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**DOCTORADO EN CIENCIAS  
AGROPECUARIAS Y RECURSOS NATURALES**

**RESPUESTA DE LA HERPETOFAUNA A LA PERTURBACIÓN DEL HÁBITAT:  
UN ANÁLISIS MULTIESCALAR**

**TESIS**

**QUE PARA OBTENER EL GRADO DE DOCTOR EN CIENCIAS  
AGROPECUARIAS Y RECURSOS NATURALES**

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## Índice

|      |                                    |    |
|------|------------------------------------|----|
| I.   | RESUMEN.....                       | 6  |
| II.  | INTRODUCCIÓN GENERAL.....          | 8  |
| III. | CAPÍTULO 1 (PRIMER ARTÍCULO).....  | 11 |
| IV.  | CAPÍTULO 2 (SEGUNDO ARTÍCULO)..... | 31 |
| V.   | DISCUSIÓN GENERAL.....             | 60 |
| VI.  | REFERENCIAS.....                   | 65 |

## I. RESUMEN

El cambio de uso de suelo y el cambio climático están amenazando el mantenimiento de la biodiversidad a nivel global. Estos cambios ambientales afectan negativamente parámetros poblacionales como la distribución, abundancia o diversidad genética de muchas especies, incrementando su riesgo de extinción. Los anfibios y reptiles se encuentran entre los grupos de vertebrados más amenazados. El Eje Neovolcánico Transversal (ENT) es una de las provincias biogeográficas de México con mayor riqueza de especies, muchas de ellas endémicas; sin embargo, también es una de las zonas más perturbadas. En esta tesis evaluo la respuesta de la herpetofauna del ENT a los cambios en variables ambientales medidas a diferentes escalas espaciales. El primer capítulo analiza la distribución potencial (presente y futura) de las cinco especies de *Thamnophis* que se encuentran en el ENT y las variables (climáticas y de uso de suelo) más importantes que explican dicha distribución. Los hallazgos indican que las cinco especies responden negativamente al aumento de la cobertura de vegetación árida. Para *T. scalaris* y *T. scaliger*, la distancia al bosque de oyamel (*Abies religiosa*) fue la variable más importante: su probabilidad de ocurrencia disminuyó en sitios más alejados a estos bosques. Aunque una proporción mayoritaria de la distribución de estas especies se encuentra en el ENT, los resultados sugieren que todas las especies de *Thamnophis* sufrirán reducciones en sus distribuciones potenciales dentro de esta provincia biogeográfica en el futuro. Por lo tanto, este primer capítulo contribuye a entender la persistencia de este grupo herpetofaunístico ante un escenario de cambio ambiental. El segundo capítulo evalúa la abundancia y diversidad genética de una especie de salamandra (*Pseudoeurycea robertsi*) microendémica del Nevado de Toluca, y su respuesta a cambios en la cantidad y configuración del hábitat, a escala local y de paisaje. Este estudio demuestra

que la abundancia de *P. robertsi* está más estrechamente relacionada con variables locales y del paisaje que la diversidad genética. La cantidad de hábitat a nivel local (i.e. volumen de troncos caídos) fue el predictor más importante, y se asoció positivamente con la abundancia de individuos y el número de alelos. La configuración del paisaje que rodea a los sitios de muestreo también juega un papel importante. En particular, la densidad de borde tuvo un efecto negativo en todas las variables de respuesta. En ambos estudios, el bosque de oyamel tuvo una importancia clave; en el primero para la presencia de las culebras *T. scalaris* y *T. scaliger*, en el segundo ya que se trata del macrohábitat de la salamandra *P. robertsi*. La preservación de los bosques de oyamel con áreas núcleo bien conservadas y con elevada disponibilidad de troncos caídos debe ser considerada una prioridad de conservación en el ENT. En este sentido, esta provincia biogeográfica tiene la mayor extensión de bosques de oyamel del país (91%), y en este estudio se demuestra que la extensión de estos bosques se ha mantenido estable entre 2002 y 2011. Sin embargo, las nuevas políticas llevadas a cabo en los últimos años en materia ambiental, las cuales reducen las restricciones en áreas de gran importancia ecológica, comprometen potencialmente la preservación de estos bosques y de las especies que de ellos dependen a largo plazo.

**Palabras claves:** *Thamnophis*, *Pseudoeurycea robertsi*, modelado de nicho ecológico, diversidad genética, ecología del paisaje, *Abies religiosa*.

## II. INTRODUCCIÓN GENERAL

El cambio de uso de suelo y el cambio climático están amenazando el mantenimiento de la biodiversidad a nivel global (Newbold et al. 2016), alterando las comunidades, los ecosistemas y los servicios ambientales asociados a éstos (Parmesan & Yohe 2003, Cardinale et al. 2012). Las actividades productivas como la agricultura, la cría de ganado, la extracción de madera y la urbanización han transformado una gran proporción de la superficie del planeta (Foley et al. 2005). Estos cambios ambientales pueden afectar negativamente los parámetros poblacionales de muchas especies como la distribución, abundancia o diversidad genética (Hoffmann & Willi 2008, Ehrlén & Morris 2015), incrementando su riesgo de extinción.

Los anfibios son el grupo de vertebrados más amenazado (Catenazzi 2015) y sus poblaciones están disminuyendo rápidamente en todo el mundo (Stuart et al. 2004; Mendelson III et al. 2006, Eigenbrod et al. 2008), su baja vagilidad y restricciones fisiológicas los hace especialmente vulnerables a alteraciones en el ambiente (Huey 1982) como la pérdida del microhábitat térmicamente adecuado (Nowakowski et al. 2018). El 32.5% de las 5743 especies de anfibios descritas se encuentran amenazadas (Mendelson III et al. 2006). En cuanto a los reptiles, los declives de muchas poblaciones son similares a los que experimentan los anfibios en términos de amplitud taxonómica, distribución geográfica y gravedad (Gibbons et al. 2000).

México es uno de los cinco países más ricos en biodiversidad del mundo (Groombridge & Jenkins 2000); sin embargo, está sufriendo un rápido y extensivo cambio de uso de suelo (Mas et al. 2004) debido principalmente a la expansión de las actividades agropecuarias (Arredondo-León et al. 2008). Entre los años 1976 y 2000 más de 20,000 km<sup>2</sup>

de bosque templado fueron talados en el país (deforestación anual del 0.25%; Mas et al. 2004). Los bosques templados se distribuyen en áreas de gran elevación como el Eje Neovolcánico Transversal (ENT). Esta provincia biogeográfica está conformada por un conjunto de sistemas montañosos y volcanes de diferentes edades, alineados en una franja que cruza el territorio mexicano de este a oeste. Se trata de una zona de transición entre las regiones Neártica y Neotropical que resulta en un solapamiento de las biotas de ambas regiones (Suárez-Atilano 2015). Su historia geológica y su posición geográfica la convierten en una zona muy compleja con 30 tipos climáticos distintos y diferentes comunidades vegetales como los bosques de coníferas (*Pinus* sp. y *Abies religiosa*), bosques de encino (*Quercus* sp.), bosques mesófilos, pastizales alpinos, zonas de matorral subalpino y zonas de vegetación riparia (Espinoza & Ocegueda 2007). Por estos motivos, el ENT preserva una de las comunidades herpetofaunísticas más ricas del país y la más importante en número de especies endémicas de anfibios y reptiles (Flores-Villela & Canseco-Márquez 2007, Sunny et al. 2017). Desafortunadamente, es una de las zonas más perturbadas de México ya que contiene las mayores áreas urbanas del país (CONAPO 2010).

El objetivo general del trabajo fue entender la respuesta de la herpetofauna del ENT a los cambios en variables ambientales medidos a diferentes escalas espaciales. El primer caso de estudio se enfocó en un grupo de especies relacionadas taxonómicamente y con una distribución relativamente amplia por lo que las variables de respuesta que se utilizaron fueron registros de presencia, que son los más fáciles de obtener si queremos abarcar una extensión geográfica amplia. Para este estudio se utilizaron variables ambientales a 1 km de resolución, tanto climáticas como de uso de suelo, abarcando todo el Altiplano Mexicano. El objetivo consistió en determinar la distribución potencial presente y futura de las cinco

especies de *Thamnophis* que se encuentran en el ENT y las variables más importantes que explican su distribución, con el fin de evaluar la persistencia de este grupo herpetofaunístico ante un escenario de cambio ambiental. En el segundo caso se estudió un anfibio, la salamandra *Pseudoeurycea robertsi*. Esta especie tiene una distribución muy restringida, ya que es microendémica del Nevado de Toluca (un volcán del ENT). Para este estudio se utilizaron registros de abundancia y diversidad genética de toda su distribución geográfica y variables ambientales a gran resolución (10 metros). El objetivo fue evaluar la influencia relativa de la cantidad y configuración del hábitat, a escala local y de paisaje, en la abundancia y diversidad genética de *P. robertsi*.

### III. CAPÍTULO 1 (PRIMER ARTÍCULO)

Este artículo fue publicado en la revista *Peer J* el 11 de Abril de 2018.

([https://peerj.com/articles/4618/?utm\\_source=TrendMD&utm\\_campaign=PeerJ\\_TrendMD\\_1&utm\\_medium=TrendMD](https://peerj.com/articles/4618/?utm_source=TrendMD&utm_campaign=PeerJ_TrendMD_1&utm_medium=TrendMD))



## Present and future ecological niche modeling of garter snake species from the Trans-Mexican Volcanic Belt

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### ABSTRACT

Land use and climate change are affecting the abundance and distribution of species. The Trans-Mexican Volcanic Belt (TMVB) is a very diverse region due to geological history, geographic position, and climate. It is also one of the most disturbed regions in Mexico. Reptiles are particularly sensitive to environmental changes due to their low dispersal capacity and thermal ecology. In this study, we define the important environmental variables (considering climate, topography, and land use) and potential distribution (present and future) of the five *Thamnophis* species present in TMVB. To do so, we used the maximum entropy modeling software (MAXENT). First, we modeled to select the most important variables to explain the distribution of each species, then we modeled again using only the most important variables and projected these models to the future considering a middle-moderate climate change scenario (rcp45), and land use and vegetation variables for the year 2050 (generated according to land use changes that occurred between years 2002 and 2011). Arid vegetation had an important negative effect on habitat suitability for all species, and minimum temperature of the coldest month was important for four of the five species. *Thamnophis cyrtopsis* was the species with the lowest tolerance to minimum temperatures. The maximum temperature of the warmest month was important for *T. scalaris* and *T. cyrtopsis*. Low percentages of agriculture were positive for *T. eques* and *T. melanogaster* but, at higher values, agriculture had a negative effect on habitat suitability for both species. Elevation was the most important variable to explain *T. eques* and *T. melanogaster* potential distribution while distance to *Abies* forests was the most important variable for *T. scalaris* and *T. scaliger*. All species had a high proportion of their potential distribution in the TMVB. However, according to our models, all *Thamnophis* species will experience reductions in their potential distribution in this region. *T. scalaris* will suffer the biggest reduction because this species is limited by high temperatures and will not be able to shift its distribution upward, as it is already present in the highest elevations of the TMVB.

