

RESEARCH ARTICLE

A spatially explicit risk assessment of salamander populations to *Batrachochytrium salamandrivorans* in the United States

Michael Moubarak¹  | Ilya R. Fischhoff² | Barbara A. Han² | Adrian A. Castellanos²

¹Hamilton College, Clinton, New York, USA

²Cary Institute of Ecosystem Studies, Millbrook, New York, USA

Correspondence

Michael Moubarak, Hamilton College, Clinton, NY, USA.

Email: moubarak.michael@gmail.com

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Abstract

Aim: Amphibian populations are threatened globally by anthropogenic change and *Batrachochytrium dendrobatidis* (Bd), a fungal pathogen causing chytridiomycosis disease to varying degrees of severity. A closely related new fungal pathogen, *Batrachochytrium salamandrivorans* (Bsal), has recently left its supposed native range in Asia and decimated some salamander populations in Europe. Despite being noticed initially for causing chytridiomycosis-related population declines in salamanders, Bsal can also infect anurans and cause non-lethal chytridiomycosis or asymptomatic infections in salamanders. Bsal has not yet been detected in the United States, but given the United States has the highest salamander biodiversity on Earth, predictive assessments of salamander risk to Bsal infection will enable proactive allocation of research and conservation efforts into disease prevention and mitigation.

Location: The United States, Europe and Asia.

Methods: We first predicted the environmental suitability for the Bsal pathogen in the United States through an ecological niche model based on the pathogen's known native range in Asia, validated on the observed invasive range in Europe using bioclimatic, land cover, elevation, soil characteristics and human modification variables. Second, we predicted the susceptibility of salamander species to Bsal infection using a machine-learning model that correlated life history traits with published data on confirmed species infections. Finally, we mapped the geographic ranges of the subset of species that were predicted to be susceptible to Bsal infection.

Results: In the United States, the overlap of environmental suitability and susceptible salamander species was greatest in the Pacific Northwest, near the Gulf of Mexico, and along the Atlantic coast, and in inland states east of the Plains region.

Main Conclusions: The overlap of these metrics identify salamander populations that may be at risk of developing Bsal infection and suggests priorities for pre-emptive research and conservation measures to protect at-risk salamander species from an additional pathogenic threat.

KEYWORDS

boosted regression tree, chytrid, conservation, disease susceptibility, salamander, ecological niche model, emerging infectious disease, invasive pathogen, pathogen suitability

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1 | INTRODUCTION

Globally threatened by multiple stressors, including climate change and habitat destruction, amphibians are on track for mass extinction (Alroy, 2015; IUCN, 2020; Wake & Vredenburg, 2008). The infectious disease chytridiomycosis, caused by two pathogenic chytrid fungi, *Batrachochytrium dendrobatidis* (*Bd*) and *B. salamandrivorans* (*Bsal*), has also precipitated startling declines in amphibian populations (Cheng et al., 2011; Stegen et al., 2017) and contributes substantially to the global loss of amphibians (Yap et al., 2017). *Bd* was described in 1999 (Longcore et al., 1999) prior to *Bsal*, which was first described in 2013 (Martel et al., 2013), and has since infected more than 1300 amphibian species (Olson et al., 2021). Although susceptibility to both pathogens varies among species (Bancroft et al., 2011; Carter et al., 2020; Gervasi et al., 2017; Sabino-Pinto et al., 2018), *Bd* has led to the population decline of over 200 frog species (Skerratt et al., 2007) and continues to threaten amphibian biodiversity over 20 years later (Fisher & Garner, 2020). Some evidence suggests that *Bsal* is endemic to Asia and spread to Europe around the late 2000s. Laboratory studies show that many salamander species in Europe (Martel et al., 2014) and at least one anuran (Towe et al., 2021) are susceptible to infection. Lethal infection was observed in wild populations of fire salamanders (*Salamandra salamandra*) in the Netherlands, Belgium, and Germany and northern crested newts (*Triturus cristatus*) at two sites in Germany (Lötters et al., 2020; Martel et al., 2013). There is currently no evidence for *Bsal* presence in North America (Klocke et al., 2017; Koo et al., 2021; Waddle et al., 2020), but due to the continent's high salamander biodiversity, invasion of *Bsal* poses a serious threat to North American ecosystems (Richgels et al., 2016; Yap et al., 2015). Given the potentially devastating effects of *Bsal* on salamander populations in the United States, identifying vulnerable regions and species will inform prevention and mitigation efforts.

