two different methods were used to compare results: ENMeval with Maxent algorithm and an ensemble model implemented in biomod2. The Maximum Entropy algorithm was applied using Maxent 3.3.3

software (Phillips et al., 2006), with species-specific settings selected using the ENMeval R package (Muscarella et al., 2014). Several Maxent models were calculated using different combinations of parameters to select the settings that optimized the trade-off between goodness-of-fit and over-fitting. ENMeval was set to test the regularization values of 1 and 2 steps, as well as the following feature classes: linear (L), quadratic (Q), product (P), threshold (T), and hinge (H) with the following combinations: L, H, LQ, LQP, LQH, LQHP, and LQHPT. In the ENMeval workflow, 100,000 random points were generated as background points. To avoid nonindependence between training and testing data, the 'Checkerboard' approach was adopted to test for two spatial grains: with an aggregation factor of two, as ENMeval uses this as the default value (fine-resolution Checkerboard), and with an aggregation factor of four (coarse-resolution Checkerboard). This is a spatially independent cross-validation method that avoids spatial autocorrelation between testing and training data. For model selection, the Akaike information criterion corrected for small sample sizes (AICc) was used (Burnham & Anderson, 2004).

An assembly model was also made with the biomod2 package (Thuiller et al., 2016) in R software. Seven of the ten algorithms available in the package were selected. These were generalized boosted models (GBM), generalized additive models (CTA), artificial neural networks (ANN), surface range envelop or BIOCLIM (SRE), flexible discriminant analysis (FDA), random forest (RF), and Maxent. As presence data was available, a set of 10,000 pseudo-absence datapoints was randomly generated (i.e., using the user-defined option in biomod2 to create pseudo-absences). Prevalence was set to 0.5 to give presences and absences the same importance in the calibration process (Linero et al., 2020). The models were calculated ten times, each run with a different selection of training and testing datasets. The proportion of data for calibration was set to 80% (Linero et al., 2020).

To evaluate the overall model accuracy in both Maxent and ensemble models, the scores from the area under the curve (AUC) from the

receiver operating characteristic plot (ROC) were used first (Metz, 1978; Phillips et al., 2006), followed by the transformation of AUC into partial-receiver operating characteristic curve graphics (Partial-ROC; Peterson et al., 2008). For this, the package ntbbox (Osorio-Olvera et al., 2020) in R was used. For the ensemble model, the true skill statistic (TSS) and KAPPA evaluation metric were assessed in package biomod2 (Allouche et al., 2006) based on the sum of sensitivity and specificity minus one (the sensitivity is the proportion of correctly predicted presences, and the specificity is the proportion of correctly predicted absences). In the biomod2 approach, the models were assembled by a total consensus rule, and algorithms were assembled by the weighted sum of evaluations greater than TSS > 0.4 (Linero et al., 2020). The ensemble model (seven algorithms  $\times$  10 repetitions) was then used to project the potential distribution of each salamander species under current and projected future climatic scenarios.

### 2.3. Niche overlap

Principal component analysis (PCA) was used to transform the environmental variables into a two-dimensional space defined by the first and second principal components, following Broennimann et al. (2012). Thus, the axes of the PCA maximized the ecological variance present in the study areas (Di Cola et al., 2017). Then, the two-dimensional environmental space was projected for each pair of salamander species onto a  $100 \times 100$  PCA grid of cells bounded by the minimum and maximum PCA values in the study areas. A smoothed density of occurrences for each species in each cell of the grid was then estimated using a kernel density function. The overlap between niches was calculated using Schoener's D and Hellinger's I metrics (Rödder & Engler, 2011; Schoener, 1970; Warren et al., 2008). These metrics vary from 0 (no overlap) to 1 (complete overlap). Finally, a niche similarity test was performed to assess the statistical significance of a measured niche difference against null model niches taken randomly within a given background area. These analyses were carried out in R software with packages ecospat (Di Cola et al., 2017) and SDMTools to plot the niche overlap (VanDerWal et al., 2014).

### 2.4. Land cover and climate change

Land use and vegetation variables for the year 2050 were generated using the module Land Change Modeler for Ecological Sustainability (LCMES) in IDRISI TerrSet software and land use and vegetation layers from year 2011 (series V; INEGI, 2011) and time 2 from year 2014 (series VI; INEGI, 2014). This model was based on the artificial neural network, Markov chain matrices, and transition suitability maps generated by training multilayer perceptron or logistic regression (Ansari & Golabi, 2019; Hasan et al., 2020; Mas et al., 2014). This model predicted land cover changes from different raster images (from different time periods) with the same number of classes in the same sequential order (Mas et al., 2014). This analysis provided a quick evaluation of quantitative change by charting gains and losses among different land cover types (Hasan et al., 2020; Mishra et al., 2014). It also estimated net change, persistence, and the specific transition of land cover in the geographic space (Gibson et al., 2018; Hasan et al., 2020). These changes are important to identify the dominant transition from one class to another (Hasan et al., 2020; Müller et al., 2010). Finally, the algorithm implements a Markov chain model to forecast land cover changes from time  $t = 1$  to another time  $t + 1$  (Hasan et al., 2020; Wang & Murayama, 2017) based on the transition probability matrix and the transition area matrix of each land cover class (Hasan et al., 2020). The present and future urban areas were designated as areas of zero habitat suitability. All graphs were made using the ggplot2 package (Wickham, 2011) for R.

To generate the future potential distributions maps, future bioclimatic variables of the Community Climate System Model, version 4 (CCSM4), were obtained for the year 2050 considering two climate

change scenarios: Representative Concentration Pathways, RCP 45 (middle-moderate) and RCP 85 (the most extreme scenario). From WorldClim downscaled CMIP5 data ([https://worldclim.org/data/cmip5\\_2.5m.html](https://worldclim.org/data/cmip5_2.5m.html)), this climate model was chosen as it is one of the top best for Central America according to Hidalgo and Alfaro (2015) and one of the six with the best performance of the 40 existing climate models and second in precision in precipitation values according to Kamworapan and Surussavadee (2019). Then, continuous maps were reclassified to binary using the 10th percentile training presence threshold, which sets the threshold as the value that excludes 10% of the localities having the lowest predicted values. (Radosavljevic & Anderson, 2014). These binary maps were used to assess the change in the potential distribution of each species in the future with both climate change scenarios.

### 2.5. Connectivity analysis

A connectivity model was generated for the present and future considering both climate change scenarios and for each species using Circuitscape V 4.0 software (McRae et al., 2013), which is based on the circuit theory (CT) that considers population connectivity as an analog of an electrical current (McRae et al., 2008; McRae, 2006). The model uses a graph-theoretical approach to predict movement patterns and quantify the effects of landscape features in impeding species movement (Cushman et al., 2013). The inverse of the habitat suitability map (1-ENM) was used as the landscape resistance surface layer, depicting the difficulty of animal movement within any location in the landscape (Mateo-Sánchez et al., 2014). Each calculation used focal points in pairwise modelling mode and a four-neighbor connection scheme that allowed connectivity amongst the four nearest cells, since salamanders have a low dispersal capacity (Sunny et al., 2019; Velo-Antón et al., 2013).