**Subjects** Conservation Biology, Zoology, Climate Change Biology, Environmental Impacts, Spatial and Geographic Information Science

**Keywords** Climate change, Environmental niche models, *Thamnophis*, Potential distribution, Land-use change

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## INTRODUCTION

Land use and climate change are affecting the abundance and distribution of species, altering biological communities, ecosystems, and their associated services to humans (Parmesan & Yohe, 2003; Cardinale et al., 2012; Kortsch et al., 2015; Nadeau, Urban & Bridle, 2017). Both factors are the main contributors to the global decline of reptiles (Ribeiro et al., 2009; Schneider-Maunoury et al., 2016; Sunny, González-Fernández & D'Addario, 2017). In fact, some studies indicate that 20% of the world's reptile species are threatened (Böhm et al., 2013) because they are particularly sensitive to environmental changes due to their low dispersal capacity and thermal ecology (Huey, 1982; Castellano & Valone, 2006; Ribeiro et al., 2009; Russildi et al., 2016). Studies predicting biological responses to land use and climate change are therefore necessary to assess the potential impacts of these changes and develop management decisions and conservation strategies (Jimenez-Valverde & Lobo, 2007; Nadeau, Urban & Bridle, 2017) to mitigate negative impacts. Information concerning species' distributions is essential in these cases (Liu, White & Newell, 2013). Through species occurrence data and environmental information, we can generate environmental niche models that can be used to predict the location of particular areas where environmental conditions are favorable for the presence of the species of study (Suárez-Atilano, 2015).

The Trans-Mexican Volcanic Belt (TMVB) is a set of mountain ranges and volcanoes of different ages, aligned on a strip that crosses Mexico from west to east. It is a transition area between Nearctic and Neotropical regions that results in an overlap of biotas from both regions (Suárez-Atilano, 2015). Its geological history and geographic position make it a very complex area with 30 distinct climatic types and several different vegetation communities, such as coniferous forests (*Pinus* sp. and *Abies* sp.), oak forests (*Quercus* sp.), mesophyll forests, alpine pastures, subalpine scrub, and riparian vegetation zones (Espinoza & Ocegueda, 2007). For these reasons, the TMVB has the second highest herpetological richness in Mexico and is the most important biogeographic region of the country in number of endemic amphibian and reptile species (Flores-Villela & Canseco-Márquez, 2007; Sunny, González-Fernández & D'Addario, 2017). Due to the complex characteristics of the TMVB, the montane taxa of this region have been exposed to a sky-island dynamic through climate fluctuations (Mastretta-Yanes et al., 2015), consequently, the high-altitude-adapted species could be especially vulnerable to climate change as they may be limited by future rising temperatures (Sunny, González-Fernández & D'Addario, 2017). Moreover, the TMVB is one of the most disturbed regions in the country as it contains the biggest metropolitan areas of Mexico (CONAPO, 2010; Sunny, González-Fernández & D'Addario, 2017).

Garter snakes are among the most abundant snake species in North America (Rossman, Ford & Seigel, 1996; De Queiroz, Lawson & Lemos-Espinal, 2002) and they are distributed from Canada to Costa Rica (Rossman, Ford & Seigel, 1996; Manjarrez, 1998; De Queiroz, Lawson & Lemos-Espinal, 2002). However, we lack information on the ecology and current conservation status of most *Thamnophis* species that are endemic to, or primarily distributed in, Mexico (Manjarrez, Venegas-Barrera & García-Guadarrama, 2007). They are also the most abundant snake genus in the TMVB (Flores-Villela, Canseco-Márquez

& Ochoa-Ochoa, 2010), thus they have an important ecological role in the ecosystem (Montoya, Pimm & Solé, 2006). These garter snakes also have great ecological plasticity in reproduction, feeding, and thermal ecology (Seigel, 1996).

For this study, we chose the five *Thamnophis* species that occur in the TMVB. *Thamnophis melanogaster* is endemic to the Mexican Central Plateau. It is a semiaquatic species that inhabits the edges of water bodies and specializes in underwater foraging, preying on aquatic animals such as fish, tadpoles and leeches (Rossman, Ford & Seigel, 1996). *Thamnophis scalaris* is endemic to high elevations across the TMVB (Rossman, Ford & Seigel, 1996). It lives in grasslands and the periphery of forests, and feeds mainly on earthworms, although it can eat vertebrates such as mice and lizards (Uribe-Peña, Ramírez-Bautista & Casas-Andreu, 1999; Manjarrez, Venegas-Barrera & García-Guadarrama, 2007). *Thamnophis scaliger* is a poorly-known montane species, endemic to central Mexico (Rossman, Ford & Seigel, 1996). It inhabits forests where it feeds on frogs, salamanders and lizards (Uribe-Peña, Ramírez-Bautista & Casas-Andreu, 1999). *Thamnophis cyrtopsis* extends from the southern United States to Guatemala, although is mainly distributed in Mexico (Hammerson, 2013). It is an amphibian specialist in aquatic habitats from subtropical deciduous and mixed forests (Rossman, Ford & Seigel, 1996). *Thamnophis eques* is widely distributed over the Mexican Plateau, reaching southern Arizona and New Mexico (Rossman, Ford & Seigel, 1996). It is a generalist predator because it feeds on both aquatic and terrestrial prey—mostly frogs, tadpoles, and fish, supplemented by lizards and mice (Drummond & Macías García, 1989; Manjarrez, 1998).

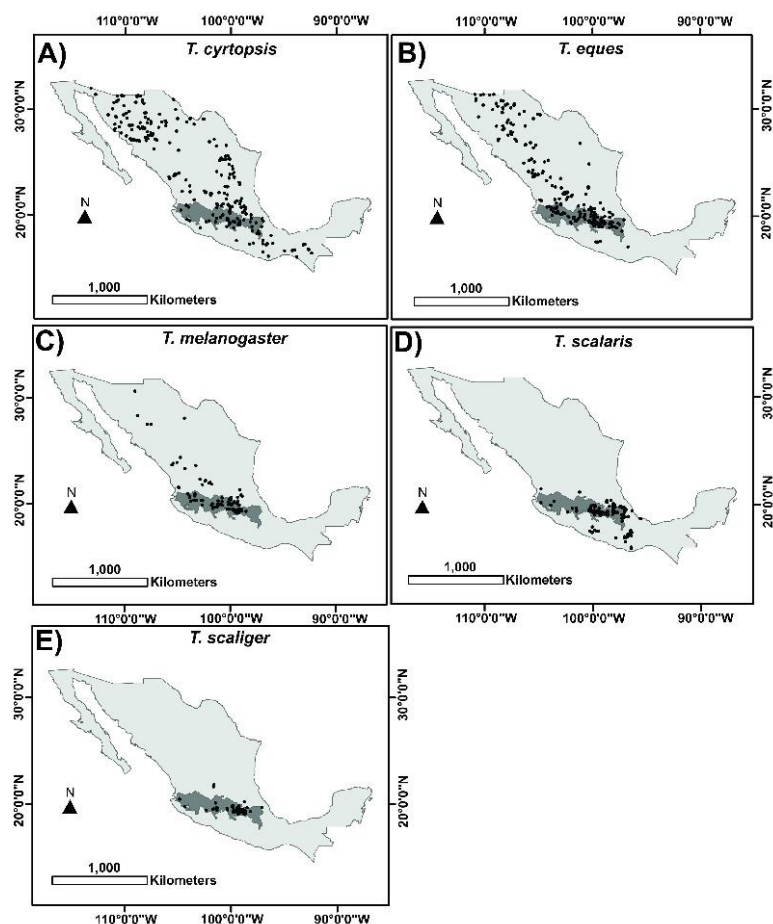
Despite their widespread distribution and relatively high abundance in comparison to other reptiles, this group has suffered critical reductions in the last 10 years (Canseco-Márquez & Mendoza-Quijano, 2007; Hammerson, 2013; Vázquez Díaz & Quintero Díaz, 2007; Hammerson, Vázquez Díaz & Quintero Díaz, 2007). Thus, knowledge regarding their ecological niche and their present and future potential distribution is key to better understanding the causes of their population decline. Moreover, due to the geological history and geographic position of the TMVB, the animals of this region constitute a cenocron (a group of animals originated in a defined area that have coexisted for a long period, thus sharing a common biogeographic history and a distribution pattern; Halffter & Morrone, 2017), therefore, changes in garter snake species' distributions in the TMVB may represent future changes in other species' distributions of this region. We expect that land use and climate change will reduce the future potential distribution of these five garter snake species (i.e., a reduction in the suitable area available for each species). In this study, we aimed to answer the following four questions. (1) Which climatic, topographic and land use variables determine each species' distribution? (2) Considering land use and climate change, what are the present and future potential distributions of each species? (3) What changes in suitable available area in the TMVB will each species undergo in the future? (4) What changes in suitable available area in the entire country will each species undergo in the future?

## MATERIALS AND METHODS

We modeled the potential distribution of the five *Thamnophis* species that occur in the TMVB (*T. cyrtopsis*, *T. eques*, *T. melanogaster*, *T. scalaris*, and *T. scaliger*). Occurrence records were obtained from fieldwork (60% or more; [Table S1](#)) and online databases such as Global Biodiversity Information Facility (GBIF) and iNaturalist. We selected only the records from the last 20 years for the analysis, as extensive land use changes occurred in Mexico during the 1990s ([FAO, 1993](#)) and we included some land use variables (such as extent of induced grasslands and agriculture areas) in the analysis. Maps of occurrence data for all five species were generated to check for obvious errors. We also filtered these data to eliminate duplicated observations from the same pixel (1-km resolution). We defined a polygon (background) for each species that represents the accessibility area ([Suárez-Atilano, Burbrink & Vázquez-Domínguez, 2014](#); [Suárez-Atilano et al., 2017](#)). These polygons were generated considering biogeographic regions with geographical records or records near their borders ([Sunny, González-Fernández & D'Addario, 2017](#)). Three of the species are endemic to Mexico and the other two have only a marginal distribution outside the country ([Rossman, Ford & Seigel, 1996](#); [Hammerson, 2013](#)), therefore all polygons are large representative regions of species distribution ranges. We obtained bioclimatic variables from WorldClim ([Hijmans et al., 2005](#)); topographic and land cover variables were obtained from the National Institute of Statistics and Geography ([INEGI, 2013](#)). We reclassified the land use map (series V, 1:250,000, generated during the period 2011 to 2013; [INEGI, 2013](#)) in different exclusive classes that were converted to raster and transformed from categorical to continuous using a resample method that averages the value of the surrounding pixels to assign a new value to each pixel. All layers were processed in a raster format, with 1-km resolution, using ARC GIS 10.5 and the packages RASTER ([Hijmans, 2016](#)) and RGDAL ([Bivand, Keitt & Rowlingson, 2017](#)) for R software (version 3.4.0; [R Development Core Team, 2017](#)). After a bibliographic review and Pearson correlation analysis to discard highly correlated variables ( $R^2 > 0.8$ , [Suárez-Atilano, 2015](#)) we selected the following variables: elevation, percent natural grasslands, percent human-induced grasslands, percent arid vegetation, percent *Pinus* forest, distance to *Pinus* forest, percent *Quercus* forest, distance to *Quercus* forest, percent *Abies* forest, distance to *Abies* forest, distance to water sources, percent agriculture, minimum temperature of the coldest month, maximum temperature of the warmest month, precipitation of the wettest month, and precipitation of the driest month.

