Anticipating the potential impacts of *Batrachochytrium salamandrivorans* on Neotropical salamander diversity

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Associate Editor: Jennifer Powers
Handling Editor: Amanda Zellmer

Abstract
Emergent infectious disease caused by the fungal pathogens *Batrachochytrium dendrobatidis* (*Bd*) and *Batrachochytrium salamandrivorans* (*Bsal*) represents one of the major causes of biodiversity loss in amphibians. While *Bd* has affected amphibians worldwide, *Bsal* remains restricted to Asia and Europe, but also could be a major threat for salamanders in the Western hemisphere, including the 320 bolitoglossine species described. Here, we predict the suitable areas for *Bsal* in the Neotropics and assess its potential impact on bolitoglossine diversity. For this, we determined the geographic patterns of taxonomic, phylogenetic, and functional diversity for bolitoglossines and modeled the potential distribution of *Bsal* in the Neotropics. We identified which species and regions could be at risk from an eventual introduction of *Bsal* in the region, quantified the degree of overlap between regions of high diversity and the suitable conditions for the pathogen, and considered species IUCN Red List status, and geographic range size. We found that regions of high taxonomic, phylogenetic, and functional diversity are concentrated in the Trans-Mexican Volcanic Belt, Sierra Madre Oriental, the southern portion of Sierra Madre del Sur and the mountains of Oaxaca in México, as well as the Chiapan-Guatemalan highlands, and the Cordilleras of Costa Rica and Panama. Alarmingly, the regions of high diversity for bolitoglossines and over 75% of the ranges of the more threatened species could be affected by *Bsal*.

Given the unknown vulnerability of these species, we strongly recommend measures to avoid the introduction of *Bsal* in the continent.

Abstract in Spanish is available with online material.

Keywords
amphibians, chytridiomycosis, decline, emergent diseases, extinction, species distribution models
1 | INTRODUCTION

Amphibians are one of the most threatened groups of vertebrates (Monastersky, 2014), with approximately 56% of described species experiencing population declines and even extinction in the last 40 years (Stuart et al., 2008; Wake & Vredenburg, 2008). One widely studied cause of amphibian declines is chytridiomycosis (Berger et al., 1999), an emergent infectious cutaneous disease caused by the fungal pathogens Batrachochytrium dendrobatidis (Bd) (Longcore et al., 1999) and Batrachochytrium salamandrivorans (Bsal) (Martel et al., 2013). While Bd disrupts osmoregulation and eventually leads to death (Van Rooij et al., 2015; Voyles et al., 2009), Bsal erodes skin, promoting secondary bacterial overgrowth that may result in lethal septicemia (Bletz et al., 2018). The presence of Bd has been linked to drastic population declines and extinctions of many amphibian species around the globe (Lambert et al., 2020; Scheele et al., 2019); meanwhile, the recent emergence of Bsal has been associated with rapid population collapses in European salamanders (Martel et al., 2014; Stegen et al., 2017).

Current evidence suggests that both fungal pathogens have their origin in East Asia (O’Hanlon et al., 2018). While Bd has been found in all regions of the globe where amphibians occur (Lips, 2016; Olson et al., 2013), the current known distribution of Bsal remains restricted to Asia and Europe (Beukema et al., 2018; Laking et al., 2017; Lötters et al., 2020; Martel et al., 2014; Yuan et al., 2018). The detection of Bsal in the pet trade suggests that this activity might be the primary cause for its spread to naïve regions and continents (Cunningham et al., 2015; Gray et al., 2015; Laking et al., 2017; Martel et al., 2014, 2020; Nguyen et al., 2017; Yuan et al., 2018). Additionally, experimental studies have demonstrated that Bsal infections are lethal to several North American salamander species from the Plethodontidae and Salamandridae families and cause more erosive skin lesions than Bd (Carter et al., 2020; Friday et al., 2020; Martel et al., 2014; North American Bsal Task Force, 2020). On the contrary, anurans might be more tolerant or resistant to Bsal, potentially acting as Bsal-reservoirs species (Martel et al., 2014; Stegen et al., 2017). Although some amphibian species may not become infected with Bsal and the knowledge on species-specific vulnerability to Bsal is still limited, the current evidence suggests that the introduction of Bsal in naïve ecosystems could be devastating, even in populations resistant or tolerant to Bd (Longo et al., 2019; Martel et al., 2014; Stegen et al., 2017). Therefore, the potential introduction and spread of this pathogen must be considered a latent threat for salamander-rich regions in continents where this pathogen is not currently present or still undetected (e.g., the Western hemisphere).