## 3. Results

### 3.1. Ecological niche modelling

Regarding the results of ENMeval, for *P. robertsi*, the best model was the combination LQH with a regularization multiplier value of 2. For *P. leprosa*, the best model was the combination LQ with a regularization multiplier value of 1. For *A. cephalica*, the best model was the combination LQ with a regularization multiplier value of 2, while for *I. bellii*, the best model was the combination LQ with a regularization multiplier value of 1. The Maxent models run in ENMeval (present and future with both RCP estimations) performed better than expected by random chance according to AUC (0.823 to 0.989; p-value < 0.001). Additionally, the Partial-ROC bootstrap tests showed significant ratio values of empirical AUC over null expectations (AUC ratios  $\geq$  from 1.759 to 1.985 and p-value < 0.001 in all cases, Table 1). Ensemble models, both present and future for the four species, had very good performance (TSS values from 0.737 to 0.993, Kappa values from 0.536 to 0.906, Partial-ROC values from 1.846 to 1.986, and ROC values from 0.908 to 0.999; Table 2; Allouche et al., 2006).

The most important environmental variables associated with the

**Table 1**

Predictive performance of present and future ENMeval distribution models developed for the four salamander species.

| Year                | 2014  |             | 2050 RCP 45 |             | 2050 RCP 85 |             |
|---------------------|-------|-------------|-------------|-------------|-------------|-------------|
|                     | ROC   | Partial-ROC | ROC         | Partial-ROC | ROC         | Partial-ROC |
| <i>P. robertsi</i>  | 0.985 | 1.982       | 0.990       | 1.983       | 0.989       | 1.985       |
| <i>P. leprosa</i>   | 0.971 | 1.949       | 0.968       | 1.941       | 0.975       | 1.941       |
| <i>A. cephalica</i> | 0.929 | 1.858       | 0.943       | 1.9         | 0.947       | 1.901       |
| <i>I. bellii</i>    | 0.823 | 1.706       | 0.864       | 1.759       | 0.833       | 1.759       |

**Table 2**

Predictive performance of present and future Biomod2 ensemble distribution models developed for each salamander species.

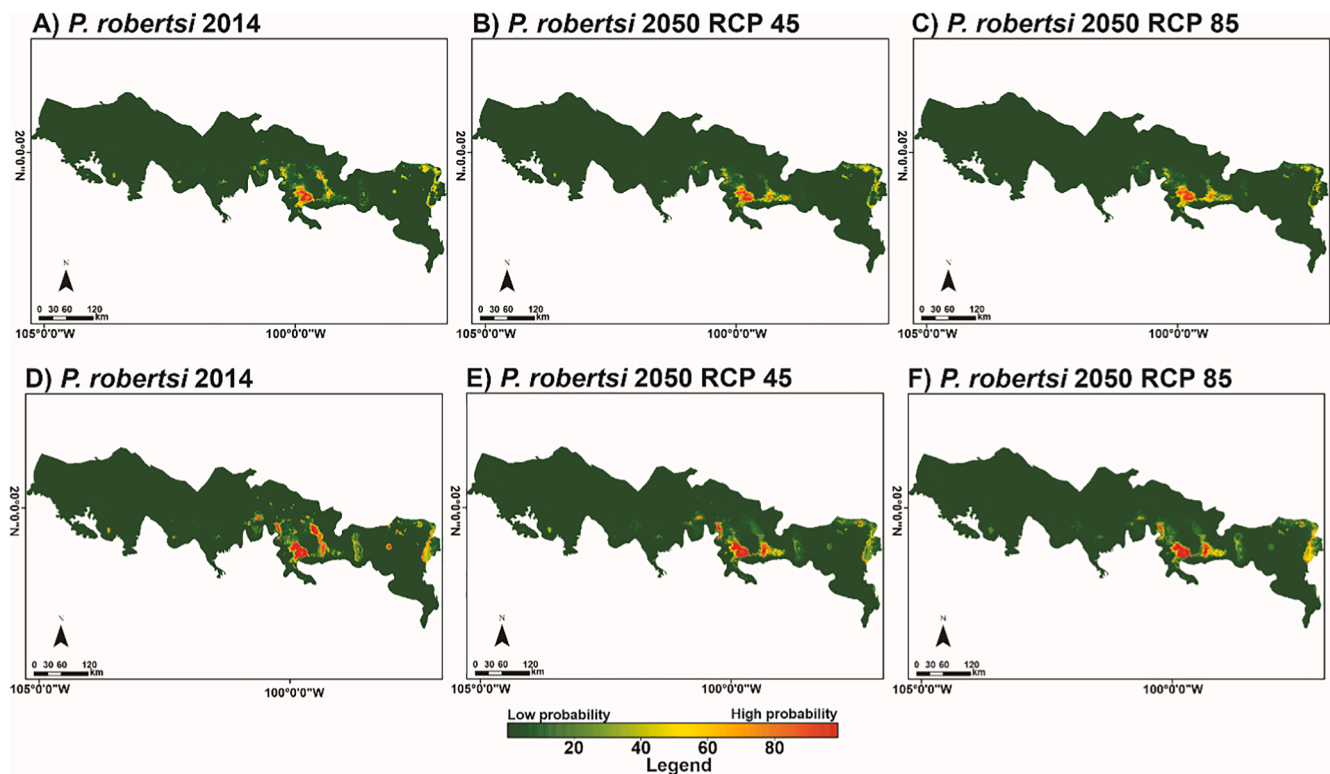
| Year                | 2014  |       |       |             | 2050 RCP 45 |       |       |             | 2050 RCP 85 |       |       |             |
|---------------------|-------|-------|-------|-------------|-------------|-------|-------|-------------|-------------|-------|-------|-------------|
|                     | TSS   | KAPPA | ROC   | Partial-ROC | TSS         | KAPPA | ROC   | Partial-ROC | TSS         | KAPPA | ROC   | Partial-ROC |
| <i>P. robertsi</i>  | 0.991 | 0.906 | 0.999 | 1.985       | 0.993       | 0.903 | 0.998 | 1.985       | 0.992       | 0.882 | 0.998 | 1.986       |
| <i>P. leprosa</i>   | 0.906 | 0.740 | 0.986 | 1.968       | 0.899       | 0.739 | 0.986 | 1.961       | 0.922       | 0.782 | 0.988 | 1.963       |
| <i>A. cephalica</i> | 0.768 | 0.589 | 0.908 | 1.903       | 0.841       | 0.623 | 0.968 | 1.942       | 0.855       | 0.696 | 0.976 | 1.948       |
| <i>I. bellii</i>    | 0.737 | 0.718 | 0.934 | 1.846       | 0.772       | 0.565 | 0.939 | 1.849       | 0.739       | 0.536 | 0.936 | 1.846       |