We used the maximum entropy modeling software (MAXENT; [Phillips, Anderson & Schapire, 2006](#)) which estimates species' distributions by finding the distribution of maximum entropy (the most spread out, or closest to uniform), subject to constraints imposed by a known distribution of the species, and by the environmental conditions across the study area ([Anderson & González Jr, 2011](#)). First, we ran the model for each species in MAXENT with 10 replicates and we selected the most important variables that explained the distribution of each species ([Anderson, Lew & Peterson, 2003](#); [Chefaoui, Hortal & Lobo, 2005](#); [Suárez-Atilano et al., 2017](#)). We only used linear and quadratic features because we had less than 80 records of *T. scaliger* ([Merow, Smith & Silander, 2013](#)) and, for an easier

comparison, we used the same methodology for all species. All analyses were performed using the logistic output for an easier interpretation and a convergence threshold of  $1 \times 10^{-5}$  with 500 iterations (Pearson, 2007; Suárez-Atilano, 2015). We modeled again, this time with only the most important variables for each species (Guisan & Zimmerman, 2000; Guisan & Thuiller, 2005; Araujo & Guisan, 2006) and projected these models to the future using both clumping (restricting the variables to the range of values encountered during model calibration) and extrapolation methods (Merow, Smith & Silander, 2013). We obtained the future bioclimatic variables CCSM4 for the year 2050 considering the climate change scenario rcp45 (middle-moderate) from WorldClim. Land use and vegetation variables for the year 2050 were generated using the module LAND CHANGE MODELER FOR ECOLOGICAL SUSTAINABILITY in IDRISI SELVA 17.0 software (Clark Labs, 2012) and land use and vegetation layers from years 2002 and 2011 (series III and V; INEGI, 2005; INEGI, 2013). We also used elevation, slope (obtained from the elevation layer), and distance to urban settlements, for a better prediction of land use change. We designated present urban areas (from the present distribution maps) and future urban areas (from the future distribution maps) as areas of zero habitat suitability. We did not include distance to urban areas as a variable in the models because this can generate a bias, as these areas are more easily accessed by observers (Araujo & Guisan, 2006). We generated present and future potential distribution maps for each species. We preferred to show the continuous maps because binary outputs can obscure important biological detail (Liu, White & Newell, 2013). To evaluate model performance, we used partial Receiving Operating Characteristic (partial ROC) analyses (Peterson, Papes & Soberón, 2008; Osorio-Olvera, 2016) as recommended based on criticisms of area under the curve analyses (AUC) (Lobo, Jiménez-Valverde & Real, 2008; Peterson, Papes & Soberón, 2008). While AUC evaluates only the environmental niche model (under the omission-commission framework) performance, partial-ROC allows for statistical significance from the AUC itself, based on a null distribution of expectations created via bootstrapping replacement of 50% of the total available points and 1,000 resampling replicates (Suárez-Atilano, 2015). One-tailed significance of the difference between AUC and the null expectations was assessed by fitting a standard normal variate (the z-statistic) and calculating the probability that the mean AUC ratio was  $\leq 1$ . We used 75% of occurrence localities for model training and 25% for model testing (Suárez-Atilano, 2015). We used the platform NICHE TOOLBOX for partial-ROC calculations (Osorio-Olvera, 2016). We generated the species potential distribution binary maps using Max SS threshold (Liu, White & Newell, 2013), a threshold selection method based on maximizing the sum of sensitivity and specificity. This is considered an adequate method to use when reliable absence data are unavailable (Liu, White & Newell, 2013). For each species, we used these binary maps to calculate the present and future high-suitability areas (Suárez-Atilano, 2015) in both all of Mexico, and the TMVB only, to assess whether the distribution of each species will decrease or increase in the future.



**Figure 1** Occurrence records used to build the distribution model for each *Thamnophis* species, showing the Trans-Mexican Volcanic Belt (TMVB) in dark gray.

[Full-size !\[\]\(1ac7c971e7df5bf204fbb84fd617a50a\_img.jpg\) DOI: 10.7717/peerj.4618/fig-1](https://doi.org/10.7717/peerj.4618/fig-1)

## RESULTS

After filtering the data, we worked with 267 records of *T. cyrtopsis* (Fig. 1A), 274 of *T. eques* (Fig. 1B), 103 of *T. melanogaster* (Fig. 1C), 186 of *T. scalaris* (Fig. 1D), and 76 of *T. scaliger* (Fig. 1E). The most important variables for each *Thamnophis* species are summarized in Table 1. In all cases these variables together explained 60% or more of the species' potential distribution. It is important to note that arid vegetation had an important negative effect

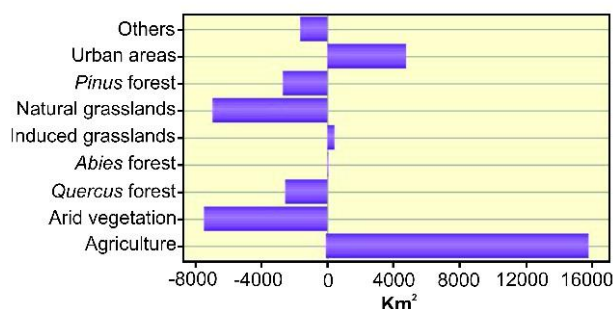
**Table 1** Contribution percent of the most important variables that explain the distribution of each *Thamnophis* species.

| Variables                                | <i>T. cyrtopsis</i> | <i>T. eques</i> | <i>T. melanogaster</i> | <i>T. scalaris</i> | <i>T. scaliger</i> |
|------------------------------------------|---------------------|-----------------|------------------------|--------------------|--------------------|
| Minimum temperature of the coldest month | 33.7                | 19.2            | 11.3                   |                    | 26.5               |
| Maximum temperature of the warmest month | 5.2                 |                 |                        | 36                 |                    |
| Elevation                                |                     | 28.4            | 27.3                   |                    |                    |
| Arid vegetation                          | 26.4                | 15.6            | 11.5                   | 4.9                | 5.3                |
| Agriculture                              |                     | 9.6             | 12.9                   |                    |                    |
| Distance to <i>Quercus</i> forest        | 8.5                 |                 |                        |                    |                    |
| Distance to <i>Abies</i> forest          |                     |                 |                        | 44.9               | 40.6               |
| Total                                    | 73.8                | 72.8            | 63                     | 85.8               | 72.4               |

on habitat suitability for all species (Fig. S1) and the minimum temperature of the coldest month was important in four of the five models. This latter variable was the most important to explain *T. cyrtopsis* potential distribution, which was the species with the lowest tolerance to minimum temperatures (5 °C). Habitat suitability for *T. scalaris* and *T. cyrtopsis* steadily decreased when maximum temperatures increased. Low agriculture percentages were positive for *T. eques* and *T. melanogaster* but, at higher values (above 30%), agriculture had a negative effect on habitat suitability for both species. Elevation was the most important variable to explain *T. eques* and *T. melanogaster* potential distribution. It was a positive variable for *T. melanogaster*, while habitat suitability for *T. eques* was optimal near 2,500 m above sea level (masl). Distance to *Abies* forests was the most important variable to explain *T. scalaris* and *T. scaliger* potential distribution. It had negative effects on these species (as distance to *Abies* forests increase, habitat suitability decrease), which means that proximity to *Abies* forests was positive for both species. Distance to *Quercus* forests had a negative effect on habitat suitability for *T. cyrtopsis*, which means that proximity to these forests was positive for the species.

Between 2002 and 2011, there was an increase of almost 16,000 km<sup>2</sup> in agriculture and about 5,000 km<sup>2</sup> in urban areas (Fig. 2). There was also an increase in human-induced grasslands. A reduction in arid vegetation and natural grasslands occurred, mainly because of its conversion to agriculture lands. The area of *Pinus* and *Quercus* forests also fell, but *Abies* forests held steady. For the year 2050, an increase of 82,865 km<sup>2</sup> in agriculture areas is expected according to the model (Figs. 3A, 3B). The urban areas will increase by 20,392 km<sup>2</sup> (Figs. 3C 3D), most of it taking place in the area around Toluca city (Figs. 3C, 3D), and induced grasslands will increase by 24,796 km<sup>2</sup> (Figs. 3E, 3F). Potential distribution maps for each species are in Figs. 4A–4J. We found no differences in future projections between extrapolation and clumping methods. Partial-ROC bootstrap tests showed significant ratio values of empirical AUC over null expectations (mean AUC ratios  $\geq 1.5$  and *p*-values  $< 0.001$  in all cases; Fig. S1).

All species had a high proportion of their potential distribution in the TMVB. However, according to high-suitability area calculations for present and future, all *Thamnophis* species will experience reductions in their distribution in this region (Table 2). *T. scaliger* was only distributed in the TMVB, while *T. scalaris* had a small part of its potential distribution in the Sierra Madre del Sur. *T. cyrtopsis*, *T. eques*, and *T. melanogaster* were



**Figure 2** Land use change by category (km<sup>2</sup>) between years 2002 and 2011.

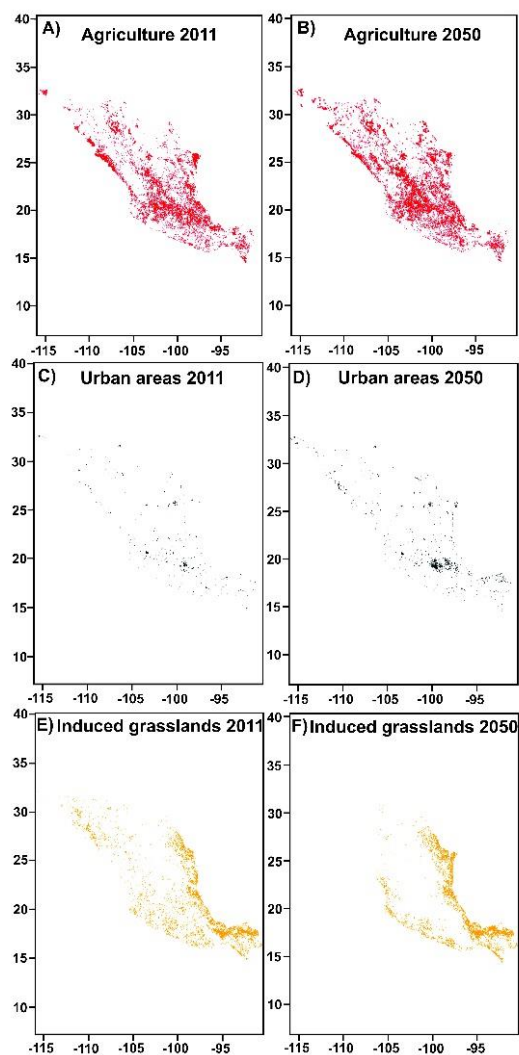
Full-size [DOI: 10.7717/peerj.4618/fig-2](https://doi.org/10.7717/peerj.4618/fig-2)

also distributed in the Sierra Madre Occidental, Sierra Madre Oriental, Sierra Madre del Sur, and Oaxaca mountain ranges. Unlike the TMVB, these biogeographic regions will not suffer important reductions in suitable habitat for *T. eques* and *T. melanogaster* in the future. *T. cyrtopsis* will suffer important reductions in all its potential distribution, which also includes Chiapas Highlands. The potential distribution of *T. melanogaster* will increase in the future, considering the entire country, and *T. scalaris* will suffer the biggest reduction of the five species (reductions of 54.08% for the TMVB, and 54.30% for all of Mexico, Table 2; Figs. 4A–4J).