There are approximately 763 described salamander species worldwide, 75% of which occur in the New World (AmphibiaWeb, 2021). Among them, the most diverse group are the Neotropical salamanders (hereafter bolitoglossines: Wake, 2012) containing 320 species grouped in 14 genera within the family Plethodontidae (AmphibiaWeb, 2021). Bolitoglossines have radiated in mountainous regions of the Neotropics and most species exhibit micro-endemic distributions (Boza-Oviedo et al., 2012; García-París et al., 2000; Hanken & Wake, 1994; Parra-Olea et al., 2020). Their highly restricted distributions, together with significant ongoing threats, make species within this group highly prone to extinction (Ripple et al., 2017), with nearly 60% of its species categorized as Endangered (EN) or Critically Endangered (CR) on the International Union for Conservation of Nature Red List of Threatened Species™ (hereafter IUCN Red List of Threatened Species™: IUCN, 2021).

Historical declines in several bolitoglossine populations (e.g., Cheng et al., 2011; Olivares-Miranda et al., 2020; Parra-Olea et al., 1999; Rovito et al., 2009) have been associated with the presence of Bd within the geographic range of many bolitoglossines (Bolom-Huet et al., 2019; Olson et al., 2013; Zumbado-Ulate et al., 2019). Although Bsal still remains undetected in the New World (Parrott et al., 2017; Waddle et al., 2020), Neotropical amphibians have shown high vulnerability to chytridiomycosis caused by Bd (Lips et al., 2006; Scheele et al., 2019). Pioneering efforts to model the potential distribution of Bsal in new areas have been already conducted in the US, Europe, and Mexico (Basanta et al., 2019; Feldmeier et al., 2016; Katz & Zellmer, 2018; Richgels et al., 2016; Yap et al., 2015, 2017). Studies in North America have classified several salamander hotspots as suitable for Bsal (Basanta et al., 2019; Richgels et al., 2016; Yap et al., 2015). However, the potential effects of Bsal on the megadiverse bolitoglossine fauna across the entire Neotropical region have yet to be evaluated.

Currently, much of our knowledge of biodiversity is derived from analyses focused on the biological richness at the species level—that is, taxonomic diversity (TD) (Järzyna & Jetz, 2016). Although important, TD measures alone ignore species relatedness and ecological functions, limiting the understanding of the underlying processes of diversity patterns (Cardoso et al., 2014). In recent years, this species-based approach has been complemented with the quantification of the phylogenetic diversity (PD) and functional (FD) dimensions of biodiversity. While PD provides insights on the evolutionary history of the biotic assemblage (Faith, 2013), FD captures the diversity of relevant traits for ecosystem functioning (Petchey & Gaston, 2006). Efforts linking such dimensions have recently improved our understanding of the eco-evolutionary processes underlying the conformation of the rich amphibian biota in the Neotropics (Ochoa-Ochoa et al., 2020). A further required step is anticipating the potential impacts of contemporary threats (e.g., climate change, biological invasion, and emerging diseases) on such dimensions to develop effective and integrative conservation strategies.

In the specific context of emergent disease, identifying high-risk areas for the establishment of a pathogen and determining the most vulnerable host groups are essential to implement effective conservation strategies (Gray et al., 2015; Mendelson et al., 2019; Woodhams et al., 2011). Addressing these tasks from a framework that considers the multiple facets of salamander biodiversity and the potential areas the pathogen may colonize could ideally prevent or at least mitigate another collapse of the region’s amphibian fauna. Here, we assessed the potential impact of Bsal outbreaks on bolitoglossines using two different approaches: 1. Assemblage-based analyses to formally describe the geographic patterns of different facets of bolitoglossine biodiversity (i.e., taxonomic, phylogenetic, and functional) and determine...
their potential overlap with suitable areas for Bsal, and 2. Clade-based methods to determine which species could be at risk from an eventual introduction of Bsal in the region. Using species distribution modeling, phylogenetic approaches, and comparative methods, we identified both the geographic regions where most species occur and the portions of the bolitoglossine phylogeny that might be most drastically pruned. The incorporation of this eco-evolutionary perspective aims to better guide conservation priorities for these Neotropical species.

