RESEARCH ARTICLE

Potential risk of *Batrachochytrium salamandrivorans* in Mexico

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Abstract

The recent decline in populations of European salamanders caused by the chytrid fungus *Batrachochytrium salamandrivorans* (*Bsal*) has generated worldwide concern, as it is a major threat to amphibians. Evaluation of the areas most suitable for the establishment of *Bsal* combined with analysis of the distribution of salamander species could be used to generate and implement biosecurity measures and protect biodiversity at sites with high salamander diversity. In this study, we identified the areas most suitable for the establishment of *Bsal* in Mexico. Mexico has the second-highest salamander species diversity in the world; thus, we identified areas moderately to highly suitable for the establishment of *Bsal* with high salamander diversity as potential hotspots for surveillance. Central and Southern Mexico were identified as high-risk zones, with 13 hotspots where 30% of Mexican salamander species occur, including range-restricted species and endangered species. We propose that these hotspots should be thoroughly monitored for the presence of *Bsal* to prevent the spread of the pathogen if it is introduced to the country.

Introduction

Chytridiomycosis, an emergent disease caused by the fungal pathogen *Batrachochytrium dendrobatidis* (*Bd*), has caused alarming population collapses and extinctions of amphibians worldwide [1–7]. In many regions throughout the world, *Bd* infections have transitioned from epidemic to endemic states after declines occurred, and at present, some amphibian populations are either stable or recovering after more than a decade since the disease outbreaks occurred [4, 8, 9]. The recent emergence of a second chytrid fungus, *Batrachochytrium salamandrivorans* (*Bsal*), has unleashed great concern among researchers and conservation agencies since this pathogen has already caused die-offs of native salamander species in Europe [10]. The potential effects of *Bsal* infections in other regions of the world are still unclear. However, recent studies in European salamander populations determined that the combination of *Bsal*’s transmission strategy, virulence and host population dynamics could have...
catastrophic effects on naïve salamander populations [11, 12], including those species that were not previously affected by Bd. The urgency of this situation requires estimation of the potential effect of Bsal if introduced to naïve regions.

The available ecological data can provide some indicators regarding the potential of Bsal to contribute to the global decline in amphibians. Although Bd affects all groups of amphibians, experimental studies have documented that Bsal infections are harmful to urodeles even at very low Bsal zoospore levels [11, 12], whereas anurans can coexist with Bsal infections and act as reservoirs [12, 13]. Bsal physiological studies have shown that the thermal growth range of Bsal in the laboratory is between 5˚C and 25˚C, with optimal growth between 10˚C and 15˚C [10], which is considerably lower than the optimal temperature range of Bd (between 17˚C and 25˚C) [14]. However, recent surveys in Vietnam and China found Bsal in ponds and streams with water temperatures between 20˚C and 25˚C [15, 16], suggesting a wide thermal niche for this pathogen.

Since Bsal is lethal to some urodele species, its spread to naïve regions with high salamander diversity, such as North America, could cause significant reductions in amphibian diversity [11, 17, 18]. Thus, areas that are moderately to highly suitable for Bsal with high salamander diversity could be considered as hotspots in which surveillance strategies should be implemented to prevent potential amphibian declines.

The use of ecological niche modeling (ENM) to infer the suitable distribution of Bsal could provide an estimate of sites with the potential risk of infection based on bioclimatic variables and salamander distributions [18–23]. Yap et al. [18] created a species distribution model for Bsal using the native ranges of the three putative native Bsal host species in Asia (Cynops cyanurus, C. pyrrhogaster, and Paramesotriton deloustali) and projected these results to North America. These analyses identified the southern part of the Appalachian Mountains, the Pacific Northwest, the Sierra Nevada, and the mid-Atlantic as high-risk zones in the USA and the Sierra Madre Oriental (SMO) and the Trans-Mexican Volcanic Belt (TVB) as high-risk zones in Mexico. However, Yap et al. [18] analyzed the native host niche under the assumption that it is a proxy for the Bsal ecological niche.

Since Bsal has been found in different environmental conditions outside the native host range of Asia (introduced areas in Europe), we constructed a potential distribution model to identify areas susceptible to invasion. We modelled Bsal’s niche considering environmental layers and the occurrences of Bsal in its native and invasive areas to create projections of Bsal suitability in Mexico. Based on the obtained Bsal model and the salamander richness distribution, we identified major hotspots for salamander decline in the event of Bsal introduction in Mexico. This information will be relevant to implement conservation strategies in Mexico, which has the world’s second-highest salamander richness, with 146 described species [24].