## DISCUSSION

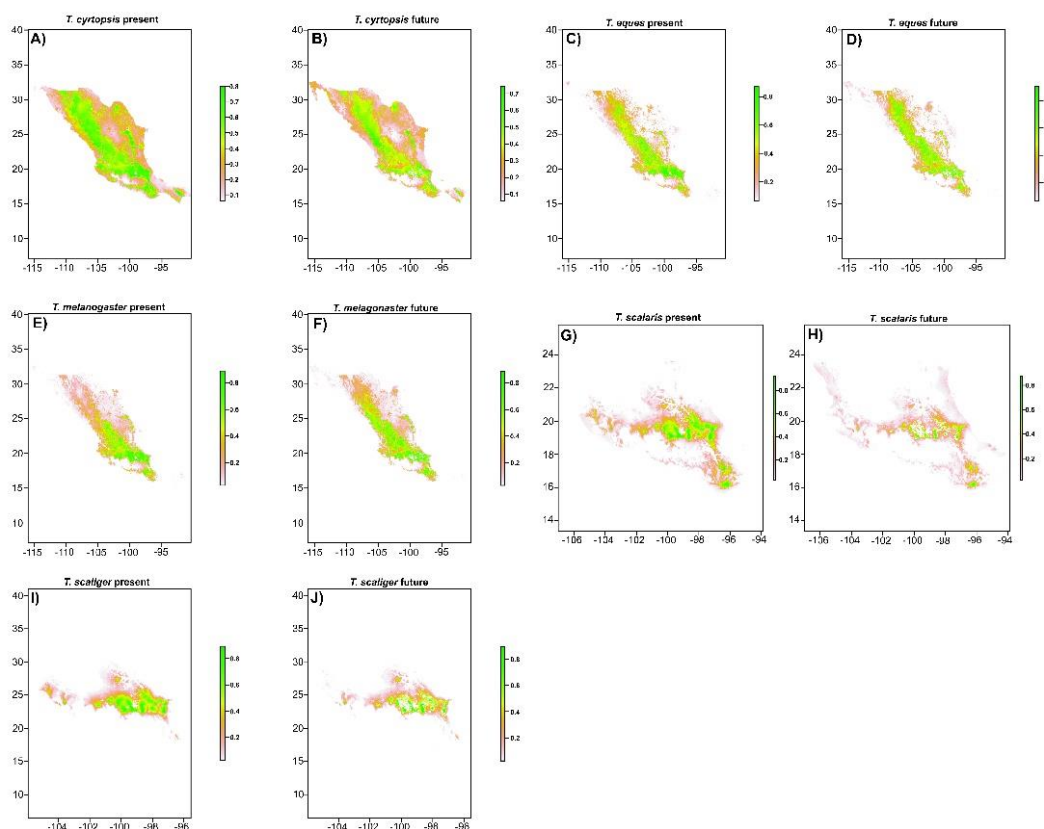
### Environmental variables

Although current records and literature support the idea that grasslands and water sources are essential for *Thamnophis* species in Mexico (Jones, 1990; Manjarrez & Drummond, 1996; Venegas-Barrera & Manjarrez, 2011), these variables were not selected by the model as important to explain the distribution of the species. Both variables are more related to the microhabitat of the species, but for this study, we modeled the macrohabitat. Although most records of *Thamnophis* are in grasslands or near water sources (lakes, ponds and streams), these habitat features are present throughout most of the country, including areas where the species is not present, therefore, these variables are not limiting the species at a macro level. The percent of arid vegetation (which can be interpreted as the opposite of water sources) was a negative limiting factor for all species (Table 1). Distances to forests were more important for explaining the presence of *Thamnophis* species than the percent of these forests. This was especially important for *T. scalaris* and *T. scalariger* as distance to *Abies* forest was the most important variable determining their potential distribution. These results are consistent with our fieldwork observations, as we found only a few individuals inside forests; the majority were found in grasslands near coniferous forests. This could be because coniferous forests occur in a moist (1,000–3,800 mm annual precipitation) and cold microclimate (2°–24 °C; Sáenz-Romero et al., 2012; Sunny, González-Fernández &



**Figure 3** Present (2011) and future (2050) maps of (A, B) agriculture, in red; (C, D) urban, in gray; and (E, F) induced grasslands, in orange.

Full-size [DOI: 10.7717/peerj.4618/fig-3](https://doi.org/10.7717/peerj.4618/fig-3)



**Figure 4** Present (2011) and future (2050) potential distribution maps for each *Thamnophis* species: (A, B) *T. cyrtopsis*, (C, D) *T. eques*, (E, F) *T. melanogaster*, (G, H) *T. scalaris* and (I, J) *T. scaliger*.

Full-size [DOI: 10.7717/peerj.4618/fig-4](https://doi.org/10.7717/peerj.4618/fig-4)

*D'Addario, 2017*) that is preferred by *Thamnophis* species (*Manjarrez & Drummond, 1996*). Therefore, microclimatic conditions of grasslands surrounded by forests and large areas of grasslands without forest, may be different. Grasslands surrounded by forests offer the climatic benefits of forests (moist and cold), and the food benefits of grasslands (higher availability of small prey; (*Bastos, Araújo & Silva, 2005; Reinert et al., 2011; Wittenberg, 2012; Mociño Deloya, Setser & Pérez-Ramos, 2014*).

Low percent of agriculture was positive for *T. eques* and *T. melanogaster*, but a high percent was negative for both species. This could be because agriculture is a tradeoff for many reptile species, especially snakes. It provides benefits for them, such as higher prey

**Table 2** Present and future high suitability area (km<sup>2</sup>) and percent of reductions in these areas for each *Thamnophis* species in Mexico and the Trans-Mexican Volcanic Belt (TMVB).

|                        | MEXICO                                  |                                        |               | TMVB                                    |                                        |               |
|------------------------|-----------------------------------------|----------------------------------------|---------------|-----------------------------------------|----------------------------------------|---------------|
|                        | Present distribution (Km <sup>2</sup> ) | Future distribution (Km <sup>2</sup> ) | Reduction (%) | Present distribution (Km <sup>2</sup> ) | Future distribution (Km <sup>2</sup> ) | Reduction (%) |
| <i>T. cyrtopsis</i>    | 661,888.53                              | 387,393.67                             | 41.47         | 103,190.15                              | 56,172.18                              | 45.56         |
| <i>T. eques</i>        | 583,936.04                              | 554,336.36                             | 5.07          | 102,001.64                              | 88,928.44                              | 12.82         |
| <i>T. melanogaster</i> | 255,647.78                              | 317,411.39                             | -24.16        | 83,237.55                               | 67,581.46                              | 18.81         |
| <i>T. scalaris</i>     | 110,441.63                              | 50,474.08                              | 54.30         | 54,057.65                               | 24,825.27                              | 54.08         |
| <i>T. scaliger</i>     | 58,682.16                               | 37,278.67                              | 36.47         | 42,804.76                               | 26,617.94                              | 37.82         |

availability, but also exposes them to human interactions (i.e., people kill *Thamnophis* out of fear even though these species are not dangerous to humans; [Sunny et al., 2015](#)). Moreover, the persistent practice of crop burning and use of roller-chopping to prepare fields also affect their populations ([Mullin & Seigel, 2009](#)).

Environmental temperature is important for ectothermic species like garter snakes because they are more active when they can maintain a body temperature above approximately 22 °C ([Manjarrez & Drummond, 1996](#)). Environmental temperature increases may lead *Thamnophis* to physiological stress that results in reduced fitness ([Peterson, Gibson & Dorcas, 1993](#)). The fact that *T. cyrtopsis* was limited by low and high temperatures could be the cause of its reduced potential distribution. The maximum temperature of the warmest month was one of the most important variables explaining *T. scalaris* potential distribution; however, for all other species, the minimum temperature of the coldest month was more important. This may be because *T. scalaris* is the species occurring at the highest elevation and, consequently, is adapted to a colder climate. Therefore, while other species are more limited by lower temperatures, *T. scalaris* is more limited by higher ones, which could make this species more vulnerable to warming temperatures associated with climate change. This scenario is consistent with the future distribution model for this species as *T. scalaris* suffered the biggest reduction of the five species. The fact that its distribution already includes the existing areas with the highest altitude implies that, as climate change progresses, this species will be limited in its ability to shift its distribution upward, increasing the possibility of becoming extinct ([Sunny, González-Fernández & D'Addario, 2017](#)). According to the International Union for Conservation of Nature (IUCN), *T. scalaris* is considered a species of Least Concern ([Canseco-Márquez & Mendoza-Quijano, 2007](#)); however, our results suggest that this risk category is likely to change in the future.

### Present and future potential distribution

The potential distribution of all species was located at high elevation areas (mountain ranges), which is consistent with the biology of this genus ([Rossman, Ford & Seigel, 1996](#)). The fact that all species had a high proportion of their potential distribution in the TMVB means that this is a very important biogeographic region for the conservation of these five *Thamnophis* species. This is especially applicable for *T. scalaris* and *T. scaliger* as their

suitable habitat was mainly found in the TMVB. However, according to our models, all species will suffer large reductions in their potential distribution in the TMVB, while in other regions some species like *T. eques* and *T. melanogaster* will not. This may be because the TMVB is one of the most disturbed regions as it contains the largest extent of urban area in Mexico (CONAPO, 2010). Considering the entire country, all species will suffer reductions in their potential distributions in the future except *T. melanogaster*. We are surprised by this fact, as this species is the most threatened of the five, according to the IUCN (Endangered, Vázquez Díaz & Quintero Díaz, 2007). This species is more aquatic than the others (Manjarrez & Drummond, 1996) and so an approach that considers both macrohabitat and microhabitat variables (such as water source and quality) may be necessary for a better prediction of *T. melanogaster* potential distribution.

### Conclusions and conservation implications

Arid vegetation has an important negative effect on habitat suitability for all species, and the minimum temperature of the coldest month is important for four of the five species. *T. cyrtopsis* has the lowest tolerance to minimum temperatures. Maximum temperature of the warmest month is important for *T. scalaris* and *T. cyrtopsis*. Low percentages of agricultural areas are positive for *T. eques* and *T. melanogaster* but at higher values agriculture has a negative effect on habitat suitability for both species. Elevation is the most important variable to explain *T. eques* and *T. melanogaster* potential distribution while distance to *Abies* forests is the most important variable to explain *T. scalaris* and *T. scalaris* potential distribution. As we predicted, all *Thamnophis* species will experience reductions in their distributions in the TMVB, however, for the entire country, *T. melanogaster* seems to increase its distribution in the future. We feel more studies should be conducted to evaluate *T. melanogaster* distribution and abundance. These studies should consider microhabitat variables such as water source and their quality. We also consider it essential to carry out studies of *T. scalaris* abundance, as this species will suffer the biggest reduction in potential distribution of the five species. Current abundance data of this species will be key to deciding if a change in its conservation status is needed. We are especially concerned about our finding that a relatively abundant species like *T. scalaris* may suffer severe reductions in its potential distribution, as this suggests that reptile species with similar distributions (such as the lizard *Barisia imbricata*; Sunny, González-Fernández & D'Addario, 2017) may undergo similar reductions. For less abundant species with similar distributions (such as the rattlesnake *Crotalus triseriatus*; Sunny et al., 2015), even larger reductions may result. Reductions in suitable area available for *Thamnophis* and other species will cause the reduction and isolation of their populations. Small populations are susceptible to demographic stochasticity (Gibbs, 1998; Hicks & Pearson, 2003) that can convert normal population fluctuations into local extinctions (Gibbs, 1998). Moreover, while certain isolation levels between populations may facilitate precise evolutionary adaptations to local conditions (Tschamtker et al., 2012), the high isolation levels affecting populations of many species in the TMVB, which are expected to increase in the future and that are limiting species distributions to the highest altitudes of the volcanoes, will lead to important losses of genetic diversity in these populations, thereby affecting their capacity

to cope with environmental changes and increasing their susceptibility to extinction (Johansson, Primmer & Merila, 2006; Sunny et al., 2014).