2 | METHODS

2.1 | Geographic patterns of bolitoglossine biodiversity

We compiled range maps for 304 bolitoglossine species (~95% of the bolitoglossines in the region) from the IUCN Red List of Threatened Species™ (IUCN, 2021). Because range polygons are based on collection points instead of suitability surfaces, they might potentially underestimate or overestimate the geographic range of some of our study species, especially those that lack many collection points (deficient species or species that have restricted distributions). This uncertainty in geographic area estimation can affect some of our metrics. However, to reduce geographic uncertainty, we used updated IUCN range polygons, which were generated by (1) plotting point data, (2) drawing a minimum convex polygon (MCP) around the points, (3) expanding the range considering the knowledge of habitat preferences, (4) removing areas known to be unsuitable (e.g., unsuitable habitat, elevation limits, or climate/temperature restrictions), and (5) smoothing polygons. Major modifications in range maps (steps 3 and 4) are based on IUCN protocols using environmental data and IUCN expert criteria (Bland et al., 2017; IUCN Red List Technical Working Group, 2018).

Additionally, we generated maps for other 16 bolitoglossines not included in the IUCN dataset, but for which occurrences were available in the literature or in the Global Biodiversity Information Facility (GBIF.org; Table S1), by applying 5-km radius buffers around each occurrence. By combining all maps, we were able to account for 100% of the region’s known salamander diversity. To describe relevant indicators of bolitoglossine diversity across space, we quantified five metrics within three dimensions of biodiversity: (a) taxonomic diversity (species richness and endemism), (b) phylogenetic diversity (Faith’s phylogenetic diversity and evolutionary distinctiveness), and (c) functional diversity (body size).

2.2 | Taxonomic diversity

We calculated two measures of taxonomic diversity: species richness and endemism. With the full set of range maps, we created a presence–absence matrix at 50-km resolution and estimated species richness by summing all species co-occurring within each grid cell using the R package “letsR” (Vilela & Villalobos, 2015). Given that spatially restricted species may be more prone to extinction risk (Gaston, 1996; Lawler et al., 2003), we also quantified a proxy of endemism by dividing species richness by the mean range sizes of the species occurring within each cell to obtain an estimation of corrected weighted endemism (Crisp et al., 2001). This metric highlights regions of high endemism by assigning greater proportional weight to pools of spatially restricted species. For both metrics, we used all bolitoglossine species with available geographic data (320 species) and performed the analyses using the R package “raster” (Hijmans & van Etten, 2010).

2.3 | Phylogenetic diversity

We calculated two measures of phylogenetic diversity: Faith’s phylogenetic diversity (PD) and evolutionary distinctiveness (ED). Conservation policy has found that the phylogenetic dimension of biodiversity is a valuable way to incorporate evolutionary history into decision-making (Faith, 2018; Isaac et al., 2007). Therefore, we reconstructed the phylogeny of bolitoglossines based on the matrix data used in Rovito et al. (2015), which includes seven mitochondrial markers (ND1, COI, COII, cyt b, tRNAs, 12S, and 16S) and three nuclear markers (POMC, RAG1, and SLC8A3). We compiled new data available from Genbank (www.ncbi.nlm.nih.gov) for these same markers to enhance the species representation in the phylogenetic reconstruction. With this process, we added 33 species (Table S2) to the Rovito, Vásquez-Almazán, et al. (2015) dataset for a total of 267 species included in our phylogeny, representing 83% of known bolitoglossines.

Using the CIPRES data portal (Miller et al., 2010), we conducted a Bayesian inference analysis in BEAST 1.8.2 (Drummond et al., 2012) with four chains of 50 million generations, sampled every 1000 generations. We configured the input file under the uncorrelated log-normal relaxed clock, with a Yule process tree prior. We assigned the substitution model to each partition according to the results estimated in PartitionFinder v1.0 (Lanfear et al., 2012). We used Tracer v1.7.1 (Rambaut & Drummond, 2007) to assess convergence of the runs, appropriate burn-in, and ensure that effective sample size values were sufficiently high (>200). Finally, a maximum clade credibility tree with median heights was calculated with TreeAnnotator 1.8.2 (Drummond et al., 2012).