presence of *P. robertsi*, according to Maxent, were *Abies* forest cover percentage (39%), maximum temperature of the warmest month (33%), and precipitation of the wettest month (13%). The presence of *P. leprosa* and *A. cephalica* was mainly influenced by the maximum temperature of the warmest month (54 and 42%, respectively) and *Abies* forest cover percentage (18 and 22%, respectively), whereas the most important variable associated with the presence of *I. bellii* was the minimum temperature of the coldest month (54.4%). *Abies* forest cover percentage had a positive effect on *P. robertsi*, *P. leprosa*, and *A. cephalica*. The probability of presence of these three species decreased as the maximum temperature increased (around 27 °C the probability of presence of *P. robertsi* and *P. leprosa* fell below 0.1%. At 30 °C, the probability of presence of *A. cephalica* fell below 0.1%). *P. robertsi* had an optimum around 175 mm of precipitation during the wettest month, and the probability of presence of *I. bellii* fell below 0.1% with minimum temperatures lower than 0 °C (Fig. A3). In the current distribution models with and without elevation, there were no differences between both maps, and elevation showed, in general, a low contribution value for the salamander species; it was a bit higher for *I. bellii* (7.4%; Table. A2). The four salamander species were distributed mainly in the mountains of the TMBV (Figs. 2–5). *A. cephalica* was also distributed in the Sierra Madre Oriental (Fig. 4) and *I. bellii* in the Sierra Madre Oriental, Sierra Madre Occidental, Sierra Madre del Sur, Cuenca del Balsas, and Costa Pacifica Mexicana (Fig. 5). With both methods (Maxent model and ensemble

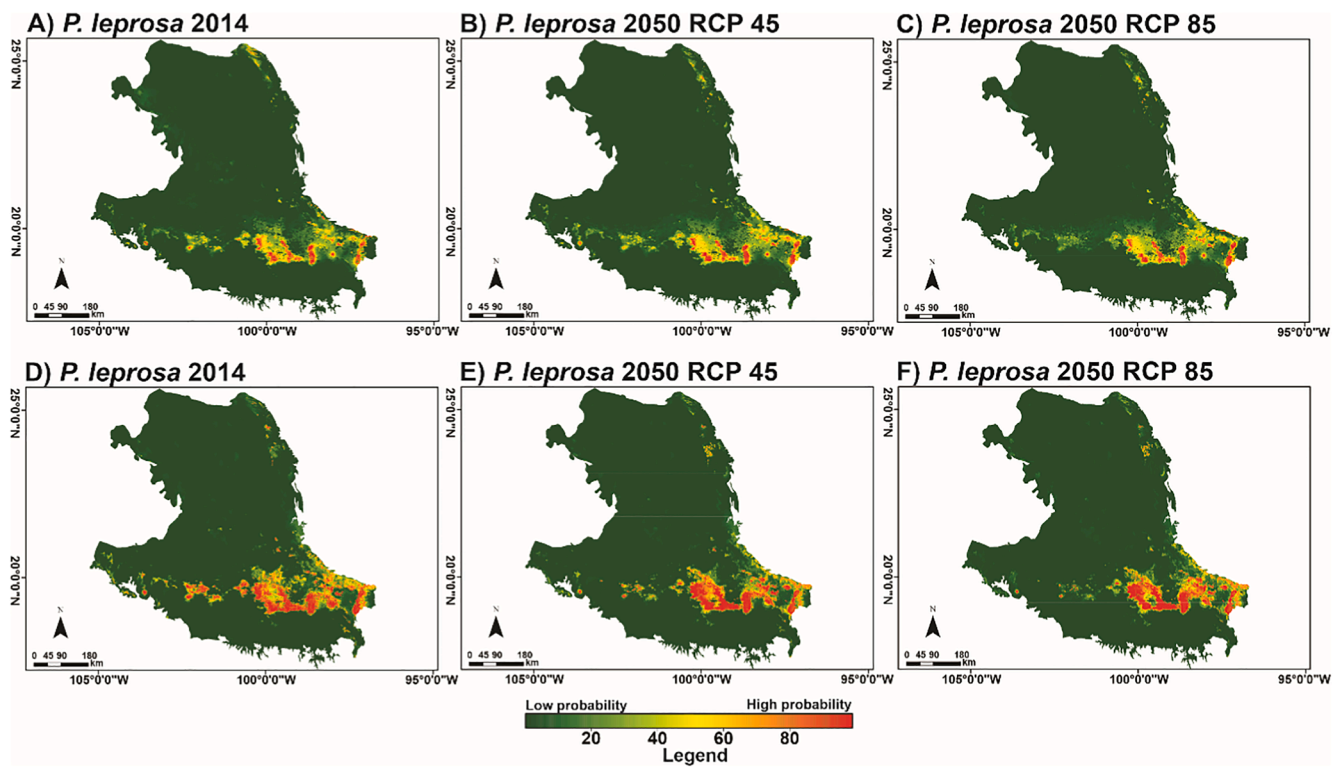
model), all salamander species were predicted to face a reduction in their potential distribution under future scenarios of climate and land cover change (Table 3 and Figs. 2–5). The ensemble model predicted a larger potential distribution area for all species and scenarios, except for *I. bellii* under the RCP85 scenario (Figs. 2D–F, 3D–F, 5D–F, Table 3). However, there was little consistency between the different methodologies and climate change scenarios to determine which species would suffer the greatest loss in potential distribution in the future. With Maxent and RCP45, *A. cephalica* suffered the greatest loss with a reduction of 16.34% in its potential distribution, and with Maxent and RCP85, *P. robertsi* suffered the biggest reduction (30.17%). With the ensemble model and RCP45, *P. leprosa* suffered the biggest reduction (16.47%), and with the ensemble model and RCP85, *I. bellii* suffered the biggest reduction (32.16%).