The TMVB has the highest area of *Abies* forests (91.14%) of the country (Sunny, González-Fernández & D'Addario, 2017); however, it only represents 1.10% of TMBV area (Sunny, González-Fernández & D'Addario, 2017). Unfortunately, governmental laws have recently changed the protection status of some areas of the TMVB, like the Nevado de Toluca Volcano (DOF, 2013). This change could lead to logging and changes in land use (Mastretta-Yanes et al., 2014). The extent of *Abies* forests have held steady from 2002 to 2011 (Fig. 2) but we are afraid this could change as a consequence of this new protection status, thus affecting *Thamnophis* populations and many other species. Moreover, land use changes are expected to accelerate due to climate change (Madsen & Wilson, 2011; Urban, 2015; Nadeau, Urban & Bridle, 2017) so garter snakes and other species of the TMVB could suffer the synergistic effect of both factors. The process of reversing climate change involves world-wide economic systems and government decisions, so there is little we can say about this here. However, we consider the conservation of TMVB forests, especially *Abies* forests and grasslands associated with them, of great importance for the conservation of many reptile and amphibian species that live in this region (Figueroa-Rangel, Willis & Olvera-Vargas, 2010; Vargas-Rodríguez et al., 2010; Ponce-Reyes et al., 2012; Bryson et al., 2014). Moreover, in the short term, we think is essential to implement environmental education activities to teach everyone the importance of our natural environments. This in turn may lead to fewer reptiles being killed out of fear, and use of fewer wildlife-destructive agricultural practices such as roller chopping and crop burning.

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## Competing Interests

The authors declare there are no competing interests.

## Author Contributions

- Andrea González-Fernández and Armando Sunny conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Javier Manjarrez conceived and designed the experiments, contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, approved the final draft.
- Uri García-Vázquez contributed reagents/materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Maristella D'Addario conceived and designed the experiments, authored or reviewed drafts of the paper, approved the final draft.

## Data Availability

The following information was supplied regarding data availability:

The raw data is provided as a [Supplemental File](#).

## Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.4618#supplemental-information>.

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#### IV. CAPÍTULO 2 (SEGUNDO ARTÍCULO)

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1    **Local and landscape drivers of the abundance and genetic diversity of a**

2    **microendemic and critically endangered salamander**

3

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40

41 **Abstract**

42 *Context* Conversion of forest ecosystems to human-modified landscapes threatens the  
43 persistence of forest-specialist species. Yet, the local and landscape drivers of the  
44 abundance and genetic diversity of these species are largely unknown, especially for  
45 elusive and critically endangered species, such as the salamander *Pseudoeurycea robertsi* –  
46 a species microendemic to the Nevado de Toluca volcano, Mexico.

47 *Objectives* To assess the relative influence of local- and landscape-scale habitat amount and  
48 habitat spatial configuration on the abundance and genetic diversity of *P. robertsi*. Given  
49 the low vagility of the species, we expected stronger responses to local habitat amount than  
50 to landscape variables, with habitat configuration showing the weakest effects on all  
51 responses.

52 *Methods* Using multiscale and multimodel inference approaches, we tested the relative  
53 effect of local habitat amount (fallen logs volume), landscape habitat amount (forest cover)  
54 and landscape configuration (forest edge density and forest fragmentation per se) on the  
55 abundance and genetic diversity of *P. robertsi*.

56 *Results* The abundance of individuals was more strongly related to local and landscape  
57 variables than genetic diversity. As predicted, local habitat amount showed stronger  
58 positive effects on salamander abundance and number of alleles than forest cover. Yet, all  
59 response variables also increased in landscapes with higher fragmentation and lower edge  
60 density (i.e., larger core areas).

61 *Conclusions* Fallen logs volume is a major driver of this (and potentially others) forest-  
62 specialist salamanders. Yet, landscape configuration also shapes salamander populations,

63 especially the number of individuals. Retaining fallen logs in forests and increasing forest  
64 core areas are critical for salamander conservation.

65 **Keywords:** Plethodontidae, splitting index, Trans-Mexican Volcanic Belt, genetic  
66 diversity.

67

## 68 **Introduction**

69 Productive activities such as agriculture, cattle ranching, timber extraction, and  
70 urbanization have transformed a large proportion of the planet's land surface (Foley et al.  
71 2005). In fact, deforestation between 2000 and 2012 resulted in the loss of 2.3 million km<sup>2</sup>  
72 of tree cover (Hansen et al. 2013). These land use changes are threatening the maintenance  
73 of global biodiversity (Newbold et al. 2016), and is causing rapid changes in the  
74 composition and configuration of terrestrial landscapes (Fahrig et al. 2011). Landscape  
75 changes are also typically followed by a number of local disturbances, such as edge effects  
76 (i.e., biotic and abiotic changes at habitat edges) and resource exploitation (e.g., hunting,  
77 logging) by human populations (Laurance et al. 2002; Tuff et al. 2016; Arroyo-Rodríguez  
78 et al. 2017). These local and landscape disturbances are expected to have stronger effects  
79 on forest-specialist species (Laurance 1991; Kouki 2001; Tuff et al. 2016; Pfeifer et al.  
80 2017), but this topic remains poorly understood, especially for elusive species, such as most  
81 amphibians.

82 Amphibians are among the most threatened vertebrates on Earth (Catenazzi 2015),  
83 and their populations are rapidly declining worldwide, mainly due to the loss and  
84 degradation of their natural habitats (Stuart et al. 2004; Eigenbrod et al. 2008).

85 Salamanders, like other low-vagility ectotherms, are highly vulnerable to local-scale  
86 disturbances, such as the loss of thermally suitable habitat (Nowakowski et al. 2018).  
87 Salamanders are important as top-down controls of many invertebrates, and can also be a  
88 source of high energy prey for other predators (Davic and Welsh 2004). They can also  
89 provide an important indirect regulatory role in the processing of detritus-litter by ingestion  
90 of detritivore prey (Davic and Welsh 2004). Although many species are narrowly  
91 distributed, salamanders can represent an important proportion of the vertebrate biomass in  
92 old-growth forests (Davic and Welsh 2004). In temperate ecosystems, terrestrial  
93 salamanders prefer areas with high relative moisture like *Abies*, *Pinus* and *Pinus-Quercus*  
94 forests, which provide important microhabitats, such as fallen logs, which are particularly  
95 used by the Plethodontidae family for shelter (Sánchez-Jasso et al. 2013). Landscape-scale  
96 disturbances can also shape amphibian communities (e.g., Skelly et al. 1999; Lowe and  
97 Bolger 2002; Van Buskirk 2005; Russildi et al. 2016), but the relative effect of local vs.  
98 landscape disturbances on salamanders is not well understood. In fact, some studies of  
99 salamanders assess the association between landscape structure and population genetics  
100 (Spear et al. 2005; Wang et al. 2009; Savage et al. 2010; Velo-Antón et al. 2013), but they  
101 are focused on genetic responses to landscape connectivity, overlooking other potential  
102 local and landscape predictors of genetic diversity, such as habitat amount. Filling this gap  
103 of information is critically needed to improve conservation strategies.

104 Mexico is within the five biologically richest countries in the world (Groombridge  
105 and Jenkins 2000), but it is suffering rapid and extensive land use changes (Mas et al.  
106 2004), especially for the expansion of agricultural lands (Arredondo-León et al. 2008).  
107 Between 1976 and 2000, more than 20,000 km<sup>2</sup> of temperate forests were cleared in

108 Mexico (annual deforestation rate = 0.25%; Mas et al. 2004). Temperate forests are  
 109 distributed in high elevation areas, such as the Trans-Mexican Volcanic Belt, which  
 110 preserves one of the most species-rich herpetological communities in Mexico, and the most  
 111 important in terms of endemic amphibian species (Flores-Villela and Canseco-Márquez  
 112 2007; Sunny et al. 2017). Unfortunately, it is one of the most disturbed regions of the  
 113 country due to the expansion of big cities, such as Mexico City, Puebla and Toluca  
 114 (CONAPO 2010; González-Fernández et al. 2018).

115         Here, we assessed the relative influence of local- and landscape-scale habitat  
 116 amount and habitat spatial configuration (i.e., forest fragmentation per se and forest edge  
 117 density) on the abundance and genetic diversity of *Pseudoeurycea robertsi*. This little-  
 118 known salamander of the Plethodontidae family is classified as Critically Endangered, and  
 119 is microendemic to the Nevado de Toluca volcano (SEMARNAT 2010; IUCN SSC  
 120 Amphibian Specialist Group 2016), located in the Trans-Mexican Volcanic Belt. This  
 121 species inhabits fallen logs, where it finds refuge and food (Bille 2009). Given its low  
 122 vagility, we expect stronger responses to local habitat amount (i.e., fallen logs volume) than  
 123 to landscape structure (Miguet et al. 2016). Yet, as this is a forest-specialist species (Davie  
 124 and Welsh 2004), when assessing the effect of landscape-scale patterns, we expect stronger  
 125 responses to forest cover (a proxy of landscape-scale habitat amount) than to forest spatial  
 126 configuration (Fahrig 2003; Jackson and Fahrig 2016). If forest fragmentation is relevant  
 127 for this species, we could expect either positive or negative effects. Positive effects are  
 128 predicted because mean inter-patch isolation distance typically decreases with increasing  
 129 fragmentation per se, thus favoring dispersal movements across the landscape (Fahrig 2003,  
 130 2017; Jackson and Fahrig 2016). Yet, fragmentation also increases edge-affected habitats in

131 the landscape, and this forest-interior specialist can be negatively affected by the abiotic  
132 changes (e.g. lower relative humidity and higher temperature) that usually occur at forest  
133 edges (Arroyo-Rodríguez et al. 2017). In this sense, we predicted that forest edge density  
134 can have negative effects on the abundance and genetic diversity of salamanders.

135

## 136 **Methods**

### 137 **Study area**

138 We conducted this study in the Nevado de Toluca volcano (18°59'- 19°18'N, 99°40'-  
139 99°59' W), the fourth highest peak in Mexico (Bille 2009), located in the Trans-Mexican  
140 Volcanic Belt at 22 km of southwest Toluca city. The region has a temperate semi-cold  
141 climate, with precipitations during the summer and an average annual temperature ranging  
142 between 5 and 12 °C. Annual precipitation averages 1200-1800 mm (CONABIO 2000).  
143 The dominant land cover types of the volcano are old-growth and secondary forest patches  
144 of fir (*Abies religiosa*) and pine (*Pinus hartwegii* and *P. pseudostrobus*). There are also  
145 broad-leaved forests (oak and alder) in a lower extent, at the eastern part of the volcano,  
146 and alpine grasslands at the highest elevations. There is an important extension of  
147 agricultural lands in addition to induced grasslands and human settlements (Franco-Maass  
148 et al. 2006). Between 1972 and 2000, *Abies* forests experienced an important recovery,  
149 whereas *Pinus* forest cover had decreased by 40% due to timber extraction for commercial  
150 purposes (Franco-Maass et al. 2006). The Nevado de Toluca volcano is considered a  
151 priority terrestrial region for biodiversity conservation (CONABIO 2000), and was declared  
152 a National Park in 1936, although the Mexican Government has recently changed this  
153 highly restrictive protection category to a less restrictive one (DOF 2013) – a controversial

154 decision that could lead to further degradation of the last well-preserved *Abies* forests  
155 (Mastretta-Yanes et al. 2014).