With this tree, we estimated two evolutionary metrics that account for phylogenetic diversity: (1) Faith’s phylogenetic diversity (PD), which was calculated for the assemblage of all bolitoglossine species occurring in a given grid cell by summing up all their branch lengths (Faith, 1992). Because the branch lengths count the relative number of new features arising in a specific portion of a phylogenetic tree, the PD summarizes the evolutionary history accumulated by the set of species occurring in a given region. In contrast, (2) evolutionary distinctiveness (ED) is a metric that measures species uniqueness as determined by means of phylogeny (Redding & Mooers, 2006). ED scores are assigned to each species by applying a value to each branch equal to its length divided by the number of species composing the branch (Redding et al., 2008). With these
species’ values, we calculated means considering all species occurring in a grid cell. All phylogenetic analyses were conducted with the R package “ape” (Paradis & Schliep, 2019) over our newly generated phylogenetic hypothesis.

2.4 | Functional diversity

Finally, we calculated one value of functional diversity based on body size. Due to its capacity to reflect morphological, physiological, and ecological traits within biological communities, functional diversity provides relevant information to safeguard ecosystem functioning (Petchey & Gaston, 2006). Body size is a commonly used trait in functional ecology due to the availability of body measurements for many species and because it co-varies with many other species features (Gaston & Blackburn, 2008). To determine the variability of this trait, we estimated the standard deviation of adult body size based on the species assemblage occurring in each cell. For this, we compiled data on body size (measured as maximum snout-vent length—SVL) for 311 species (>95% of the total diversity of Neotropical salamanders) representing all genera included in this study. Maximum SVL data for each species were obtained from the literature and from direct measurements on museum specimens (Table S3).

2.5 | Climatic suitability for Bsal in the Neotropics

We estimated the potential distribution of Bsal in the Neotropics using the Maximum Entropy algorithm (MaxEnt; Phillips et al., 2006). To build the models, we gathered data of proven presence for Bsal available in Beukema et al. (2018), Dalbeck et al. (2018), Feldmeier et al. (2016), Laking et al. (2017), Lötters et al. (2018, 2020), Martel et al. (2013, 2020), Sluijs et al. (2016) and Yuan et al. (2018), and eliminating duplicates. The updated combined dataset consists of 32 unique localities for Asia and 16 for Europe (Table S4). Further details on the climatic predictors used as well as on the model tuning and evaluation approaches are thoroughly described in Appendix S1.

2.6 | Regions and species potentially threatened by Bsal

We used our maps of bolitoglossine biodiversity and the potential distribution of Bsal to define priority regions for conservation. To this end, we overlaid the prediction of Bsal suitability with each of the six regional maps of diversity using ArcGIS v.10.2 (ESRI, 2010). We then identified the highest-risk areas as those where high Bsal suitability (>0.7) and high bolitoglossine diversity overlapped.

We also used a cross-species approach to define species at risk by Bsal. In this case, we first converted the prediction of Bsal suitability (logistic output) to a binary presence-absence map of potential distribution for the pathogen using the equal training sensitivity and specificity threshold (Liu et al., 2005). Additionally, we used the minimum training threshold for a sensitive analysis. To keep the more conservative approach, we downstream analyses using the equal training sensitivity and specificity threshold. This threshold is considered conservative and suitable for the purpose of delimiting priority conservation areas based on the precautionary principle (Liu et al., 2005). Then, using ArcGIS v.10.2 (ESRI, 2010) we estimated the overlap among Bsal and each species range polygon to quantify the proportion of the range that is predicted to be suitable for the pathogen. We also mapped species-specific information on conservation status according to the IUCN Red List (IUCN, 2021) across the bolitoglossine phylogeny. To facilitate visualization, we split the phylogeny into those belonging to the genus Bolitoglossa and species in the other genera. Finally, to define species’ risk, we ranked them considering a higher risk for those having (1) a category of EN or CR according to the most recent IUCN Red List assessment, (2) the most restricted distributions, and (3) a high percentage of their geographic range suitable for Bsal.