### 3.2. Niche overlap

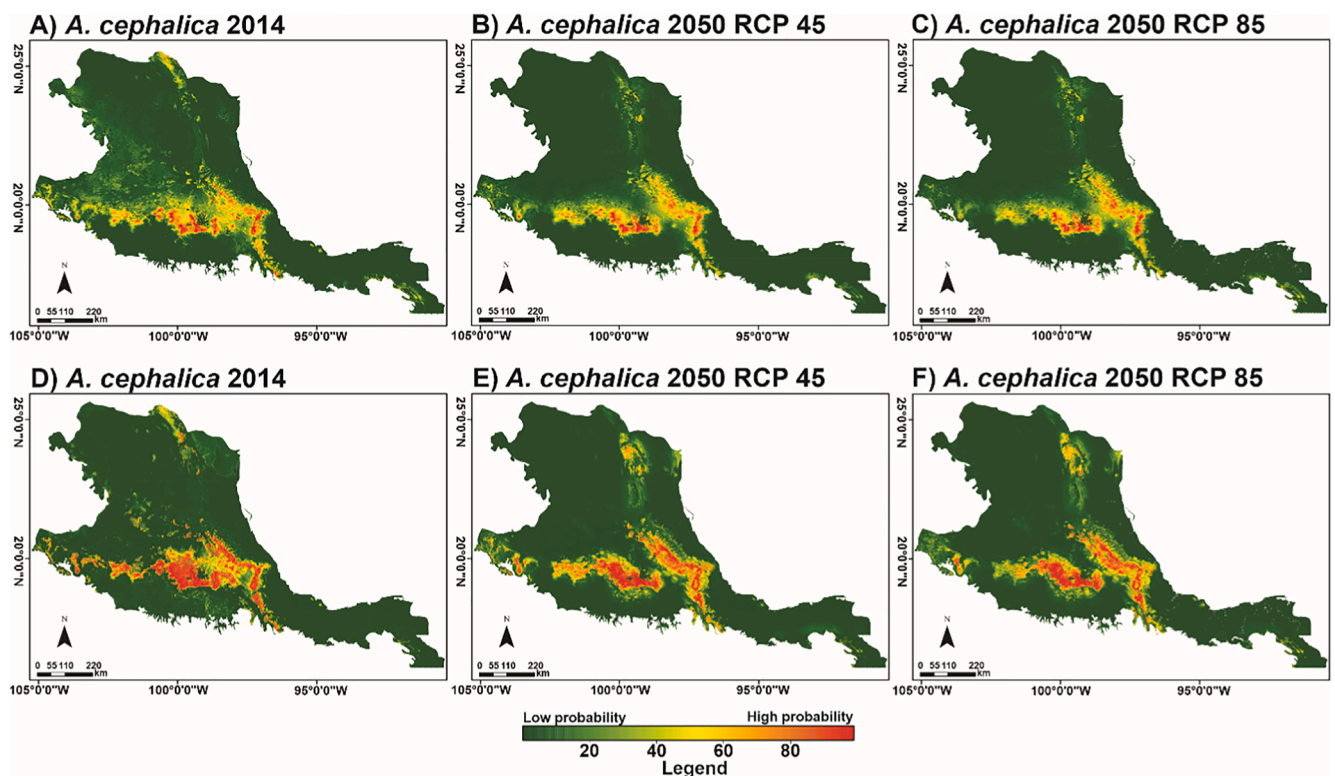
Environmental niches of *P. leprosa* and *A. cephalica* were significantly similar ( $D = 0.637$ ,  $I = 0.801$ ,  $p$ -value = 0.02), as well as the environmental niches of *P. robertsi* and *P. leprosa* ( $D = 0.640$ ,  $I = 0.797$ ,  $p$ -value = 0.01). The lowest niche overlap occurred between *P. leprosa* and *I. bellii* ( $D = 0.150$ ,  $I = 0.296$ ; Fig. 6; Table 4). Notably, the environmental niche of *P. robertsi* was within the environmental niches of *P. leprosa* and *A. cephalica* (Fig. 8A, B).



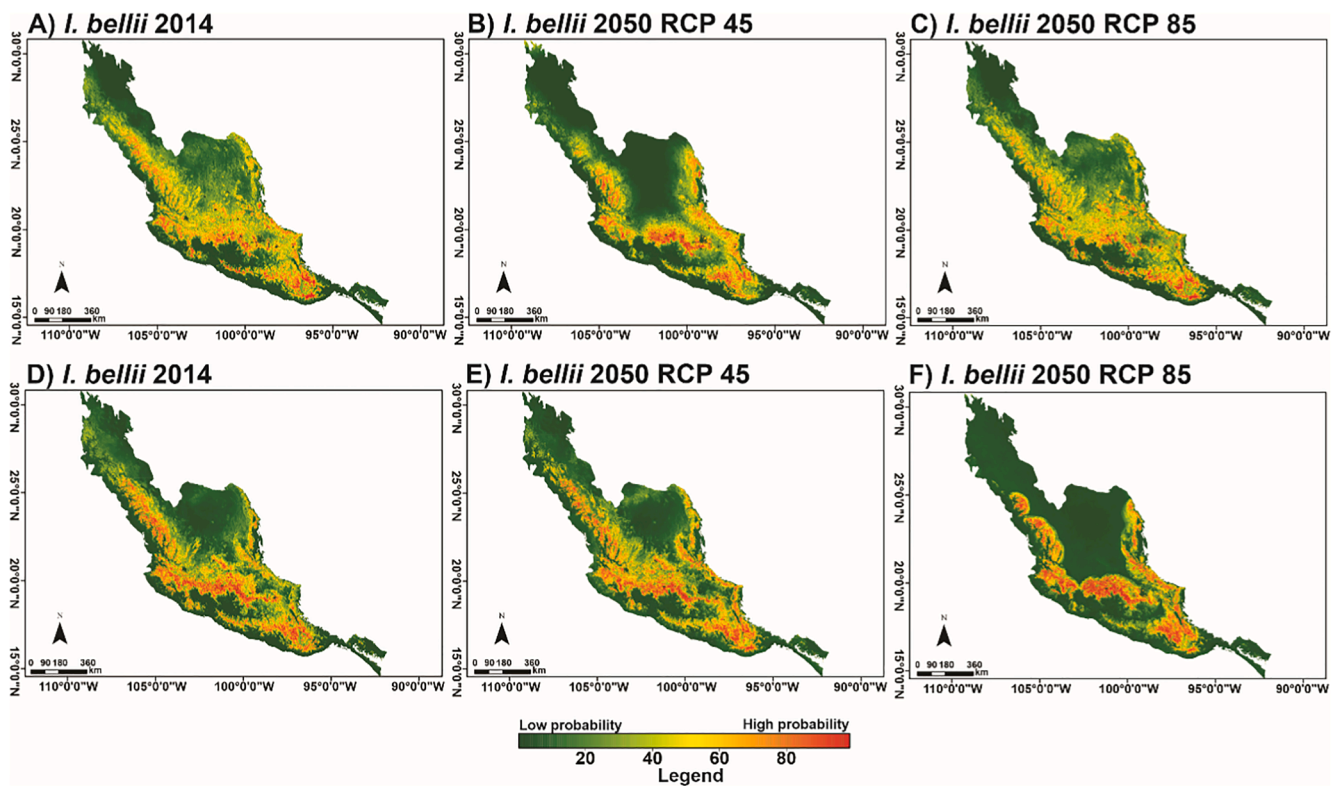
**Fig. 2.** Present (2014) and future (2050) potential distribution maps developed for *Pseudoeurycea robertsi*. A–C considering the Maxent algorithm, D–F considering the ensemble model.