156

#### 157 Experimental design

158 We sampled 14 forest sites distributed across the volcano, all located in *Abies-Pinus* forest,  
159 between 2850 and 3450 m asl (Fig. 1). We used a site-landscape approach; i.e., response  
160 variables were recorded in equal-sized sample sites, and landscape variables were measured  
161 within different-sized and concentric buffers from the geographic center of these sample  
162 sites (Fahrig 2013). We considered buffers of 10, 50, 100, 200, 300, 400 and 500 ha to  
163 assess the scale of effect, i.e., the spatial extent that yields the strongest response-landscape  
164 relationship (Fahrig 2013; Jackson and Fahrig 2015; Miguet et al. 2016). The smallest  
165 landscape size (10 ha) was selected because salamanders have low dispersion capacity  
166 (Petranka et al. 1993), which can decrease the scale of effect (Miguet et al. 2016). To avoid  
167 pseudoreplication problems, we located each study site isolated enough to avoid spatial  
168 overlap between landscapes (Eigenbrod et al. 2011; Fig. 1).

169

#### 170 Salamander sampling and response variables

171 We sampled salamanders via visual encounter surveys (sensu Crump and Scott 1994). As  
172 there is no information on the timing of peak of *Pseudoeurycea robertsi* abundance, we  
173 carry out a pilot study to identify the annual season with higher abundance of salamanders  
174 in *Abies* and *Pinus* forests. In particular, we surveyed three study sites from April to  
175 October 2015 and visited each site once per month. We did not record any individual in  
176 April and October. In May and September the abundance of individuals was two times

177 lower than in June-August. We therefore recorded the abundance of individuals in all 14  
178 sites from mid-June to mid-August 2016. In particular, during each visit 2 people looked  
179 for salamanders under the bark of fallen logs with a diameter of  $\geq 5$  cm and length of  $\geq 30$   
180 cm. We started at 9:00 am and spent 2 effective hours of search (i.e., excluding stops),  
181 covering an area of about 10 ha in each site (the size of our smallest landscape).

182 The genetic survey was carried out at the same time, but we re-visited some sites in  
183 September to collect additional genetic samples, but in these extra-surveys we did not  
184 record individual abundances. We sampled 2 mm of tail tips of adult salamanders for DNA  
185 extraction (license number SGPA/DGVS/05701/16). This methodology is a low-invasive  
186 method that does not affect the survival or growth of salamanders (Arntzen et al. 1999;  
187 Polich et al. 2013). We released all individuals immediately after data collection in the  
188 same place where they were found.

189 Tail tissues were preserved in 90% ethanol and then frozen at  $-20^{\circ}\text{C}$  until  
190 processed. We extracted the DNA according to the commercial kit protocol “GF-1 Tissue  
191 DNA” of “Vivantis” mark. We used nine fluorescently labelled microsatellite primers  
192 developed for *Pseudoeurycea leprosa* by Velo-Antón et al. (2009). We multiplexed and run  
193 PCR microsatellite products on an ABI Prism3730xl (Applied Biosystems), with Rox-500  
194 as an internal size standard by a commercial laboratory (Roy. J. Carver Biotechnology  
195 Center in Illinois University, USA). We obtained allele sizes with PEAKSCANNER 1.0  
196 software (Applied Biosystems) and the fragment lengths with TANDEM 1.08 (Matschiner  
197 and Salzburger 2009). To avoid wrong data interpretation, we tested the presence of null  
198 alleles and other typing errors in the software MICROCHECKER 2.2.3 (Van Oosterhout et  
199 al. 2004). In POPPR 2.4.1 (Kamvar et al. 2014) for the R software (version 3.4.0; R

200 Development Core Team 2017), we made an analysis to create a genotype accumulation  
 201 curve, useful to determining the minimum number of loci necessary to discriminate  
 202 between individuals in a population (Kamvar et al. 2014). This function will randomly  
 203 sample loci without replacement and count the number of observed multilocus genotypes  
 204 (Kamvar et al. 2014). The genotype accumulation curve showed that the minimum number  
 205 of loci necessary to discriminate between individuals in this population is eight (Appendix  
 206 Fig. A1 in Supplementary Material). Therefore, we can assume that our study has enough  
 207 microsatellite primers (N = 9).

208 We used up to 16 samples per site (150 samples in total) but in some sites we found  
 209 less than 16 individuals. We finally excluded 3 forest sites where we found less than 4  
 210 genetic samples. To estimate the accuracy of allelic accounts we used the coverage  
 211 estimator recommended by Chao and Jost (2012), which is usually used to estimate the  
 212 accuracy of species inventories. Sample coverage was very high in all sites (>0.91),  
 213 indicating that our sampling effort was adequate to estimate diversity metrics within each  
 214 site (Chao and Jost 2012). Yet, we calculated the expected values of allele richness based  
 215 on coverage extrapolations performed with the *entropart* package (Marcon and Hérault  
 216 2014) for R 3.0.1 (R Development Core Team 2014) to avoid any potential bias in our  
 217 results due to differences in sample coverage among sites (Chao and Jost 2012). We  
 218 calculated genetic diversity using true diversity measures (Hill 1973):

219 Diversity  $\Delta \equiv \left( \sum_{i=1}^k p_i^q \right)^{1/(1-q)}$ , where  $p_i$  is the population frequency of the  $i$ -th allele and  
 220 the exponent  $q$  determines the measure's sensitivity to allele frequencies. When  $q = 0$ , the  
 221 equation gives the allele number ( $Na$ ), and when  $q = 2$  it gives Kimura and Crow's (1964)  
 222 effective number of alleles ( $Ne$ ) (Jost 2008). We calculated all diversity metrics with the

223 *entropart* package (Marcon and Hérault 2014) for R (version 3.4.0; R Development Core  
 224 Team 2017).  $Na$  is not sensitive to allele abundances, and thus gives disproportional weight  
 225 to rare alleles, while  $Ne$  can be interpreted as the effective number of dominant alleles in  
 226 the population. These true diversity measures have the linear behavior implicit in the  
 227 geneticists' concept of diversity (i.e., the “doubling” property sensu Hill 1973), while  
 228 heterozygosity and Shannon entropy do not (Jost 2008).

229

230 Explanatory variables

231 Using ArcGis 10.5 software and satellite images (SPOT 6/7) of very high resolution (1.5  
 232 m) for year 2015, we made a supervised classification considering six land cover types:  
 233 *Pinus* forest, *Abies* forest, grasslands, agriculture, urban areas, and water sources. Within  
 234 each landscape, and at each scale, we calculated two metrics of landscape composition: (i)  
 235 the percentage of remaining forest cover; and (ii) the percentage of *Abies* cover (from the  
 236 total forest cover). We also evaluated two metric of landscape configuration: (iii) forest  
 237 fragmentation per se, and (iv) forest edge density. We calculated forest fragmentation with  
 238 the splitting index (S) proposed by Jaeger (2000):  $S = A_t^2 / \sum_{i=1}^n A_i^2$ , where  $A_t$  is the area  
 239 covered by forest in the landscape and  $A_i$  is the area of the forest patch  $i$ . This index  
 240 represents the ‘effective number of forest patches’ and is a measure of fragmentation per se  
 241 because it is independent of the total forest cover in the landscape (Fahrig 2003). At the  
 242 local scale, we also evaluated (v) fallen logs volume using the formula of the cylinder  
 243 volume:  $V = h\pi r^2$ , where  $h$  is the sum of the length of all sampled logs in each 10-ha  
 244 sample site (see above) and  $r$  is the mean radius of these logs, as fallen logs showed a  
 245 similar diameter.

246

## 247 Data analyses

248 We used generalized linear models to assess the effects of local and landscape attributes on  
249 each response variable. We fixed a Gaussian error distribution for continuous response  
250 variables (expected values of  $N_a$  and  $N_e$ ) after verifying that model's residuals followed a  
251 Normal distribution (Shapiro-Wilk test). Abundance (count-dependent variable) was  
252 assessed by fixing a Poisson error distribution. To assess collinearity among predictor  
253 variables we estimated their variance inflation factors (VIF) using the *car* package for R  
254 version 3.0.1. A VIF > 4 suggests possible collinearity, and a VIF > 10 indicates severe  
255 collinearity (Neter et al. 1996). We found severe collinearity between forest cover (i.e.,  
256 *Abies* and *Pinus* forest) and splitting index in all models. Thus, we decided to exclude  
257 forest cover from the models. We then included only *Abies* forest cover, which was not  
258 collinear with the splitting index. In fact, *Abies* forest is probably the main habitat of the  
259 species, as in our pilot survey we did not record any individual in *Pinus* forest. We used a  
260 multimodel inference approach to assess the relative effect of each predictor on each  
261 response variable (Burnham and Anderson 2002). To obtain model-averaged parameter  
262 estimates we used Akaike weights ( $w_i$ ). The set of models for which  $\sum w_i$  was 0.95  
263 represents a set that has 95% probability of containing the true best model (Burnham and  
264 Anderson 2002). To be more conservative in our selection of important explanatory  
265 variables, we considered that a given predictor was important for a given response variable  
266 if accomplishing these three conditions simultaneously: (i) the predictor showed a high sum  
267 of Akaike weights (i.e., considering each candidate model in which it appeared); (ii) the  
268 model-averaged unconditional variance was lower than the model-averaged parameter

269 estimate, and (iii) the goodness-of-fit of the model was relatively high (Russildi et al. 2016;  
270 Sánchez-de-Jesús et al. 2016). All models were built using the package *glmulti* for R  
271 version 3.0.1 (Calcagno and Mazancourt 2010).

272

## 273 **Results**

274 In total, we recorded 185 individuals and 33 alleles (from the 150 genotyped individuals).  
275 Both local and landscape variables showed a relatively high explanatory power, being  
276 higher for salamander abundance (75% of explained deviance) than for genetic diversity  
277 (44-56%) (Fig. 2). As predicted, local habitat amount (fallen logs volume) was relatively  
278 more important than landscape habitat amount (*Abies* forest cover), positively affecting  
279 salamander abundance (Fig. 2a) and number of alleles (Fig. 2b). Yet, contrary to our  
280 expectations, forest cover generally showed a weaker effect than forest spatial  
281 configuration, especially on salamander abundance, which responded negatively to forest  
282 edge density ( $\sum w_i = 1.0$ ; Fig. 2a). Genetic diversity also responded negatively to increasing  
283 edge density (Fig. 2b and 2c). Although more weakly, forest fragmentation (i.e., splitting  
284 index) showed a consistently positive association with all response variables.

285

## 286 **Discussion**

287 This study assesses the relative effect of local- and landscape-scale habitat amount and  
288 habitat spatial configuration on the abundance and genetic diversity of *Pseudoeurycea*  
289 *robertsi* – a critically endangered salamander microendemic to the Nevado de Toluca  
290 volcano, Mexico. Our findings show that salamander abundance is more strongly

291 associated with all predictor variables than genetic diversity. As expected, local habitat  
292 amount (i.e., fallen logs volume) has stronger positive effects on salamander abundance and  
293 allele number than landscape-scale habitat amount (i.e., *Abies* forest cover). Yet, contrary  
294 to our expectations, landscape-scale habitat amount shows a relatively weaker impact on  
295 salamanders than forest spatial configuration. In particular, as predicted, forest edge density  
296 is negatively related to salamander abundance, and although weaker, the effect of forest  
297 fragmentation per se tended to be positive. As discussed below, these findings have  
298 important theoretical and conservation implications.