3 | RESULTS

3.1 | Geographic patterns of bolitoglossine biodiversity

The highest levels of bolitoglossine species richness were associated with high elevation sites, especially in Costa Rica (where some cells had up to 13 species), Mexico, Guatemala, and Panama (with up to nine species per cell in some regions). Furthermore, we found that the most important centers of endemism occurred in the same countries, with the highest scores in the Sierra Madre Oriental and the southern portion of Sierra Madre del Sur in México, the Chiapan-Guatemalan highlands, and the Cordilleras of Costa Rica and Panama (Figure 1a).

Our results showed the highest accumulation of evolutionary history (Faith’s PD) in the Costa Rican highlands and the Trans-Mexican Volcanic Belt, where PD reaches values of 0.98 and 1.06, respectively. The mountains of Oaxaca in Mexico and the Guatemalan assemblages showed intermediate values for this metric, ranging between 0.62 and 0.86. Regarding evolutionary distinctiveness (ED), we found the highest values for this metric in the eastern portions of the Trans-Mexican Volcanic Belt and the Sierra Madre del Sur in Mexico, the complex of Guatemalan highlands (e.g., Sierra de los Cuchumatanes and Sierra de las Minas), the Cordillera Nombre de Dios in Honduras, and the Cordillera Volcánica Central and the Cordillera de Talamanca in Costa Rica and Panama (Figure 1b).

The distribution of body size showed the highest variability (SD of maximum SVL) in some Mexican regions, including the mountains of Oaxaca and sections of the Trans-Mexican Volcanic Belt (Figure 1c). In some of these regions, species may vary in size between 166 mm SVL (Isthmura gigantea) and <25 mm SVL (e.g., Parvimolge or Thorius spp).
The best-fit species distribution model for Bsal had a parametrization of regularization multiplier of four with a linear–quadratic–product (LQP) feature class combination (Table S6). This model showed good performance with high accuracy (average test AUC = 0.88, omission rate = 0% at minimum training presence, 0.13% excluding the 10 percent of training localities with the lowest predicted suitability). For the independent validation, this model assigned a mean suitability of 0.84 for the validation.
occurrences, and a 0% omission rate for the equal training sensitivity and specificity threshold (logistic threshold = 0.271; Table S6) applied. The MESS analysis also confirmed the similarity of climatic conditions between the current niche of Bsal in Europe and Asia with that of the Neotropics (Figure S2). The climatic predictor with the highest contribution to the species distribution model was the maximum temperature of warmest month (BIO5), which explained 53.6% of the predicted distribution of Bsal.

The projected model into the Neotropics (Figure 2; Figure S3) predicted variable levels of suitability for Bsal occurrence, with the highest suitability values in the Trans-Mexican Volcanic Belt, Sierra Madre Oriental, Sierra Norte de Oaxaca and the Caribbean coasts of Mexico and Central America. In South America, the highest Bsal suitability was found in the Andean region, eastern and southern Amazon, and the northeastern coasts of Brazil (Figure 2a). Our binary map predicted a potential distribution of Bsal in more than 65% of the Neotropical region, including the Trans-Mexican Volcanic Belt, Sierra Madre del Sur, Sierra Madre Oriental, Sierra Norte de Oaxaca, Caribbean coasts, mountain ranges of Central America, Andean, and Amazon regions of South America (Figure 2b).

3.3 | Regions and species potentially threatened by Bsal

We found a high concordance between high suitability areas for Bsal and high bolitoglossine diversity (Figure 3). The mountains of Costa Rica (e.g., Cordillera de Talamanca) and Mexico (e.g., eastern Trans-Mexican Volcanic Belt) were the regions with the highest overlap in all indexes. Hotspots of taxonomic diversity, such as the Sierra Madre Oriental, the extreme eastern Trans-Mexican Volcanic Belt, southeastern Sierra Madre del Sur, mountains of Chiapas in Mexico, and the major mountain ranges of Guatemala, Honduras, and Costa Rica, were all suitable for Bsal (Figure 3a). Similarly, the pathogen shows high expected suitability in regions of high phylogenetic diversity, including some of the previously cited speciose mountain ranges and other regions, such as the highlands of the northern portion of nuclear Central America (Figure 3b). Regions hosting high functional diversity for neotropical salamanders also are within areas with high suitability for Bsal (Figure 3c).