**Fig. 3.** Present (2014) and future (2050) potential distribution maps developed for *Pseudoeurycea leprosa*. A-C considering the Maxent algorithm, D-F considering the ensemble model.



**Fig. 4.** Present (2014) and future (2050) potential distribution maps developed for *Aquiloeurycea cephalica*. A-C considering the Maxent algorithm, D-F considering the ensemble model.



**Fig. 5.** Present (2014) and future (2050) potential distribution maps developed for *Isthmura bellii*. A-C considering the Maxent algorithm, D-F considering the ensemble model.

**Table 3**

Present and future suitability area (km<sup>2</sup>) and percentage of area loss for each salamander species with different niche modelling algorithms.

| Ensemble            | 10 percentile training presence |                                      |                                 |                                      |                                 |
|---------------------|---------------------------------|--------------------------------------|---------------------------------|--------------------------------------|---------------------------------|
|                     | 2014<br>(km <sup>2</sup> )      | 2050<br>RCP 45<br>(km <sup>2</sup> ) | Loss (%)                        | 2050<br>RCP 85<br>(km <sup>2</sup> ) | Loss (%)                        |
| <i>P. robertsi</i>  | 6011                            | 5371                                 | <b>10.65</b>                    | 4770                                 | <b>20.65</b>                    |
| <i>P. leprosa</i>   | 48,764                          | 40,733                               | <b>16.47</b>                    | 40,404                               | <b>17.14</b>                    |
| <i>A. cephalica</i> | 95,792                          | 89,992                               | <b>6.05</b>                     | 82,961                               | <b>13.39</b>                    |
| <i>I. bellii</i>    | 365,531                         | 353,960                              | <b>3.17</b>                     | 247,964                              | <b>32.16</b>                    |
| ENMeval             |                                 |                                      |                                 |                                      |                                 |
| Species             | 2014<br>(km <sup>2</sup> )      | 2050<br>RCP 45<br>(km <sup>2</sup> ) | Loss<br>2014–2050<br>RCP 45 (%) | 2050<br>RCP 85<br>(km <sup>2</sup> ) | Loss<br>2014–2050<br>RCP 85 (%) |
| <i>P. robertsi</i>  | 3513                            | 3250                                 | <b>7.49</b>                     | 2453                                 | <b>30.17</b>                    |
| <i>P. leprosa</i>   | 34,824                          | 33,091                               | <b>4.98</b>                     | 32,082                               | <b>7.87</b>                     |
| <i>A. cephalica</i> | 94,438                          | 79,007                               | <b>16.34</b>                    | 78,750                               | <b>16.61</b>                    |
| <i>I. bellii</i>    | 335,740                         | 326,886                              | <b>2.64</b>                     | 299,713                              | <b>10.73</b>                    |

### 3.3. Land use and vegetation cover change

Between 2011 and 2014, there was an increase of 16,241 km<sup>2</sup> in agriculture and 3,195 km<sup>2</sup> in urban areas (Fig. 7). Similarly, there was a reduction in *Pinus* forest of 19,085 km<sup>2</sup>, in grasslands of 1821 km<sup>2</sup>, and in *Abies* forest of 70.37 km<sup>2</sup>, mainly due to its conversion to agriculture lands (Fig. 7). The biogeographic region that showed the greatest increase in urban areas was the TMVB (Fig. 8A). Although there was an increase in agricultural areas in all the country, the areas that showed the biggest increase were the highlands of Chiapas and the central part of the Yucatan peninsula (Fig. 8B). The area with the greatest loss of *Abies* forest was located in the Corredor Biológico Chichinautzin, especially in the Lagunas de Zempoala, and the greatest gain was in Los Azufres, Michoacan (Fig. 8C). Finally, the largest loss of *Pinus* forest was

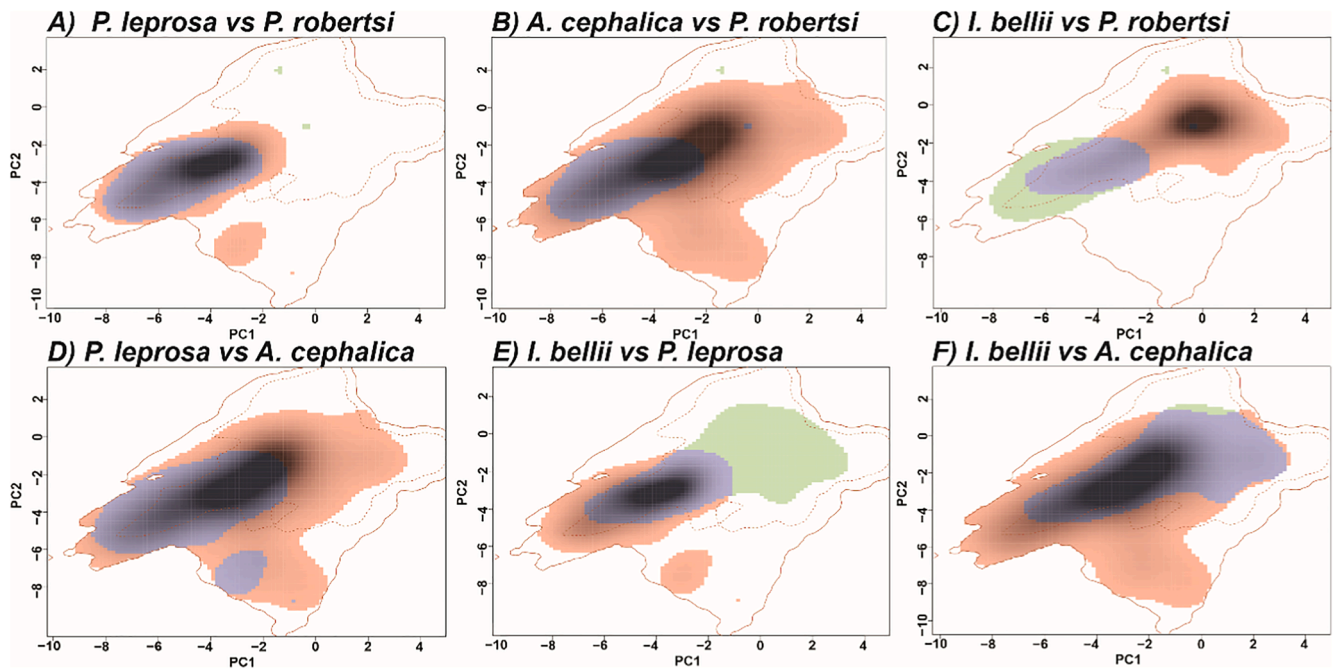
recorded in the Sierra Madre Oriental, Sierra Madre Occidental, Sierra Madre del Sur, the Highlands of Chiapas, and in the TMVB in the area of the Sierra de las Cruces and the Corredor Biológico Chichinautzin (Fig. 8D).