Bsal is thought to have originally spread from its endemic range in Asia to Europe through the trade of wild-caught salamanders (Fitzpatrick et al., 2018), which supports a focus on import centres as the potential entry point of *Bsal* (Richgels et al., 2016; Yap et al., 2015). In the United States, assessments of salamander importation and trade centres, together with predicted environmental suitability and salamander richness, suggest preventative action could benefit the Pacific coast, southern Appalachian Mountains and mid-Atlantic regions, which have the highest risk of *Bsal* infection (Richgels et al., 2016; Yap et al., 2015). In previous studies, environmental suitability for *Bsal* was predicted by comparing county-level temperatures with laboratory-measured optimal temperatures for *Bsal*. Here, we expand on this work by considering multiple environmental factors that influence environmental suitability for the *Bsal* pathogen. Even if various environments are suitable for the *Bsal* pathogen, there is wide variation in host responses to infection. As *Bsal* is known to display a wide range of pathogenicity among host species (Carter et al., 2020; Sabino-Pinto et al., 2018), we also model differential host susceptibility to *Bsal* among salamanders.

We applied presence-only ecological niche modelling (ENM) to *Bsal* using a suite of environmental predictors known to influence other chytrid fungi, including *Bd* (Murray et al., 2011; Olson et al., 2013, 2021; Xie et al., 2016). ENM estimates the geographical distribution of an organism's environmental suitability based on correlations between the presence of the species and local multi-dimensional environmental constraints on that species, such as temperature and precipitation. Allowing for the opportunistic use of available data, presence-only methods do not require explicit absence information, instead using pseudo-absence or background points to sample the environmental conditions in the study area (Johnson et al., 2019).

A previous study used an ENM based on the range of native host species in Asia to investigate the suitability of *Bsal* in the United States (Yap et al., 2015). In their study, the southeastern US and Pacific Coast were predicted to have the highest risk for *Bsal*. The most active ports for salamander trade were within areas of high species richness and high predicted suitability for *Bsal*. However, suitability predictions for the United States that extrapolate from *Bsal*'s native range in Asia (Yap et al., 2015) may not accurately capture potential co-occurrences of *Bsal* and susceptible hosts in the United States due to two challenges that we address.

The first challenge in predicting the places and species most at risk in the United States is that environmental conditions in the US may not match the native range and may be differentially suitable for the *Bsal* pathogen and its native hosts, raising the question of whether an ENM based on data from Asia can make accurate predictions in the potential US range. To address this challenge, we train our ENM using occurrence data of the *Bsal* pathogen in the native range and assess its performance on the European invasive range where some *Bsal* occurrences already exist. Yap et al. (2015) used occurrences of *Bsal* salamander hosts as a proxy for *Bsal* occurrence data. However, evidence combining wild sampling with laboratory studies of infection susceptibility suggests that *Bsal* pathogen and host ranges do not overlap completely in the native range (Feldmeier et al., 2019). Thus, environmental suitability models based on host ranges (e.g. Yap et al., 2015) may inaccurately represent parts of the pathogen's niche. Furthermore, particular combinations of environmental conditions in invasive ranges may not exist in Asia, hampering the ability to make predictions into those areas (Owens et al., 2013). In contrast to *Bd* (Weldon et al., 2004), *Bsal* has more recently left its native range and invaded other areas, suggesting its invasive range is not fully realized (Beukema et al., 2018). We explicitly check for the feasibility of transferring model predictions outside of the native range using Europe as an example of *Bsal* invasion, similar to the methods used for predicting the range of *Bsal* in Mexico by Basanta et al. (2019), and by identifying areas of high environmental dissimilarity from the native Asian range in Europe and the United States (Owens et al., 2013).