**Materials and methods**

*Batrachochytrium salamandrivorans* potential distribution model

To assess the potential distribution of Bsal in Mexico, we mapped its climatic niche based on environmental layers and Bsal occurrences from both Europe and Asia [25] (S1 Fig). Bsal occurrence records were obtained from Martel et al. [11], Laking et al. [15], Yuan et al. [16], Spitzen-van der Sluijs et al. [26], and Beukema et al. [27] (S1 Table).

The model was built using the maximum entropy algorithm MaxEnt [23]. This software estimates the probability of species occurrence by finding the distribution of maximum entropy, which is subject to constraints defined by the environmental variables being analyzed [23]. To avoid model overfitting and multicollinearity of predictors [28], we selected the non-correlated variables chosen by MaxEnt. Briefly, we first ran MaxEnt using all 19 bioclimate
layers from Wordclim [29] at 30 arcsecond (~1 km) resolution to let the software select the variables (S2 Table). Then, we calculated pairwise Pearson correlations between the variables using ENM tools [30], and we selected those with the maximum contribution percent in the model and with a Pearson’s $r < 0.75$ (S3 Table): mean diurnal range (Bio2), maximum temperature of warmest month (Bio5), temperature annual range (Bio7), precipitation seasonality (Bio15), precipitation of warmest quarter (Bio18), and precipitation of coldest quarter (Bio19).

The MaxEnt model was optimized using the ENMeval package [31] implemented in R 3.2.4 [32], which provides an automated method to execute MaxEnt models across a user-specified range of regularization multiplier (RM) values and feature combinations (FCs). We set the RM range from 0.5 to 2.5 with increments of 0.5 and three FCs, i.e., linear (L), linear and quadratic (LQ), and linear, quadratic and product (LQP), resulting in 15 possible combinations of features and regularization multipliers. The fine-tuned MaxEnt models were made by seeking the lowest delta value of Akaike’s information criterion corrected for small samples sizes (AICc) among candidate models, which reflects both model goodness-of-fit and complexity providing the most conservative results. In addition, AICc balances predictability against model complexity due to penalties for overparameterization [21, 31]. The models were built based on an approach proposed by Phillips [33]. Briefly, we modelled $Bsal$’s niche using the native area (Asia) to train the model (occurrences and background) and the invasive area (Europe) as testing data. We also used a block method to generate AUC scores [31].

We selected the model with the lowest delta AICc score, which had a parametrization of regularization multiplier of 2.5 and a LQP feature combination; it exhibited good predictive power, with high accuracy and an average test AUC value of 0.87 (S4 Table, S2 Fig). This model was used to project $Bsal$ in Mexico to create the bioclimatic suitability model (logistic output). Because the logistic output from Maxent ranges from 0 to 1, with 0 indicating unsuitable habitat and 1 indicating the highest suitability, we reclassified the predicted values using 0.25 intervals to obtain four suitability classes: no suitability when values were less than 0.25, low suitability when the occurrence probability ranged between 0.25 and 0.5, moderate suitability when the values ranged between 0.5 and 0.75, and high suitability when the values were greater than 0.75 [34–36]. In addition, we defined the potential presence and absence areas in Mexico using the minimum training presence threshold, which correspond to the lowest predicted presence value of an occurrence record [37].

**Salamander distribution and richness areas**

We estimated salamander richness in Mexico by overlapping 161 distribution maps [18]. 136 of the distribution maps were obtained from the IUCN Red List [38], and the remaining 25 were expert-based maps (Aquileurycea cafetalera, Bolitoglossa chinanteca, B. odonelli, Bradytriton silus, Chiropterotriton sp. I, Chiropterotriton sp. C, Chiropterotriton sp. E, Chiropterotriton sp. F, Chiropterotriton sp. G, Chiropterotriton sp. H, Chiropterotriton sp. J, Chiropterotriton sp. K, Chiropterotriton aureus, Chiropterotriton chico, Chiropterotriton cieloensis, Chiropterotriton infernalis, Chiropterotriton miquihanuus, Chiropterotriton nubilus, Isthmura corrugata, Isthmura sierraoccidentalis, Thorius hankeni, T. longicaudus, T. maxillabrochus, T. pinicola, T. tlaxiacus). Expert-based maps were obtained based on records from the Global Biodiversity Information Facility (GBIF, http://www.gbif.org), National Biodiversity Information System of Mexico (SNIB) and published papers [39–41]. These records were carefully reviewed, and we added a 1-km buffer radius to each record according the registered plethodontids home ranges [42]. Moreover, we modified distributions of three species from IUCN (Ambystoma granulosum, A. rivulare, Chiropterotriton multidens) considering the occurrences and last updates published [43, 44]. We also consulted the International Union for Conservation of
Nature (IUCN)-The Global Amphibian Assessment (GAA) to obtain the conservation status for all Mexican salamanders listed in the database. We used ArcGIS 10.2 [45] to produce all GIS layers and calculate the distribution area. In addition, we used the R statistical software package to overlap the species distribution and perform the richness map at a resolution of 30 arcseconds (~1 km²). Expert-based maps and modified maps are available at https://github.com/delibasanta/Mexican-salamanders.git

**Geographic overlap**

We created a salamander-vulnerability model by calculating the overlap of suitable areas of Bsal and the salamander-richness distribution. This model retrieved biodiversity hotspots in which Bsal has suitable bioclimatic conditions (Bsal suitability >0.5) and salamander diversity is high (more than five salamander species).