### 3.4. Landscape resistance surface and connectivity

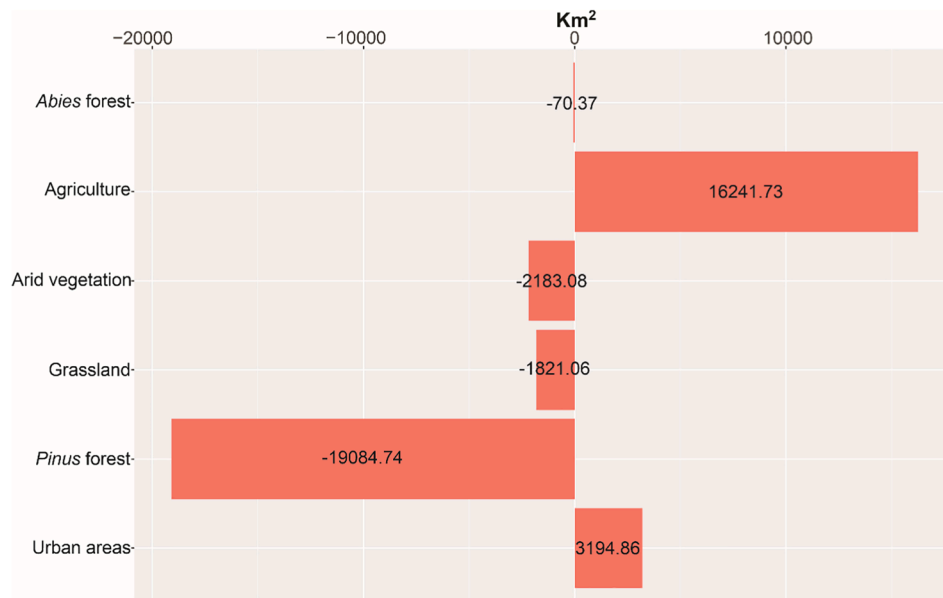
Landscape connectivity values for the four species and the different scenarios ranged from low to medium connectivity (Fig. 9). For *P. leprosa* and *A. cephalica*, the areas with the highest connectivity were Sierra de las Cruces and Corredor Biológico Chichinautzin. Additionally, for *I. bellii*, these were very important areas in terms of connectivity. Landscape connectivity for the four species were predicted to experience a reduction in the future according to both climate change scenarios, and *P. robertsi* was predicted to experience the greatest reduction (Fig. 9; Table 5), with a reduction of 35.73% in landscape connectivity considering RCP 45 and a reduction of 73.92% considering RCP 85. *P. leprosa* was predicted to experience a reduction of 24.23% considering RCP45 and a reduction of 43.61% considering RCP 85, mainly in Sierra de las Cruces and in Iztaccihuatl-Popocatepetl volcanoes. *A. cephalica* was predicted to experience a reduction of 22.12% considering RCP 45 and a reduction of 50.44% considering RCP 85, mainly in NTV and the Reserva de la Biósfera Santuario Mariposa Monarca. Finally, *I. bellii* was predicted to experience a reduction of 4.93% considering RCP 45 and a reduction of 16.23% considering RCP 85, mainly in Sierra de las Cruces and Iztaccihuatl-Popocatepetl volcanoes.

## 4. Discussion

This study adds important information to previous ENM reports about the current and future distributions of *P. leprosa* and *A. cephalica* (Parra-Olea et al., 2005). Here, the current and future potential distributions of two more plethodontid salamanders (*P. robertsi* and *I. bellii*) endemic to Mexico were assessed considering not only climate change,



**Fig. 6.** Environmental niche overlap between the four-salamander species as the pairwise salamander species are already indicated in the panel's label. A) Environmental niche overlap between *Pseudoeurycea leprosa* and *Pseudoeurycea robertsi* B) Environmental niche overlap between *Aquiloerycea cephalica* and *Pseudoeurycea robertsi* C) Environmental niche overlap between *Isthmura bellii* and *Pseudoeurycea robertsi*. D) Environmental niche overlap between *Pseudoeurycea leprosa* and *Aquiloerycea cephalica*. E) Environmental niche overlap between *Isthmura bellii* and *Pseudoeurycea leprosa*. F) Environmental niche overlap between *Isthmura bellii* and *Aquiloerycea cephalica*.



**Fig. 7.** Connectivity maps sites for each salamander species. The resistance map was estimated using CIRCUITSCAPE and based on habitat suitability from ENM reconstructions. A). *Pseudoeurycea robertsi*. B) *Pseudoeurycea leprosa*. C) *Aquiloerycea cephalica*. D) and *Isthmura bellii*.

but also land use change, using two different environmental niche methods (Maxent and an ensemble model).

The four salamander species were mainly distributed in the mountains of the TMBV, and *Abies* forest cover and maximum temperature of the warmest month were the most important variables to explain the potential distribution of three of the four salamanders (*P. robertsi*, *P. leprosa*, and *A. cephalica*). *Abies* forest cover was positively correlated with the presence of these three species, suggesting that *Abies* forest is the main habitat of these salamander species, which has also been

reported in other studies for *P. robertsi* (Bille, 2009; González-Fernández et al., 2019; Sunny et al., 2021). *I. bellii* also inhabits *Abies* forest; however, this cover type is not determinant to this species as it also inhabits cloud mountain, *Quercus*, and *Pinus* forests. Thus, this species has a wider distribution than the other species, including other biogeographic provinces apart from the TMVB. *I. bellii* also has the widest elevation range (750–3,300 m a.s.l.) in the TMVB (Parra-Olea et al., 2005) and can inhabit well-preserved forests, forest margins, and open areas, even in dry conditions (Domínguez-Vega et al., 2018). As

**Table 4**

Niche overlap between salamander species in the environmental space. The proportion of niche overlap is shown by the Schoener's D (above the diagonal) and Hellinger's I (below the diagonal) metrics. In bold the significant values according to the niche similarity value "D".