The second challenge is that *Bsal* infection in the United States requires the presence of susceptible salamanders, and salamanders vary widely in their susceptibility to *Bsal*. For example, in a laboratory test, *Ambystoma maculatum* was resistant to *Bsal* infection, while infection

was lethal in *Hydromantes strinatii* (Martel et al., 2014). However, previous risk assessments do not explicitly incorporate these differences in risk evaluation. Instead, these studies (e.g. Richgels et al., 2016; Yap et al., 2015) assess where salamander species richness overlaps with *Bsal* suitability, which oversimplifies the range of potential responses that salamanders may have to the pathogen. We directly model the susceptibility of salamander species using intrinsic traits to predict which species may be susceptible to *Bsal* infection.

Determinations of *Bsal* susceptibility across host species require either positive field samples from infected individuals, or experimental inoculations of individuals from multiple species with *Bsal* in controlled laboratory settings. As a result, comparative data on species susceptibility remain limited. Moreover, some salamanders are asymptomatic to *Bsal* infection (Carter et al., 2020; Sabino-Pinto et al., 2018), making visual inspection an unreliable diagnostic for field surveys. While lab and field confirmations of differential susceptibility remain sparse, intrinsic traits underpinning this differential susceptibility are more abundant. Traits are informative about species susceptibility to pathogens because of evolutionary linkages and trade-offs between these traits and immune defence in vertebrates (Becker et al., 2018; Butler et al., 2013). Trait-based modelling has been applied successfully in the past for predicting hosts of other pathogens in both amphibians (*Bd*: Gervasi et al., 2017; Greenberg et al., 2017; Bancroft et al., 2011; ranaviruses: Hoverman et al., 2011) and mammals (zoonotic pathogens: Han et al., 2020; Yang & Han, 2018; Han et al., 2015). To make species-level predictions for salamander susceptibility, we constructed a trait-based machine-learning model of *Bsal* susceptibility. Similar to past studies for *Bd* (Bancroft et al., 2011; Greenberg et al., 2017), we modelled whether intrinsic traits accurately predict confirmed infection with *Bsal*. Traits include qualitative and quantitative features of a species' ecology (e.g. habitat, diet), morphology (e.g. body mass, longevity), and reproduction (e.g. clutch size, breeding strategy).

Together, machine-learning models of environmental suitability and host susceptibility to infection can generate useful predictions about the risk of salamander populations to *Bsal* infection in the United States. While previous assessments define risk at the intersection of salamander imports, salamander species richness and environmental suitability for the host or the pathogen (e.g. Richgels et al., 2016; Yap et al., 2015), we sought to identify locations where biological interactions may lead to *Bsal* occurrence through a suitable environment that leads to plausible exposure and infection in susceptible salamander species. Herein, we describe areas within the United States that appear to provide the most suitable environments for the *Bsal* pathogen and also overlap the geographic ranges of particular salamander species predicted to be susceptible to *Bsal* infection.

2 | METHODS

We combined two models to create a spatially explicit risk assessment for salamander infection by *Bsal*. First, we used an ENM to

determine the environmental suitability of the *Bsal* pathogen, trained on its native range in Asia. We projected this output into the invaded range of Europe to check model accuracy, and then made predictions to the yet to be invaded US. Second, we applied a machine-learning model to intrinsic traits to classify salamander species susceptibility to *Bsal* infection, which was trained on all salamander species and their current infection status. By combining these two methods, we determine where in the United States there is both a high likelihood of ecological suitability for *Bsal* and the presence of salamanders most likely to be susceptible to infection.

2.1 | Ecological niche model

To predict the environmental suitability of *Bsal* in the United States, we used the MaxEnt algorithm as implemented in the 'dismo' package version 1.1-4 (Hijmans et al., 2017; Phillips & Dudík, 2008) in R version 4.0.1 (R Core Team, 2020). We collected spatially explicit datasets for variables deemed potentially important for predicting *Bsal* occurrence based on past research. These variables were used to create an ENM of *Bsal* in its native range in Asia. To assess how well our model of *Bsal* in the native range transfers to a known invasive range for the pathogen, we tested the accuracy of model predictions for *Bsal* occurrences in its European invasive range. Testing the model on another invasive range guided our interpretation of its efficacy outside of the native range, because there are no recorded occurrences of *Bsal* to validate the model's accuracy in the United States. Based again on the model of the native range, we then made predictions about the occurrence of *Bsal* in the United States.