299         The fact that habitat disturbance has stronger effects on salamander abundance than  
300 on genetic diversity is not surprising. The colonization or loss of a given allele in the  
301 population can require many generations, and thus, genetic diversity is expected to be  
302 regulated by a larger number of generations than abundance (Jackson and Fahrig 2014). In  
303 this sense, as most of the forested area in the study region was converted to agricultural  
304 lands in the second half of the nineteenth century (Mastretta-Yanes et al. 2014), the history  
305 of land-use change is probably not large enough to allow the full spectrum of local and  
306 landscape effects on genetic diversity be exhibited. Therefore, additional long-term  
307 monitoring studies may be necessary before we can draw stronger conclusions about the  
308 effect of habitat disturbance on the genetic diversity of this species.

309         As predicted, both salamander abundance and allele number were positively related  
310 to fallen logs volume. This species inhabits forest areas with high relative moisture  
311 (Sánchez-Jasso et al. 2013), especially fallen logs, where it finds refuge and food (Bille  
312 2009). As this species has a very low vagility, we can expect that the probability that  
313 salamanders interact with spatial variables measured across larger spatial extents is  
314 relatively low (Jackson and Fahrig 2012; Miguet et al. 2016), thus explaining why species'

315 responses to fallen logs volume were stronger than to changes in landscape structure. In  
316 fact, as fallen logs volume can be considered a proxy of habitat amount, our findings  
317 indicate that habitat loss is a major driver of population decline.

318 Surprisingly, and in contrast to previous studies (Fahrig 2003), landscape  
319 configuration variables (i.e., forest edge density and forest fragmentation) seems to have a  
320 higher predictive power than the percentage of *Abies* forest cover, a landscape  
321 compositional variable. We expected stronger responses to forest cover because this is a  
322 forest-specialist species (Davic and Welsh 2004). Yet, the abundance of individuals  
323 decreased mainly in forest sites surrounded by higher edge density. This can be related to  
324 the loss of ‘core forest areas’ in landscapes with higher edge density (Ewers and Didham  
325 2006). This salamander species, as other ectotherms, can be negatively impacted by the  
326 abiotic changes (e.g., lower relative humidity and higher temperature) that typically occur  
327 at forest edges (Arroyo-Rodríguez et al. 2017; Nowakowski et al. 2018). Thus, as has been  
328 reported for other salamander and anuran species (deMaynadier and Hunter 1998), our  
329 findings suggest that this species can be particularly dependent on the availability of core  
330 forest areas in the landscape. In fact, changes in microclimatic conditions at forest edges,  
331 especially the loss of humidity, can have strong negative impacts on plethodontids, even  
332 stronger than on other amphibians, because salamanders from this family do not have lungs  
333 and rely on cutaneous respiration (Petranka et al. 1993; deMaynadier and Hunter 1998).  
334 Moreover, drier edge conditions also slow wood decomposition (Kapos et al. 1993), which  
335 may reduce the availability of suitable refuges for salamanders.

336 But, why forest fragmentation tended to have positive effects on all ecological  
337 responses? Forest fragmentation per se increases the amount of edge-affected habitats in the  
338 landscape, and thus, following our previous rationale, we can expect the opposite pattern.

339 However, our findings support those of Fahrig (2017), who find in a global review of  
340 fragmentation effects that this landscape variable generally shows weak effects on  
341 biodiversity, but when significant, responses to fragmentation are mostly positive. Several  
342 mechanisms can explain such positive responses, including a lower mean inter-patch  
343 isolation distance in landscapes with a higher number of forest patches, which can favor  
344 patch colonization and increase population and metapopulation persistence (Fahrig 2003,  
345 2017; Jackson and Fahrig 2016).

346

#### 347 Ecological and conservation implications

348 Our findings suggest that retaining fallen logs in the forest and increasing forest core area is  
349 critically needed to preserve *P. robertsi* populations, and potentially other forest-interior  
350 specialist species. This is consistent with previous studies that highlight the importance of  
351 leaving dead wood in the forest and avoiding clear-cutting to preserve salamanders and  
352 other forest-dwelling animals (Petranka et al. 1993; deMaynadier and Hunter 1998; Kouki  
353 2001). The positive responses to increasing fragmentation per se also suggest that  
354 preserving all forest patches in the landscape can also be critical, as this can decrease inter-  
355 patch distances, favoring patch colonization dynamics in fragmented forests (Fahrig 2017).  
356 However, to avoid negative edge effects in these emerging landscapes, we should prevent  
357 the loss of the largest forest patches in the region, and avoid deviations from circularity in  
358 patch shapes to increase the amount of interior habitat (Ewers and Didham 2006). These  
359 management strategies need to be urgently considered given the recent change of protection  
360 level of the Nevado de Toluca volcano. Originally decreed as a National Park, this reserve  
361 was recently (2013) decreed as a Flora and Fauna Protected Area. This less restrictive  
362 category threatens the preservation of the *Abies* forest – the main habitat of *P. robertsi* –

363 because it allows forest harvesting practices with commercial proposes in almost all *Abies*  
 364 forest extension (Mastretta-Yanes et al. 2014). Therefore, preventing the loss of *Abies*  
 365 forest, especially the loss of the largest forest remnants is of paramount importance to  
 366 preserve this endemic and critically endangered species.

367

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Figure 1

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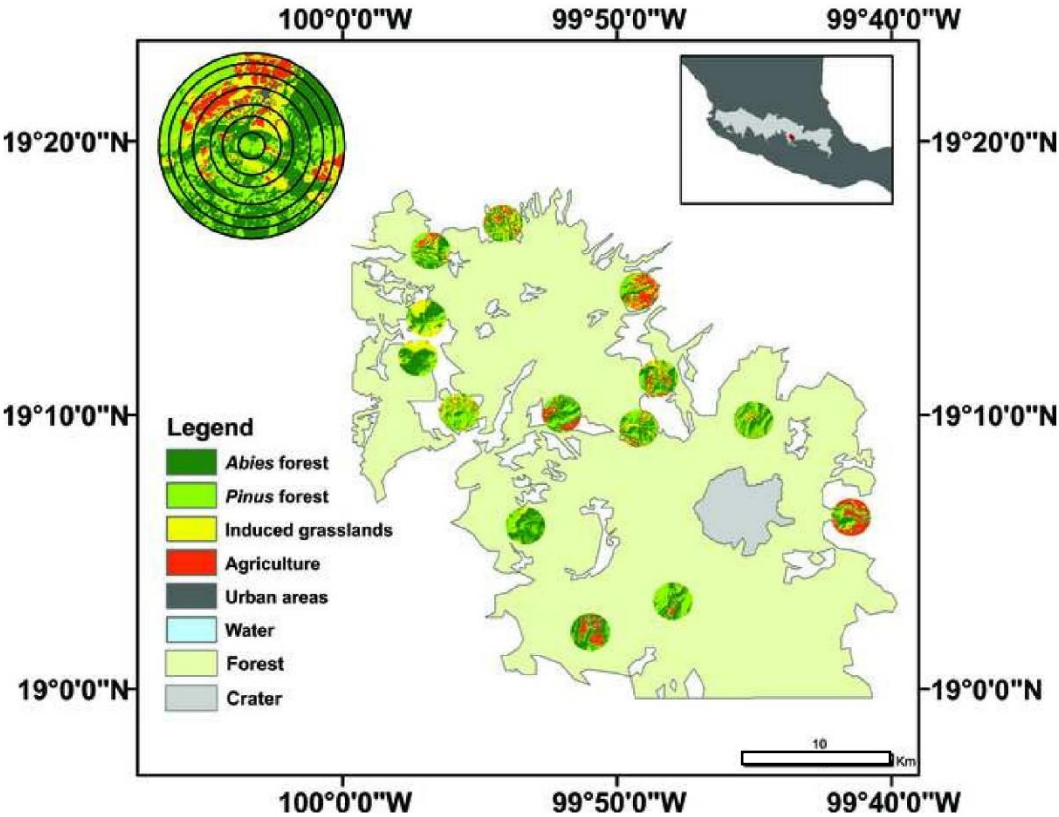
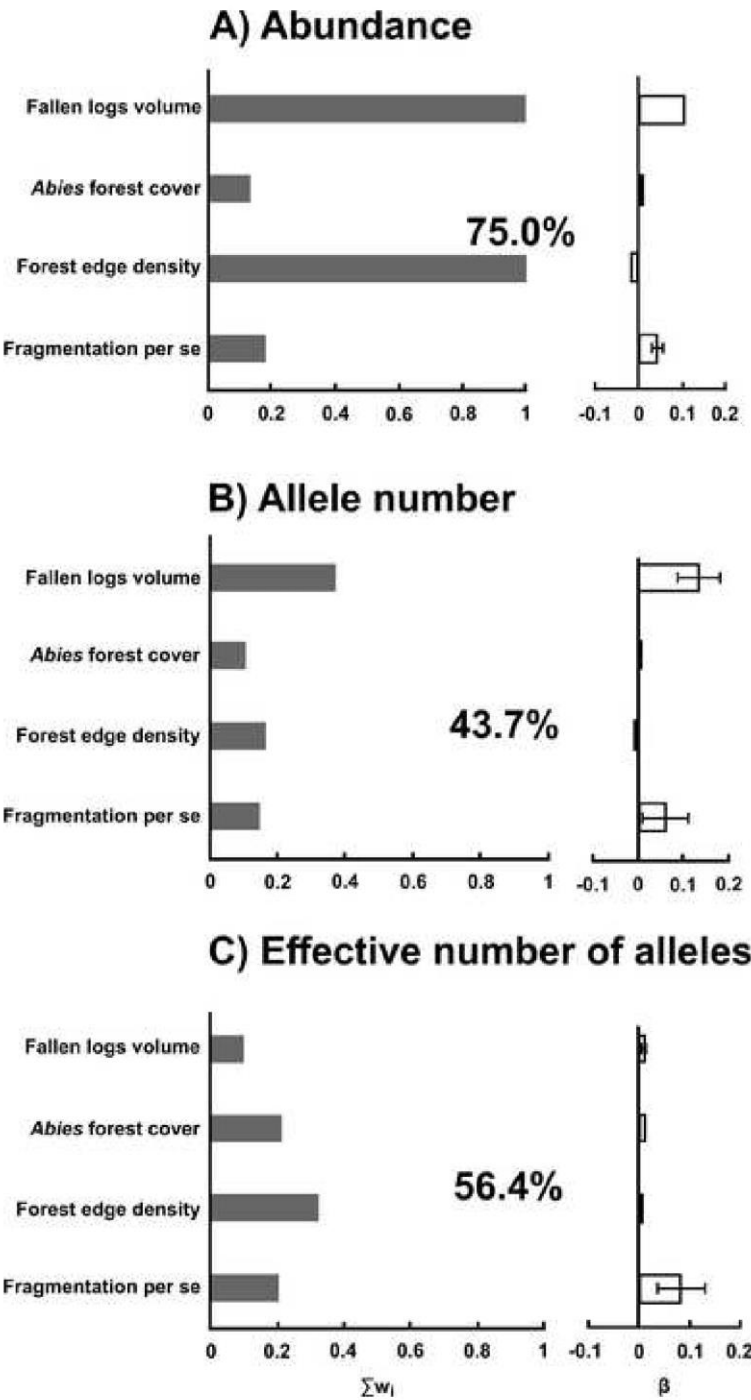


Figure 2

[Click here to access/download;Figure;Figure 2.tif](#)



1 **Figures**

2 **Figure 1.** Location of the study forest sites in the Nevado de Toluca volcano, Mexico.