|                     | <i>P. robertsi</i> | <i>P. leprosa</i> | <i>A. cephalica</i> | <i>I. bellii</i> |
|---------------------|--------------------|-------------------|---------------------|------------------|
| <i>P. robertsi</i>  | –                  | <b>0.640</b>      | 0.361               | 0.251            |
| <i>P. leprosa</i>   | <b>0.797</b>       | –                 | <b>0.637</b>        | 0.150            |
| <i>A. cephalica</i> | 0.582              | <b>0.801</b>      | –                   | 0.288            |
| <i>I. bellii</i>    | 0.347              | 0.296             | 0.388               | –                |

expected, *P. robertsi*, *P. leprosa*, and *A. cephalica* were limited by maximum temperatures as they are adapted to high elevations and temperate semi-cold climates. Similar results have been reported for other vertebrate species occurring at high elevations (*T. scalaris*; González-Fernández et al., 2018). Climate is a central determining factor for species distribution (Sexton et al., 2009), and there is evidence that climate modification causes changes and reductions in habitable areas for amphibians, in addition to alterations in survival, growth, fitness, and dispersal (Blaustein et al., 2010; Pounds et al., 1999). For species with a wide range of distribution, a greater capacity for thermal acclimatization is expected, as well as greater probabilities for colonizing new areas, compared to species with a narrow range, which suggests that the latter are more susceptible to environmental warming associated with climate change (Gifford & Kozak, 2012; Markle & Kozak, 2018). In this sense, as expected, all species will suffer reductions in their potential distributions in the future in both climate change scenarios and according to both models. However, contrary to our expectations, *P. robertsi*, the species with the smallest distribution and narrowest niche breadth, was only predicted to suffer the biggest reduction in its potential distribution in the future according to the Maxent model with the RCP85 scenario. Surprisingly, *I. bellii* suffered the biggest reduction in its potential distribution according to the ensemble model with RCP85. A possible explanation for this result may be that *I. bellii* has a larger part of its distribution in less remote areas that are more exposed to land use change compared to the other species. Although there was no consistency in determining which species' distribution would suffer the biggest reduction in the future, *P. robertsi*,

*P. leprosa*, and *A. cephalica* are at risk of suffering population reductions in the future since they inhabit relicts of the boreal forests in a context of climate change (Rzedowski Rotter & McVaugh, 1966). Moreover, the distribution of these species already includes the highest elevations, implying that, as climate change progresses, this species will be limited in its ability to shift its distribution upward (Parra-Olea et al., 2005; Velo-Antón et al., 2013). For example, other studies on the distribution of *A. cephalica* and *P. leprosa* under climate change scenarios showed higher reductions in their habitable areas than those obtained here (up to 75%, Parra-Olea et al., 2005). In particular, *P. robertsi* is especial concern, as it had the highest and most restricted distribution (Bille, 2009; Sunny et al., 2021). *I. bellii*, although it has the wider niche and distribution of the four and is limited by minimum temperatures, may be more exposed to anthropogenic activities. Moreover, this study did not consider abundance, and *I. bellii* is less locally abundant than the other three species and is increasingly difficult to find (IUCN SSC, Amphibian Specialist Group, 2020).

In general, the ensemble model predicted larger potential distributions than the Maxent model and, according to our previous knowledge of *P. robertsi* distribution, which is endemic to the Nevado de Toluca Volcano (Bille, 2009), the Maxent model was more accurate, as the species is not present in sites with a high probability of presence according to the ensemble model that are far away from the Nevado de Toluca Volcano.

Not only will species' distribution suffer future reductions, but landscape connectivity will also experience a reduction in the future for the four salamander species according to both climate change scenarios. In this case, as expected according to its narrow niche breadth, *P. robertsi* was predicted to suffer the greatest reduction in landscape connectivity under both climate change scenarios, while *I. bellii* did not show great changes in the future, which is consistent with the more generalist habitat selection that allows the species to use a greater variety of habitats for its dispersal (IUCN SSC, Amphibian Specialist Group, 2020). Sierra de las Cruces and Corredor Biológico Chichinautzin were very important areas in terms of connectivity for *P. leprosa*, *A. cephalica*, and *I. bellii*; however, the greatest loss of *Abies* forest between 2011 and 2014 occurred in the Corredor Biológico Chichinautzin (especially in Lagunas de Zempoala). In addition, important *Pinus* forest loss occurred in the

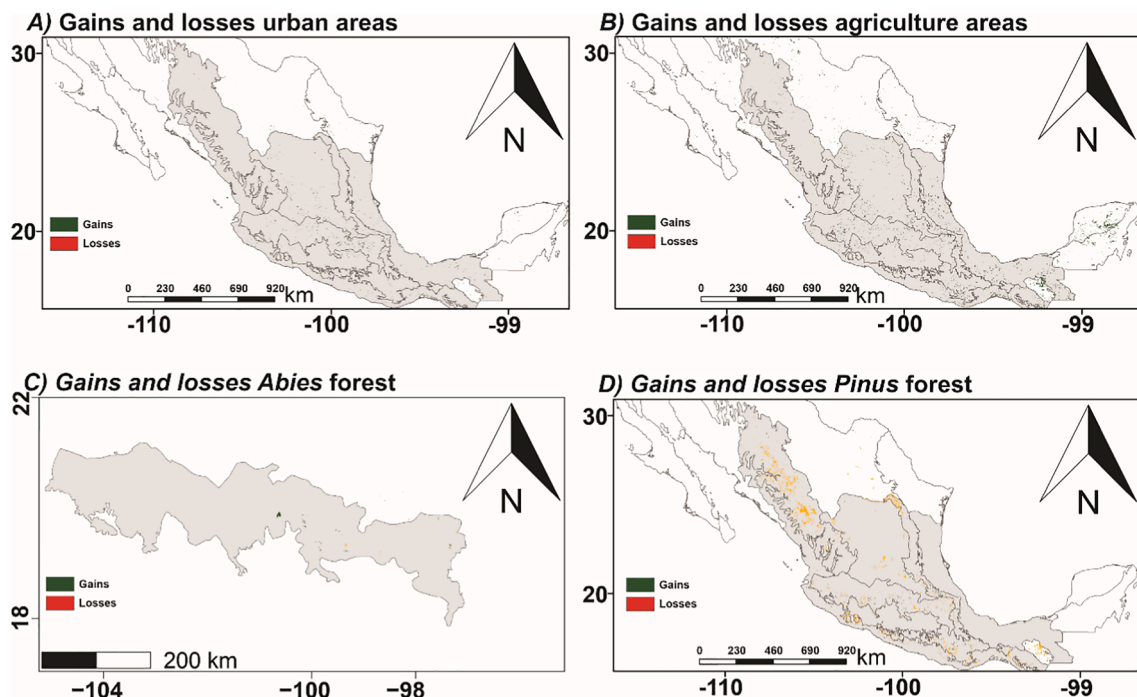


Fig. 8. Land use change by category (km<sup>2</sup>) between years 2011 and 2014 of most important variables for each salamander species.