2.1.1 | Data collection and preparation

For training, evaluating and applying the model, we defined three study extents in Asia, Europe and the United States, respectively. The native study extent in Asia encompassed an area 20 percent greater than the range of native *Bsal* host species determined by Yuan et al. (2018), Laking et al. (2017), and Martel et al. (2014). Range maps for these species are made available by the International Union for the Conservation of Nature Red List (IUCN, 2020). We used the same European study extent defined in Beukema et al. (2018) for the invasive range. Finally, our study extent for the United States bounded the lower 48 states. Occurrence points for *Bsal* in Asia ($n = 34$) and Europe ($n = 19$) were taken from González et al. (2019) and Beukema et al. (2018). All of our predictor variables were cropped to the three study extents and resampled to achieve a spatial resolution of 10 kilometres, which was chosen to capture the uncertainty in the location of *Bsal* occurrence points due to variable location measurement precision.

Background points were sampled randomly and guided by salamander occurrences in the native range to reflect locations within the study extent that would be reasonable places for *Bsal* to exist based on expected salamander presence. We downloaded salamander occurrences from the Global Biodiversity Information Facility

(GBIF) in the native range (GBIF.org, 2020a, 2020b), and we eliminated entries with spatial uncertainty higher than our study resolution, no coordinate data, duplicates or other common issues flagged by GBIF. For remaining occurrences, we defined a buffer of 50 km around each point and sampled 10,000 points randomly within the cumulative area across those buffered areas.

Previous studies have shown that anthropogenic environmental stressors, like distance to urban areas and land use, (Bacigalupe et al., 2019; Spitzen-Van Der Sluijs et al., 2014), elevation (Bacigalupe et al., 2019; Bielby et al., 2008; Olson et al., 2013), land cover (McMillan et al., 2020; Murray et al., 2011; Scheele et al., 2015), soil pH (Kärvemo et al., 2018) and climate (Basanta et al., 2019; Beukema et al., 2018; Puschendorf et al., 2009; Rödder et al., 2009) constrain *Bd* or *Bsal*, which warranted inclusion of these variables in our model. We also included soil organic carbon because salamanders increase litter retention and carbon capture (Best et al., 2014). We predicted that areas of higher soil organic carbon may indicate places with more salamanders, which may increase habitat suitability for *Bsal*. Encompassing all of these variables, we gathered data on Global Human Modification (GHM) (Kennedy et al., 2019), elevation and continuous estimates of 12 land cover classes from EarthEnv (Amatulli et al., 2018; Tuanmu & Jetz, 2014), soil pH and organic carbon data (Hengl et al., 2017), and 19 bioclimatic variables from Worldclim 2.1 (Fick & Hijmans, 2017) (see Table S1.1 for specific variables).

2.1.2 | Variable selection for model

We removed highly correlated variables as determined by a Pearson's correlation coefficient of greater than or equal to 0.8. In the event that multiple variables were highly correlated with one another, we used a principal component analysis (PCA) of all environmental variables cropped to the native study extent to assist variable selection. In this situation, we selected the variable driving most of the variation in PCA axes comprising 90% of the variation. Our retained variables were BIO-2 (mean diurnal temperature range), BIO-3 (isothermality), BIO-4 (temperature seasonality), BIO-9 (mean temperature of the driest quarter of the year), BIO-14 (precipitation of the driest month of the year), BIO-15 (precipitation seasonality), BIO-18 (precipitation of the warmest quarter of the year), BIO-19 (precipitation of the coldest quarter of the year), all land cover classifications (see Table S1.1 for bioclimatic variable definitions and equations and land cover types), elevation, soil pH and soil organic carbon.

2.1.3 | ENM implementation and prediction

We used the MaxEnt algorithm to create ENMs given previous research on its efficacy with small sample sizes (Wisz et al., 2008) and for comparison with previous *Bsal* ENMs (Basanta et al., 2019; Beukema et al., 2018; Yap et al., 2015). We created an ENM using the *Bsal* pathogen occurrence data, background points and environmental variables

associated only with the pathogen's native range (Basanta et al., 2019). We used the R package 'ENMeval' (Muscarella et al., 2014) to parameterize this model and choose appropriate regularization multipliers and feature classes. Model parameters were chosen based on minimizing Akaike's Information Criteria for small sample sizes (AICc), unless a less complex model was not noticeably different in AICc.