3 Circles within the main panel represent the 14 landscapes selected in each region,  
4 considering the largest buffer (500 ha). Yet, landscape metrics were actually measured in 6  
5 different-sized and concentric buffers from the center of each sample site (see example in  
6 the top left corner).

7  
8 **Figure 2.** Local and landscape predictors of the abundance, allele number and effective  
9 number of alleles of *Pseudoeurycea roberts* in the Nevado de Toluca volcano, Mexico *i.*

10 The sum of Akaike weights ( $\sum w_i$ , panels in the left side) is indicated. Panels in the right  
11 side show the values of model-averaged parameter estimates ( $\beta$ ) and unconditional variance  
12 of information-theory-based model selection and multimodel inference. The sign (+/-) of  
13 parameter estimates represents a positive or negative effect of each predictor on the  
14 response variable. The percentage of deviance explained by each complete model is also  
15 indicated in each panel as a measure of goodness-of-fit.

## V. DISCUSIÓN GENERAL

La presente tesis demuestra que la herpetofauna del Eje Neovolcánico Transversal (ENT) está fuertemente influenciada por variables ambientales medidas a diferentes escalas espaciales. En particular, la presencia de las cinco especies de *Thamnophis* en el ENT está negativamente asociada al incremento de la cobertura de vegetación árida. Las demás variables que mejor explican la distribución potencial de las especies varían en cada caso, sin embargo, cabe recalcar que la distancia al bosque de oyamel es la variable más importante para *T. scalaris* y *T. scaliger*; su probabilidad de ocurrencia disminuye en sitios más alejados a estos bosques. Todas las especies tienen una elevada proporción de su distribución potencial en el ENT, sin embargo, de acuerdo a nuestros modelos, todas las especies de *Thamnophis* sufrirán reducciones en sus distribuciones potenciales en esta región. En el segundo estudio, que evalúa la influencia del hábitat en la abundancia y diversidad genética de *P. robertsi*, se encontró que la abundancia de esta salamandra está más estrechamente relacionada con variables locales y del paisaje que la diversidad genética. De acuerdo con lo esperado, la cantidad de hábitat a nivel local (volumen de troncos caídos) tuvo un efecto positivo y fue más importante para explicar la abundancia de la salamandra y el número de alelos que la cantidad de hábitat a nivel de paisaje (porcentaje de bosque de oyamel). Sorprendentemente, la configuración tuvo un mayor efecto que la cantidad de hábitat a nivel de paisaje. En particular, la densidad de borde tuvo un efecto negativo en todas las variables de respuesta. Por lo tanto, retener troncos caídos en los bosques e incrementar las áreas núcleo es crítico para la conservación de esta especie de salamandra.

En ambos estudios se encontró que los bosques de oyamel tienen un papel fundamental; en el primero para la conservación de las culebras *T. scalaris* y *T. scaliger*, en

el segundo para la conservación de la salamandra *P. robertsi*. El porcentaje de cobertura de bosque de oyamel fue menos importante para explicar la abundancia y diversidad genética de la especie que otras variables. Sin embargo, todos los individuos fueron encontrados en bosques de oyamel o de oyamel-pino, por ello, podemos afirmar que estos bosques constituyen el macrohábitat de la especie; no puede haber troncos caídos sin bosque y el efecto negativo de la densidad de borde se debe al contacto con la matriz no forestal. Lo que sugieren nuestros resultados es que una extensión mayor de estos bosques pero con poco volumen de troncos caídos y una alta densidad de borde contendrá menor abundancia de salamandras y menor diversidad genética que extensiones que, aunque sean de menor tamaño, tengan un volumen de troncos caídos elevado y baja densidad de borde. Pero si los bosques de oyamel desaparecen o sufren grandes reducciones, *P. robertsi* desaparecerá con ellos. Por lo tanto, es esencial proteger estos bosques en el Nevado de Toluca. Además de *P. robertsi*, en este volcán se encuentran otras salamandras como *P. leprosa*, *Isthmura bellii* y *Aquiloerycea cefalica* (Bille 2009, observación personal). Estas especies también se refugian debajo de la corteza de los troncos caídos, que son abundantes en los bosques de oyamel de manera natural, ya que estos bosques se encuentran en zonas con elevada pendiente, donde muchos troncos se caen fácilmente debido al viento y las tormentas.

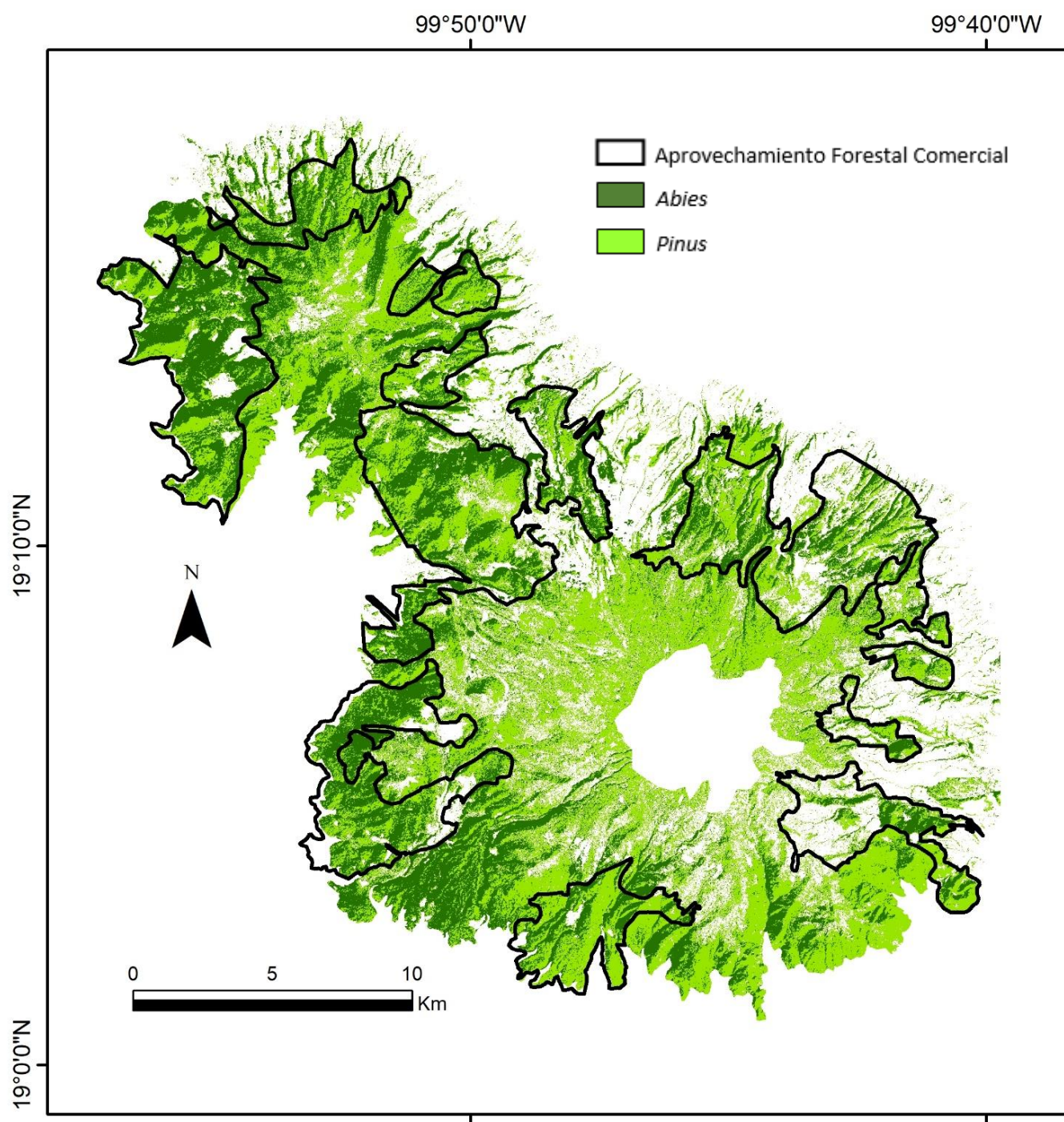
El ENT tiene la mayor extensión de bosques de oyamel del país (91%), sin embargo solamente representan el 1% de la superficie de esta provincia biogeográfica (Sunny et al. 2017). En este estudio se demuestra que la extensión de estos bosques se ha mantenido estable en el país entre 2002 y 2011, mientras que los bosques de pino han sufrido reducciones de alrededor de 3000 km<sup>2</sup> en el mismo período. Así mismo, los bosques densos de pino se redujeron en un 40% en el Nevado de Toluca entre los años 1972 y 2000 mientras

que hubo una recuperación de los bosques de oyamel del volcán durante este período (Franco-Maass et al. 2006).

El gobierno mexicano recientemente modificó la categoría de protección del Nevado de Toluca de Parque Nacional a Zona de Protección de Flora y Fauna, una categoría menos restrictiva en cuanto al uso de suelo. De acuerdo al Diario Oficial de la Federación (2013) este cambio contribuirá a preservar los bosques del Nevado de Toluca de la tala ilegal mediante la regulación de las actividades productivas. La justificación para este cambio se basa en la reducción del bosque denso de pino antes mencionada. Sin embargo, esta nueva categoría permite la tala comercial en la mayor parte de la extensión del bosque de oyamel que estuvo bien preservado bajo la categoría del Parque Nacional (Mastretta-Yanes et al. 2014) por lo que creemos que este cambio de categoría está comprometiendo el hábitat de la endémica y críticamente amenazada *P. robertsi* (Figura 1). El tipo de tala que se permite en los polígonos de la Figura 1 es la tala selectiva (práctica de remover uno o dos troncos y dejar intactos los que los rodean), este tipo de tala suele afectar extensiones grandes de bosque causando daños a los árboles circundantes, a la vegetación subarbórea y a los suelos; con impactos en los procesos hidrológicos, erosión, fuego, almacenamiento de carbono y especies de plantas y animales (Asner 2005). Aunque la tala selectiva sea menos invasiva que la tala generalizada, también puede ser muy perjudicial para especies especialistas de bosque, como la salamandra *P. robertis*, especialmente si se afectan las áreas núcleo del bosque. Además de las especies de *Thamnophis* y salamandras mencionadas, los bosques de oyamel también son importantes para la conservación de otras especies de vertebrados, como la lagartija *Barisia imbricata* (Sunny et al. 2017) y de invertebrados, como las colonias migratorias de la emblemática mariposa monarca (Saunders 2018). Por lo tanto, aunque la recuperación de

los bosques de pino del volcán es de especial importancia, la preservación de los bosques de oyamel, con áreas núcleo bien conservadas y con elevada disponibilidad de troncos caídos, debe ser una prioridad en el Nevado de Toluca y en todo el Eje Neovolcánico Transversal.

**Figura 1:** Área del antiguo Parque Nacional con los polígonos que permiten actualmente el aprovechamiento forestal comercial. El bosque de oyamel aparece en verde oscuro y el bosque de pino en verde claro.



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