**Results**

*Batrachochytrium salamandrivorans has several potential suitable regions in Mexico*

We found that areas from the Sierra Madre Oriental (SMO), Trans-Mexican Volcanic Belt (TVB), Sierra Madre del Sur (SMS), Mexican Gulf and Yucatan Peninsula were the most suitable areas for Bsal (Fig 1, S3 Fig). Of the six environmental variables, temperature annual range (Bio7), minimum temperature of the coldest month (Bio5) and precipitation seasonality (Bio15) had the largest contributions to the distribution model for Bsal (S5 Table). These three factors explained 91.3% of the modeled distribution. The contributions of the other factors, i.e., mean diurnal range (Bio2), precipitation of the warmest quarter (Bio18), and precipitation of the coldest quarter (Bio19) were 5.8%, 1.92%, and 0.97%, respectively. These results indicate that thermal conditions and precipitation seasonality were the most important variables of the obtained Bsal niche model.

![Fig 1. Suitability model for Bsal in Mexico. (A) Continuous model (B) Categorized model.](https://doi.org/10.1371/journal.pone.0211960.g001)
Salamander distribution in Mexico is highly heterogeneous

We obtained distribution maps for 161 salamander species (153 described species and 8 undescribed species, i.e., *Chiropterotriton* spp.) ([S6 Table](#)). These maps were used to generate a salamander richness map (Fig 2). The salamander distribution in the country is heterogeneous, with most of the species occurring in Central and Southern Mexico (Fig 2).

According to the areas in which salamanders occur, 44% of the salamander species exhibit a small distribution (<100 km²) and are endemic to Mexico ([S6 Table](#)). Moreover, most Mexican salamanders are threatened according the IUCN Red List classification, with 33% of the species listed as critically endangered, 29% as endangered, 8% as vulnerable, 5% as near threatened, 10% as least concern, 4% as data deficient, and 11% not evaluated ([S6 Table](#)).

Species from the family Plethodontidae represented 87.4% of the total number of species in the country, whereas Ambystomatidae, Salamandridae and Sirenidae represented 10.7%, 0.63% and 1.26%, respectively.

Geographic overlap: High correspondence between *Bsal* suitability and salamander richness

We found that 51% of salamander species of Mexico are present in areas that are suitable for *Bsal* ([S4 Fig](#), [S6 Table](#)). We identified 13 hotspots as those suitable areas categorized as moderate and high suitability for *Bsal* (Fig 1B) in which five or more salamander species were present (Fig 3). All hotspots are located in Central and Southern Mexico: eight are located on the Trans-Mexican Volcanic Belt (TVB), two in Los Tuxtlas Veracruz, one in the Sierra Madre del Sur (SMS) in Guerrero, one in Northern Oaxaca, and one in SMS in Chiapas (Fig 3). These hotspots included 47 salamander species across seven genera, including species with a restricted geographical range (<100 km²) ([Fig 4A, S6 and S7 Tables](#)) and endangered species ([Fig 4B, S6 Table](#)).

Discussion

Due to the potential risk of introducing *Bsal* to native regions through wildlife trade [13, 46], we used ENM and salamander distribution data to determine the potential areas and species that are most likely to be at risk of pathogen exposure should an introduction occur in Mexico.

![Map of salamander richness distribution in Mexico](https://doi.org/10.1371/journal.pone.0211960.g002)
Fig 3. Overlap of salamander richness with moderate suitable and high suitable areas for Bsal. (A) Areas with hotspots. Hotspots identification in: (B) TVB. (C) Los Tuxtlas. (D) SMS in Guerrero. (E) Northern Oaxaca. (F) SMS in Chiapas.