The potential distribution of Bsal coincides to some degree with the distribution of 88% of bolitoglossine species (Table S8). We found that at least 75% of the geographic ranges of 71 Bolitoglossa species are predicted to be suitable for Bsal (Figure 4a). We found a similar pattern in another 110 species of other genera of bolitoglossine salamanders (Figure 4b). In general, nearly a third of the studied species (90 out 309 excluding 11 which are considered possibly extinct) are categorized as EN or CR on the IUCN Red List, and over 75% of their ranges could be affected by Bsal (see Table S8 for the complete species ranking).

4 | DISCUSSION

Our results suggest that the potential introduction of Bsal in the Neotropics could severely affect the taxonomic, phylogenetic, and
functional diversity of bolitoglossines in a scenario where all species are assumed to be equally vulnerable. Using multiple metrics to quantify different facets of biodiversity with suitability predictions for \textit{Bsal}, we identified the regions where the outbreaks of \textit{Bsal} would be more likely to occur, potentially leading the more vulnerable species to decline. Our hope is these results can be used to identify high-priority areas and species that require immediate conservation actions and to implement effective and long-term interventions that favor the conservation of relevant habitats for these organisms. Additionally, our results highlight the urgent need to establish protocols that prevent the introduction of \textit{Bsal} into the Neotropics.

Our analyses identified at least eight different hotspots for bolitoglossine diversity in the Neotropics. We found that the highest values for all five metrics converge in Mexico and Costa Rica. The highest concentration of species richness occurred in several mountain ranges of Costa Rica. In this region, the Cerro de La Muerte-Tapanti massif has been identified as one of the highest areas of bolitoglossine species richness in the Neotropics with 18 species (García-Paris et al., 2000). The highest levels of endemism occurred principally in mountainous landscapes of Mexico, Guatemala, and Costa Rica, where the mosaic of peaks and valleys had shaped micro-endemic distributions, with many species restricted to highland forests (Boza-Oviedo et al., 2012; Rovito, Vásquez-Almazán, et al., 2015). These montane species usually show high levels of isolation and unique environmental adaptations that make them more prone to extinction in the face of current and future threats (Böhm et al., 2016; Cooper et al., 2008; La Sorte & Jetz, 2010).

In accordance with previous analyses at the genus level for salamander diversity across the Neotropics (Wake & Lynch, 1976), phylogenetic diversity is higher in Central Mexico and Costa Rica. This reflects the heterogeneous evolutionary histories contained in these regions, which are among the most important diversification centers for bolitoglossines (Rovito et al., 2015). Evolutionary distinctiveness is most evident in Costa Rica and portions of Mexico, but also in northern Guatemala and Honduras. Evolutionary distinct species represent highly isolated portions of the bolitoglossine phylogeny or representatives lacking close relatives (Redding & Mooers, 2006). For example, the species \textit{Parvimolge townsendi} (Mexico), \textit{Nycanotis pernix} (Guatemala and Mexico), and \textit{Bradytriton silus} (Guatemala and Mexico) belong to monospecific genera and are endemic to a few localities.

The functional diversity inferred from body size is notably high in Mexico. Typically, bolitoglossines range between small and medium body sizes (40–80 mm); however, Mexico is home to both miniaturized genera, such as \textit{Thorius} with some species below 19 mm SVL, and \textit{Isthmura} species exceeding 160 mm (Decena-Segarra et al., 2020). This particular trait has been widely used as a proxy of ecological interactions (Jobe et al., 2019; Rudolf et al., 2014); therefore, important hotspots of functional diversity could be mirrored in the regions showing high variability in body size. Recent evidence shows that higher functional diversity in Neotropical amphibians is strongly linked to high humidity and low precipitation seasonality (Ochoa-Ochoa et al., 2019). Such conditions are more common in mountainous regions that we also identify as relevant for the different facets of bolitoglossine biodiversity. Certainly, these regions require special attention for its conservation as species inhabiting there face multiple threats such as emerging disease and future climate change.