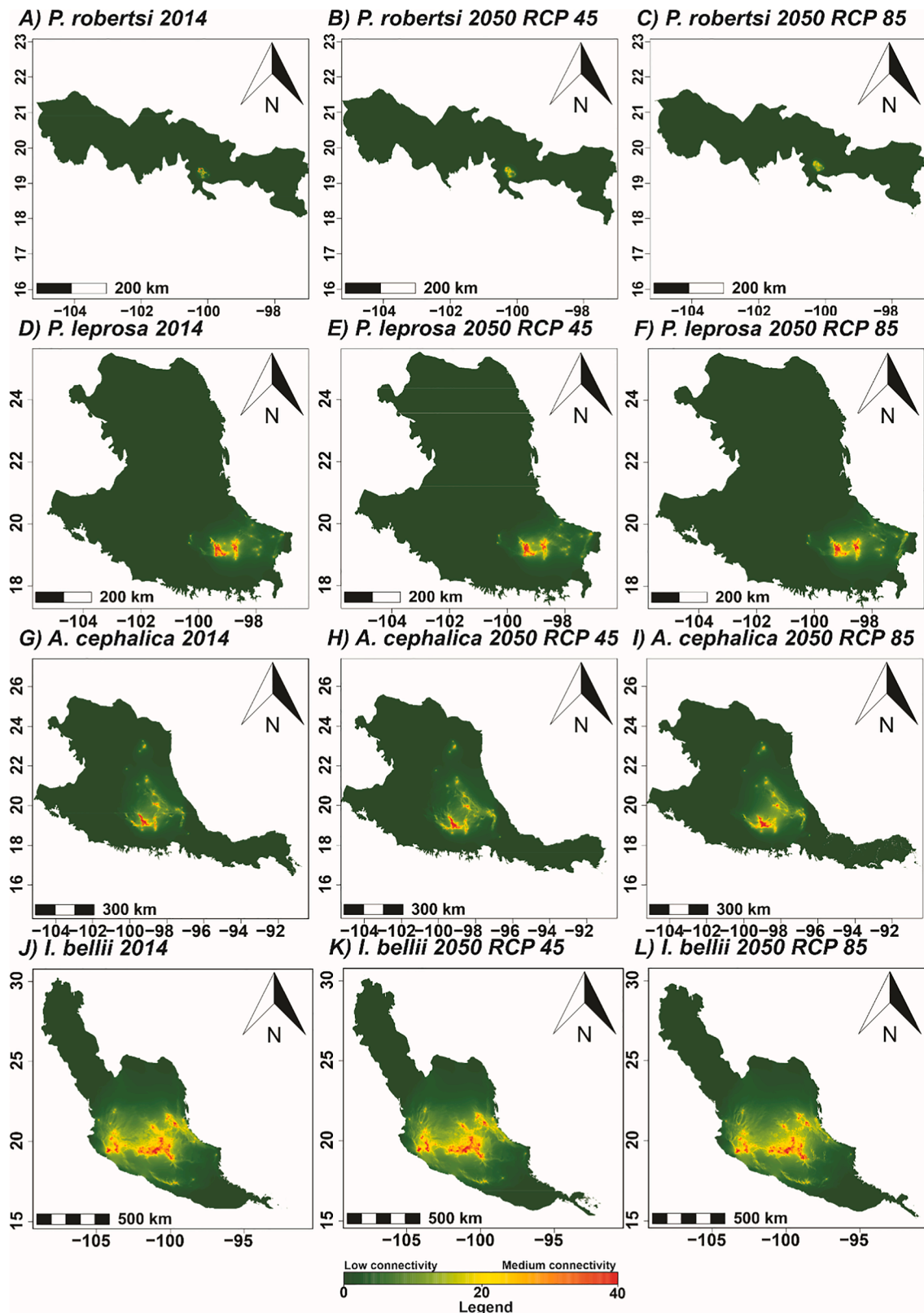


Fig. 9. Maps of losses and gains of urbanization, agriculture, *Abies* forest and *Pinus* forest between the 2011 and 2014 years.

area of Sierra de las Cruces and Corredor Biológico Chichinautzin in this period, according to our results about land use change. The degradation of this area may compromise connectivity between salamander populations.

Finally, the environmental niches of *P. leprosa* and *A. cephalica* were

significantly similar, as were the environmental niches of *P. robertsi* and *P. leprosa*. Niche overlap between similar species can increase inter-specific competition (Dehnhard et al., 2020; Navarro et al., 2013), and either could indicate a non-problematic coexistence between species in a region (de Boer & Prins, 1990). Despite that the four species coexist in

**Table 5**

Present and future landscape connectivity (km<sup>2</sup>) and percentage of area loss for each salamander species.

| Year                | Landscape connectivity     |                                      |                                 |                                      |                                 |
|---------------------|----------------------------|--------------------------------------|---------------------------------|--------------------------------------|---------------------------------|
|                     | 2014<br>(km <sup>2</sup> ) | 2050<br>RCP 45<br>(km <sup>2</sup> ) | Loss<br>2014–2050<br>RCP 45 (%) | 2050<br>RCP 85<br>(km <sup>2</sup> ) | Loss<br>2014–2050<br>RCP 85 (%) |
| <i>P. robertsi</i>  | 487                        | 313                                  | 35.73                           | 127                                  | 73.92                           |
| <i>P. leprosa</i>   | 1527                       | 1157                                 | 24.23                           | 861                                  | 43.61                           |
| <i>A. cephalica</i> | 1130                       | 880                                  | 22.12                           | 560                                  | 50.44                           |
| <i>I. bellii</i>    | 2496                       | 2373                                 | 4.93                            | 2091                                 | 16.23                           |

areas like the Nevado de Toluca Volcano (Sunny et al., 2021), there seems to be a certain degree of interspecific competition, at least between *P. robertsi* and *P. leprosa*: the low abundance and limited distribution of *P. leprosa* at the Nevado de Toluca Volcano, in contrast with its high abundance and ubiquity throughout its range, suggests the displacement of *P. leprosa* by the larger *P. robertsi* (Bille, 2009) without reaching exclusion, as both species have been found in the same study site of 10 ha (Sunny et al., 2021).

#### 4.1. Ecological and conservation implications

*Abies* forests of the TMVB were the main habitat of some Plethodontid salamanders; thus, the protection of these forests is a key factor for the conservation of *P. robertsi*, *P. leprosa*, and *A. cephalica*. Moreover, these forests are located in tropical mountains, which are areas of low climate change velocity, where many species can persist through global climate fluctuations by undertaking comparatively short elevational shifts instead of long latitudinal movements (Sandel et al., 2011). Thus, these mountains may effectively shelter many cold and temperate affinity species into the next century given the temperature increase due to climate change (Loarie et al., 2009). This may be particularly important for species with a low dispersal capacity, such as salamanders (Farallo et al., 2018). Our ENM and connectivity models can be supportive for environment managers in designing protected areas. Based on our results, the areas of Sierra de las Cruces and Corredor Biológico Chichinautzin should be prioritized in conservation programs, since these areas revealed a high suitability for salamanders and higher levels of landscape connectivity for these endemic species. Moreover, these areas are an important water supply for the metropolitan area of Mexico City and the Toluca Valley. Unfortunately, most of the Sierra de las Cruces is not protected, and the Corredor Biológico Chichinautzin area is currently being illegally deforested by organized crime.

#### 5. Compliance with ethical standards

We received the field permits and the approval of the ethics committee from Universidad Autónoma del Estado de México (4732/2019CIB) and SEMARNAT (SGPA/DGVS/05701/16).

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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