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A

Species distribution area
- >5000 km²
- 1000-5000 km²
- 500-1000 km²
- 100-500 km²
- <100 km²

Number of species

TVB | Los Tuxtlas | SMS Guerrero | Northern Oaxaca | SMS Chiapas
---|---|---|---|---

B

Number of species

TVB | Los Tuxtlas | SMS Guerrero | Northern Oaxaca | SMS Chiapas
---|---|---|---|---
Areas with high salamander diversity have climatic conditions that appear to be suitable for the establishment of \textit{Bsal} should an introduction occur. Considering the latter, the risk of \textit{Bsal} arrival is critically important, and it is essential to monitor these areas where species loss would be considerable.

Our niche model predictions differ considerably from those obtained by Yap et al. \cite{18}, in which the authors estimated the habitat suitability for invasive \textit{Bsal} in North America. Using Maxent and amphibian host occurrence records, Yap et al. \cite{18} predicted areas of Sierra Madre Occidental (SMOc), Trans-Mexican Volcanic Belt (TVB), Sierra Madre del Sur (SMS), Baja California and Oaxaca as suitable for \textit{Bsal} in Mexico. In contrast, our study predicted some parts of the TVB, SMS, Sierra Madre Oriental (SMO), Northern Oaxaca, Mexican Gulf and Yucatan Peninsula as suitable areas for \textit{Bsal}. The discrepancies between Yap et al. \cite{18} and our study (i.e., Baja California, SMOcc, Mexican Gulf and Yucatan Peninsula) can be explained by methodological differences in calibration areas and the occurrences used to estimate the potential range of \textit{Bsal} in North America. Specifically, our study used the native niche of \textit{Bsal} rather than the native Asian host distribution used by Yap et al. \cite{18}. We consider that the use of \textit{Bsal} ranges instead of \textit{Bsal} host ranges will lead to more accurate results when modeling the potential invasive range of the pathogen.

The model obtained in this study predicted that the areas suitable for \textit{Bsal} are mainly located in Central and Southern Mexico, including diverse environments such as tropical forests, pine forests and cloud forests. We found a high overlap between salamander richness and moderately to highly suitable areas for \textit{Bsal}, which is reflected in the 13 identified hotspots. These hotspots are located in the most diverse regions with respect to amphibian species (including salamanders): east of the Trans-Mexican Volcanic Belt, Northern Oaxaca and Sierra Madre del Sur in Chiapas \cite{47–49}. Thus, the arrival of \textit{Bsal} in these areas will likely have an impact on amphibian communities that include non-susceptible species (e.g., anuran species) that could act as carriers and transmission vectors \cite{13}, in addition to highly susceptible species (e.g., salamander species) \cite{12}. However, \textit{Bsal} could have different strains with genetic physiological and virulence differences such as the case with \textit{Bd} \cite{50}. In terms of \textit{Bsal}, Sabino-Pinto et al. \cite{51} has already suggested the existence of more than one \textit{Bsal} strains with differences in virulence. In this context, further investigations are needed to describe the genetic differences between \textit{Bsal} strains and it’s effect on Mexican taxa to apply better conservation strategies.

Most Mexican salamander species have a restricted distribution, including those species that inhabit hotspots. Salamander communities mainly inhabit pine-oak forests, tropical forests and cloud forests \cite{52}. These environments in Mexico are highly affected by anthropogenic activities, including deforestation and land use transformation \cite{53–55}. Thus, habitat loss has been one of the main causes of species decline: major amphibian declines were observed between 1970 and 1980 east of the Trans-Mexican Volcanic Belt, Northern Oaxaca and Sierra Madre del Sur in Chiapas, which coincide with four of the hotspots identified in this study (hotspots 4, 11, 12 and 13). Lips et al. \cite{56} reported population declines and local extinctions in the Pacific slope Sierra Madre del Sur in Guerrero (hotspot 11), Northern Oaxaca (hotspot 12) and Sierra Madre del Sur in Chiapas (hotspot 13). Later, Rovito et al. \cite{57} documented declines in salamander populations of El Chico in Hidalgo (hotspot 4) and Cerro San Felipe in Oaxaca (hotspot 12), where populations of \textit{Chiropterotriton} and \textit{Pseudoeurycea}, respectively, were the most affected.
For Mexican amphibians, in addition to habitat loss, the presence of \( Bd \) has also been considered a threat. This pathogen was detected in individuals collected in the 1970s, suggesting that chytridiomycosis has affected amphibian populations since then [7, 56]. The presence of \( Bd \) has been corroborated in many localities, including all 13 hotspots identified in this study [58, 59]. The combined effects of \( Bd \) and \( Bsal \) together in amphibian populations are unknown, but we can only assume that they could dramatically affect the amphibian populations that are already threatened by habitat loss.