Modeling and projecting the potential distribution of alien organisms are particularly challenging due to the limited available...
data and the lack of equilibrium between the organisms and their environment in ongoing invasions (Elith et al., 2010; Katz & Zellmer, 2018; Václavík & Meentemeyer, 2012). To optimize our predictions and improve model transferability (Liu et al., 2020; Yates et al., 2018), we built our SDMs using exclusively proven presences of the pathogen, and given the few and clustered existing occurrence for Bsal, we used the combination of both presences from the native and invaded range to better depict the pathogen’s niche. Moreover, we implemented a partition method that improve spatial independence of training and test data for a more robust spatial cross-validation, we used the combination of both presences from the native and invading range to better depict the pathogen’s niche. Furthermore, we included the presence of other species that might be more susceptible to Bsal, thereby favoring the long-term persistence of the pathogen in the environment (Stegen et al., 2017). Therefore, studies to detect and quantify the presence of Bsal in wild amphibians, especially from the diversity hotspots where the effects of Bsal could be the most catastrophic, are urgently needed.

Our Bsal distribution model was developed based on the climate niche of Bsal, assuming equal vulnerability across hosts. Although some species could be more tolerant than others (Martel et al., 2014), by assuming equal vulnerability across hosts we followed the precautionary principle for conservation and decision-making purposes (Persson, 2016). A recent work testing Bsal susceptibility specifically in plethodontid salamanders showed a wide spectrum of responses from species experiencing rapid and high mortality to species with moderate infections (Direnzo et al., 2021). However, for bولitoglossines the evidence remains restricted to two species (Chiropterotriton sp., Aquileuroceya cephalica) (North American Bsal Task Force, 2020) for whose susceptibility trials of Bsal infection have shown the development of disease. Then, further research is needed to understand the potential vulnerability of bولitoglossines to Bsal infection and to design and inform effective conservation strategies.

The potential distribution for Bsal also corresponds with some areas of the predicted distribution of Bd at both the regional level (Ron, 2005) and the country level in Mexico (Bolom-Huet et al., 2019) and Costa Rica (Zumbado-Ulate et al., 2020). Many amphibian species within these countries have suffered catastrophic declines associated with Bd infection (Cheng et al., 2011; Lips, 1998; Zumbado-Ulate et al., 2019), yet Bd suitability models were not generated until several decades after the introduction of the pathogen. Recent studies have shown that simultaneous infections with Bd and Bsal (1) may affect salamander populations more severely than Bsal infection alone (Longo et al., 2019; McDonald et al., 2020) and (2) that pre-existing Bd infections in some species may protect against Bsal (Greener et al., 2020). Given that both scenarios could be possible in the region, our suitability map also establishes a powerful predictive tool, especially in areas with current Bd infections in the Neotropics, as our knowledge on co-infection dynamics improves.

Our study suggests that most bولitoglossine diversity could be at risk if Bsal is introduced into the Neotropics. In this scenario, preventing the introduction of Bsal in the Neotropics is imperative for the
conservation of bolitoglossines. For this reason, we urge decision-makers to implement surveillance protocols and enact legislation to avoid the spread of Bsal into these high-diversity Neotropical regions. Furthermore, the anticipated development of conservation strategies should include continuous monitoring of priority regions that host high taxonomic, phylogenetic or functional diversity, and in particular, species whose future persistence might be jeopardized by Bsal.

ACKNOWLEDGEMENTS

We thank Eric Arias for providing some relevant genetic sequences for our phylogeny. AGR thanks Dirección General de los Asuntos del Personal Académico (DGAPA), National Autonomous University of Mexico for financial support through a postdoctoral fellowship at Instituto de Biología, UNAM. MDB and GPO thank CONACyT for assistant research scholarship (CVU/Exp. Ayte/Exp. Inv.: 509293/19525/26435).

AUTHOR CONTRIBUTIONS

AGR, MDB, MGC, and HZU conceived and designed the project. AGR, MDB, MGC, SMR, and KN involved in acquisition of data. AGR, MDB, and MGC performed the analyses. All authors interpreted the data. AGR, MDB, MGC, SMR, and KN involved in acquisition of data. AGR, MGC, and HZU wrote the first draft of the manuscript, and all authors contributed to the improvement of the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.vq83bk3tg (García-Rodríguez et al., 2021).

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**How to cite this article:** García-Rodríguez, A., Basanta, M. D., García-Castillo, M. G., Zumbado-Ulate, H., Neam, K., Rovito, S., Searle, C. L., & Parra-Olea, G. (2022). Anticipating the potential impacts of *Batrachochytrium salamandrivorans* on Neotropical salamander diversity. *Biotropica*, 54, 157-169. https://doi.org/10.1111/btp.13042