Conservation efforts for amphibians in Mexico should focus on preventing the arrival of \( Bsal \) and its transmission among populations. Amphibian trade restrictions are being implemented in the USA, Canada and the European Union, and Mexico should not be the exception. As the country with the second-highest salamander species diversity, Mexico is potentially at risk of facing dramatic declines upon the arrival of an emerging pathogen such as \( Bsal \). If \( Bsal \) is detected in Mexico, immediate management actions to prevent its spread, such as restricting site-level access, especially in hotspots, should be considered.

**Conclusions**

This study integrated ecological niche modeling of \( Bsal \) and salamander distribution in Mexico and found high overlap between them. The areas most suitable for \( Bsal \) in Mexico are Central and Southern Mexico, which coincide with the highest salamander richness areas and with the largest number of endemic and threatened species. We identified 13 areas as potential hotspots for population risk with both high salamander diversity and areas that are moderately to highly suitable for \( Bsal \). We propose that the hotspots should be monitored for the presence of \( Bsal \) to prevent the spread of the pathogen if it is introduced to Mexico.

**Supporting information**

**S1 Fig.** Occurrences and areas of \( Batrachochytrium salamandrivorans \) (\( Bsal \)) used to build the model.

(TIF)

**S2 Fig.** AICc and AUC values of \( Bsal \) models obtained with ENMeval.

(TIF)

**S3 Fig.** Binary model for \( Bsal \) obtained with the minimum training presence threshold. Areas of potential presence are in black, and areas of potential absence are in gray.

(TIF)

**S4 Fig.** Number of salamander species grouped by genus that are present or absent in \( Bsal \)-suitable areas.

(TIF)

**S1 Table.** Occurrence data used for \( Bsal \) ecological niche model.

(DOCX)

**S2 Table.** Contribution of 19 bioclimatic layers from Wordclim that made greatest contribution to the model constructed with MaxEnt.

(DOCX)

**S3 Table.** Pairwise Pearson correlations of 19 bioclimatic variables. Variables selected with less than \( r = 0.75 \) are in bold.

(DOCX)
S4 Table. ENMeval models results. (DOCX)

S5 Table. Variable contributions to Bsal distribution model. (DOCX)

S6 Table. Salamander species of Mexico, range, IUCN status, and relationship with Bsal model and hotspots. Hotspots = pixels with Bsal suitability values greater than 0.5 and more than five salamander species. IUCN status: critically endangered (CR), endangered (E), vulnerable (V), near threatened (NT), least concern (LC), data deficient (DD), and not evaluated (NE). (DOCX)

S7 Table. Species present on hotspots. (DOCX)

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References
1. Lips KR, Brem F, Brenes R, Reeve JD, Alford RA, Voyles J, et al. Emerging infectious disease and the loss of biodiversity in a Neotropical amphibian community. Proc Natl Acad Sci U S A. 2006; 103 (9): 3165–3170. https://doi.org/10.1073/pnas.0506899103 PMID: 16481617
2. Skerratt LF, Berger L, Speare R, Cashins S, McDonald KR, Philott AD, et al. Spread of chytridiomycosis has caused the rapid global decline and extinction of frogs. EcoHealth. 2007; 4 (2): 125. https://doi.org/10.1007/s10393-007-0093-5
3. Fisher MC, Garner TW, Walker SF. Global emergence of Batrachochytrium dendrobatidis and amphibian chytridiomycosis in space, time, and host. Annu Rev Microbiol. 2009; 63: 291–310. https://doi.org/10.1146/annurev.micro.091208.073435 PMID: 19575560
4. Briggs CJ, Knapp RA, Vredenburg VT. Enzootic and epizootic dynamics of the chytrid fungal pathogen of amphibians. Proc Natl Acad Sci U S A. 2010; 200912886. https://doi.org/10.1073/pnas.0912886107 PMID: 20457916
5. Vredenburg VT, Knapp RA, Tunstall TS, Briggs CJ. Dynamics of an emerging disease drive large-scale amphibian population extinctions. Proc Natl Acad Sci U S A. 2010; 107 (21): 9689–9694. https://doi.org/10.1073/pnas.0914111107 PMID: 20457913
6. Catenazzi A, Lehr E, Rodriguez LO, Vredenburg VT. Batrachochytrium dendrobatidis and the collapse of anuran species richness and abundance in the upper Manu National Park, southeastern Peru. Conserv Biol. 2011; 25 (2): 382–391. https://doi.org/10.1111/j.1523-1739.2010.01604.x PMID: 21054530
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7. Cheng TL, Rovito SM, Wake DB, Vredenburg VT. Coincident mass extirpation of neotropical amphibians with the emergence of the infectious fungal pathogen *Batrachochytrium dendrobatidis*. Proc Natl Acad Sci U S A. 2011; 108 (23): 9502–9507. https://doi.org/10.1073/pnas.1105538108 PMID: 21543713

8. Voyles J, Woodhams DC, Saenz V, Byrnes AQ, Perez R, Rios-Sotelo G, et al. Shifts in disease dynamics in a tropical amphibian assemblage are not due to pathogen attenuation. Science. 2018; 359 (6383): 1517–1519. https://doi.org/10.1126/science.aao4806 PMID: 2959242

9. Knapp RA, Fellers GM, Kleeman PM, Miller DAW, Vredenburg VT, Rosenblum EB, et al. Large-scale recovery of an endangered amphibian despite ongoing exposure to multiple stressors. Proc Natl Acad Sci U S A. 2016; 113(42): 11890–11894. https://doi.org/10.1073/pnas.1609831113 PMID: 27698128

10. Martel A, Spitzen-van der Sluijs A, Blooi M, Bert W, Ducatelle R, Fisher MC, et al. *Batrachochytrium salamandrivorans* sp. nov. causes lethal chytridiomycosis in amphibians. Proc Natl Acad Sci U S A. 2013; 201307356. https://doi.org/10.1073/pnas.1307356110 PMID: 24003137

11. Martel A, Blooi M, Adriaensen C, Van Rooij P, Beukema W, Fisher MC, et al. Recent introduction of a chytrid fungus endangers Western Palearctic salamanders. Science. 2014; 346(6209): 630–631. https://doi.org/10.1126/science.1258268 PMID: 25359973

12. Stegen G, Pasmans F, Schmidt BR, Rouffaer LO, Van Praet S, Schaub M, et al. Drivers of salamander extirpation mediated by *Batrachochytrium salamandrivorans*. Nature. 2017; 544(6650): 353. https://doi.org/10.1038/nature22059 PMID: 28425998

13. Nguyen TT, Van Nguyen T, Ziegler T, Pasmans F, Martel A. Trade in wild anurans vectors the urodelan pathogen *Batrachochytrium salamandrivorans* into Europe. Amphibia-Reptilia. 2017; 38(4): 554–556. https://doi.org/10.1163/15685381-00003125

14. Berger L, Hyatt AD, Speare R, Longcore JE. Life cycle stages of the amphibian chytrid *Batrachochytrium dendrobatidis*. Dis Aquat Organ. 2005; 68:51–63. https://doi.org/10.3354/dao068051 PMID: 16465834

15. Laking AE, Ngo HN, Pasmans F, Martel A, Nguyen TT. *Batrachochytrium salamandrivorans* is the predominant chytrid fungus in Vietnamese salamanders. Sci Rep. 2017; 7: 44443. https://doi.org/10.1038/srep44443 PMID: 28267164

16. Yuan Z, Martel A, Wu J, Van Praet S, Canessa S, Pasmans F. Widespread occurrence of an emerging fungal pathogen in heavily traded Chinese urodelan species. Conserv Lett. 2018; 11: e12436. https://doi.org/10.1111/conl.12436

17. Gray MJ, Lewis JP, Nanjappa P, Klocke B, Pasmans F, Martel A, et al. *Batrachochytrium salamandrivorans*: the North American response and a call for action. PLoS pathog. 2015; 11(12): e1005251. https://doi.org/10.1371/journal.ppat.1005251 PMID: 26662103

18. Yap TA, Koo MS, Ambrose RF, Wake DB, Vredenburg VT. Averting a North American biodiversity crisis. Science. 2015; 349(6247): 481–482. https://doi.org/10.1126/science.aab1052 PMID: 26228132

19. Richgels KL, Russell RE, Adams MJ, White CL, Grant EHC. Spatial variation in risk and consequence of *Batrachochytrium salamandrivorans* introduction in the USA. R Soc Open Sci. 2016; 3(2): 150616. https://doi.org/10.1098/rsos.150616 PMID: 26998331

20. Feldmeier S, Schefczyk L, Wagner N, Heinemann G, Veith M, Lötters S. Exploring the distribution of the spreading lethal salamander chytrid fungus in its invasive range in Europe—a macroecological approach. PLoS one. 2016; 11(10): e0165682. https://doi.org/10.1371/journal.pone.0165682 PMID: 27798698

21. Katz TS, Zellmer AJ. Comparison of model selection technique performance in predicting the spread of newly invasive species: a case study with *Batrachochytrium salamandrivorans*. Biol Invasions. 2018; 20(8): 2107–2119. https://doi.org/10.1007/s10530-018-1690-7

22. Thuiller W, Richardson DM, Pyse P, Midgley GF, Hughes GO, Rouget M. Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. Glob Chang Biol. 2005; 11(12): 2234–2250. https://doi.org/10.1111/j.1365-2486.2005.001018.x

23. Phillips SJ, Dudík M. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography. 2008; 31(2): 161–175. https://doi.org/10.1111/j.0906-7590.2008.05203.x

24. AmphibiaWeb. Amphibia Web: Information on amphibian biology and conservation. 2018 [cited 10 July 2018]. Available from https://amphibiaweb.org/.

25. Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, et al. Terrestrial Ecoregions of the World: A New Map of Life on Earth. Bioscience. 2001; 51:933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

26. Spitzen-van der Sluijs A, Martel A, Asselberghs J, Bales EK, Beukema W, Bletz MC, et al. Expanding distribution of lethal amphibian fungus *Batrachochytrium salamandrivorans* in Europe. Emerg Infect Dis. 2016; 22(7): 1286. https://doi.org/10.3201/eid2207.160109 PMID: 27070102
Potential risk of Batrachochytrium salamandrivorans in Mexico

27. Beukema W, Martel A, Nguyen TT, Goka K, Schmeiler DS, Yuan Z, et al. Environmental context and differences between native and invasive observed niches of Batrachochytrium salamandrivorans affect invasion risk assessments in the Western Palaearctic. Divers Distrib. 2018; 1–14. https://doi.org/10.1111/ddi.12795

28. Rödder D, Kielgast J, Bielby J, Schmidtlein S, Bosch J, Garner TW, et al. Global amphibian extinction risk assessment for the panzootic chytrid fungus. Diversity. 2009; 1(1): 52–66. https://doi.org/10.3390/d1010052

29. Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. Very high resolution interpolated climate surfaces for global land areas. Int J Climatol. 2005; 25(15): 1965–1978. https://doi.org/10.1002/joc.1276

30. Warren DL, Gior RE, Turelli M. ENMTools: a toolbox for comparative studies of environmental niche models. Ecography. 2010; 33(3): 607–611. https://doi.org/10.1111/j.1600-0587.2009.06142.x

31. Muscarella R, Galante PJ, Soley-Guardia M, Boria RA, Kass JM, Uriarte M, et al. ENM eval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. Methods Ecol Evol. 2014; 5(11): 1198–1205. https://doi.org/10.1111/2041-210X.12261

32. Team, R C. R: A language and environment for statistical computing [Internet]. Vienna, Austria: R Foundation for Statistical Computing; 2015.

33. Phillips SJ. Transferability, sample selection bias and background data in presence-only modelling: a response to Peterson et al. (2007). Ecography. 2008; 31(2): 272–278. https://doi.org/10.1111/j.0906-7590.2008.5378.x

34. González BA, Samaniego H, Marín JC, Estades CF. Unveiling current Guanaco distribution in Chile based upon niche structure of phylogeographic lineages: andean puna to subpolar forests. PLoS One. 2013; 8(11):e78894. https://doi.org/10.1371/journal.pone.0078894 PMID: 24265726

35. Shrestha UB, Bawa KS. Impact of climate change on potential distribution of Chinese caterpillar fungus (Ophiocordyceps sinensis) in Nepal Himalaya. PLoS One. 2014; 9(9): e106405. https://doi.org/10.1371/journal.pone.0106405 PMID: 25180515

36. Castillo AG, Aló D, González BA, Samaniego H. Change of niche in guanaco (Lama guanicoe): the effects of climate change on habitat suitability and lineage conservatism in Chile. PeerJ. 2018; 6: e4907. https://doi.org/10.7717/peerj.4907 PMID: 29868293

37. Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, et al. Ecological niches and geographic distributions (MPB-49) (Vol. 56). 2011. Princeton University Press.

38. IUCN Red List of Threatened Species. Version 2018.2. www.iucnredlist.org. Downloaded on 20th Nov, 2018.

39. Darda DM. Allozyme variation and morphological evolution among Mexican salamanders of the genus Chiroteortriton (Caudata: Plethodontidae). Herpetologica. 1994; 164–187.

40. Parra-Olea G. Phylogenetic relationships of the genus Chiroteortriton (Caudata: Plethodontidae) based on 16S ribosomal mtDNA. Can. J. Zool. 2003; 81(12): 2048–2060. https://doi.org/10.1139/z03-155

41. García-Castillo MG, Soto-Pozos AF, Aguilar-López JL, Pineda E, Parra-Olea G. Two new species of Chiroteortriton (Caudata: Plethodontidae) from central Veracruz, Mexico. Amphib Reptile Conserv. 2018; 12(2): 37–54.

42. Stebbins RC, Cohen NW. A natural history of amphibians. Princeton University Press. 1997.

43. García-Castillo MG, Revoto SM, Wake DB, Parra-Olea G. A new terrestrial species of Chiroteortriton (Caudata: Plethodontidae) from central Mexico. Zootaxa. 2017; 4363(4), 489–505. https://doi.org/10.11646/zootaxa.4363.4.2 PMID: 29245387

44. Woolrich-Piña G, Smith GR, Lemos-Espinal JA, Zamora ABE, Ayala RM. Observed localities for three endangered, endemic Mexican ambystomatids (Ambystoma altamirani, A. leorae, and A. rivulare) from central Mexico. Herpetological Bulletin. 2017; 139: 13.

45. ESRI. ArcGIS-Arcmap 10.2. 2010. Environmental Systems Research Institute, Inc., USA.

46. Cunningham AA, Beckmann K, Perkins M, Fitzpatrick L, Cromie R, Redbond J. Emerging disease in UK amphibians. Vet Rec. 2015; 176(18): 468. https://doi.org/10.1136/vetrec-h2264 PMID: 25934745

47. Ochoa-Ochoa LM, Flores-Villela OA. Áreas de diversidad y endemismo de la herpetofauna mexicana. 1st ed. UNAM-COABIO, México, D. F. 2006.

48. Ochoa-Ochoa LM, Bezaury-Creel JE, Vázquez LB, Flores-Villela O. Choosing the survivors? A GIS-based triage support tool for micro-endemics: application to data for Mexican amphibians. Biol Conserv. 2011; 144(11): 2710–2718. https://doi.org/10.1016/j.biocon.2011.07.032

49. Parra-Olea G, Flores-Villela O, Mendoza-Almerrall C. Biodiversidad de anfibios en México. Rev Mex Biodivers. 2014; 85: 460–466. https://doi.org/10.7550/rmb.32027
50. Rosenblum EB, James TY, Zamudio KR, Poorten TJ, Ilut D, Rodriguez D, et al. Complex history of the amphibian-killing chytrid fungus revealed with genome resequencing data. Proc Natl Acad Sci U S A. 2013; 110(23): 9385–9390. https://doi.org/10.1073/pnas.1300130110 PMID: 23650365

51. Sabino-Pinto J, Veith M, Vences M, Steinfartz S. Asymptomatic infection of the fungal pathogen Batrachochytrium salamandrivorans in captivity. Sci Rep. 2018; 8(1): 11767. https://doi.org/10.1038/s41598-018-30240-z PMID: 30082745

52. Wake DB, Papenfuss TJ, Lynch JF. Distribution of salamanders along elevational transects in Mexico and Guatemala. Tulane Studies in Zoology and Botany, Supplementary Publication. 1992; 1: 303–319.

53. Muñoz ALA. Riqueza, diversidad y estatus de los anfibios amenazados en el sureste de México; una evaluación para determinar las posibles causas de la declinación de sus poblaciones. 2010 [cited 10 July 2018]. Colegio de la Frontera Sur, Departamento de Fauna Silvestre. Available from: http://sp13.cepf.net/Documents/final_Ecosur_amphibians_mexico.pdf/.

54. Meza-Parral Y, Pineda E. Amphibian diversity and threatened species in a severely transformed Neotropical region in Mexico. PloS One. 2015; 10(3): e0121652. https://doi.org/10.1371/journal.pone.0121652 PMID: 25799369

55. Ochoa-Ochoa LM, Mejía-Domínguez NR, Bezaury-Creel J. Priorización para la Conservación de los Bosques de Niebla en México. Ecosistemas. 2017; 26(2): 27–37. https://doi.org/10.7550/rmb.42588

56. Lips KR, Mendelson JR III, Muñoz-Alonso A, Canseco-Márquez L, Mulcahy DG. Amphibian population declines in montane southern Mexico: resurveys of historical localities. Biol Conserv. 2004; 119(4): 555–564. https://doi.org/10.1016/j.biocon.2004.01.017

57. Rovito SM, Parra-Olea G, Vásquez-Almazán CR, Papenfuss TJ, Wake DB. Dramatic declines in neotropical salamander populations are an important part of the global amphibian crisis. Proc Natl Acad Sci U S A. 2009; 106(9): 3231–3236. https://doi.org/10.1073/pnas.0813051106 PMID: 19204286

58. Mendoza-Almeralla C, Burrowes P, Parra-Olea G. La quitridiomicosis en los anfibios de México: una revisión. Rev Mex Biodivers. 2015; 86(1): 238–248. https://doi.org/10.7550/rmb.42588

59. López-Velázquez A. Ocurrencia de la quitridiomicosis en México. In: López-Velázquez A, Basanta MD, Ochoa-Ochoa LM, editors. Quitridiomicosis en México. Publicación especial de la Sociedad Herpetológica Mexicana A. C. 2018; pp. 35–52.