Then, using the MaxEnt model we created in the native range, we predicted the environmental suitability for *Bsal* across the native, invasive and US ranges. We used both threshold-independent and threshold-dependent metrics to evaluate our model in the native range: area under the curve (AUC), omission rate and true skill statistic (TSS) (see Appendix S1 for more detail). To identify areas of high dissimilarity between the native range and either Europe or the United States we used mobility-oriented parity (MOP) surfaces, as described by Owens et al. (2013) and implemented using the 'kuenm' package in R (Cobos et al., 2019). Areas that differ completely from environmental conditions in the native range are visualized on our suitability prediction maps to guide interpretation (see Appendix S1). We also compared the permutation importance of each of our predictor variables in the final model (see Figure S2.1) and plotted the relationship between the values of each predictor and its prediction values for the likelihood of *Bsal* occurrence (see Figure S2.2). To inform areas of potential conservation concern, we show which regions of the United States contain the highest suitability to *Bsal* based on the ENM.

2.2 | Boosted regression tree analysis

To predict which salamander species are most susceptible to *Bsal* infection, we correlated salamander life history traits with *Bsal* susceptibility in each species using boosted regression trees (BRT) (Elith et al., 2008; see Appendix S1). We collected species from the literature with recorded *Bsal* infection tests to determine infection susceptibility. We then applied the fitted model to predict *Bsal* susceptibility for all species. Then, drawing on geographic range maps for salamander species, we made a risk map of the United States depicting regions with the highest richness of salamander species that were also predicted by our model to be susceptible to *Bsal*.

2.2.1 | Data collection

We gathered records from past studies that tested for *Bsal* infection or lack of infection across species. A series of Google Scholar searches with the search terms "Batrachochytrium salamandrivorans" and "infection" or "experiment" were used to find relevant studies. We distinguish surveys of *Bsal* infection in the wild versus studies of captive or experimental animals, because a negative test result for a wild population of salamanders may reflect the absence of *Bsal* in the area rather than a species' resistance to the fungus. We were more confident that negative test results reflected resistance to the fungus in captive studies than in wild studies, because *Bsal* is

considered to be widespread in captive (pet) populations in Europe (Sabino-Pinto et al., 2018), where the majority of captive studies occurred (Fitzpatrick et al., 2018; Sabino-Pinto et al., 2018). Similarly, we were more confident in negative results from controlled experimental inoculations in the lab than from the wild. We collected data from studies that experimentally tested, using quantitative PCR, whether or not a species was susceptible to *Bsal* infection through inoculation with the fungus (Barnhart et al., 2020; Bates et al., 2019; Carter et al., 2020; Martel et al., 2014). If a subspecies was positive for *Bsal*, we labelled the species from which they stem as positive, given that life history trait data were not available at the subspecies level. If any records among multiple records for a species were positive, we recorded the species as positive, even if there were other negative test results recorded for the species. If any species tested positive in the wild, including data sources from our ENM model, we recorded them as positive. Furthermore, if there were other species in the same location in the wild as the species that tested positive, and those sympatric species tested negative, we recorded those species as negative, because we assumed they had high likelihood of contact with *Bsal* (e.g. González et al., 2019) (see Table S1.2 for a list of studies from which infection data were collected).

We collected trait data for 619 salamander species from the AmphiBIO dataset, which relies on Frost's amphibian taxonomy from 2011 (Oliveira et al., 2017). Traits could be grouped into the following categories: habitat, diet, diel, seasonality and breeding strategy. Each species had a combination of binary traits within these categorical variables. The infection status of each species for *Bsal* fell into one of three categories: a positive record for *Bsal* ($n = 42$), a negative record from the literature ($n = 53$) or a negative record for species that had not yet been tested for *Bsal* ($n = 524$). For additional details about the treatments of NAs and assignment of weights to each species, see Appendix S1.

2.2.2 | Model preparation and execution

We used the 'gbm' package version 2.1.8 (Greenwell et al., 2020) in R version 4.0.1 (R Core Team, 2020) to implement our BRT model. The BRT uses a subset of the data to generate an ensemble of regression models and then tests the accuracy of the model using the remaining data (Elith et al., 2008). In all model runs described below, we used 80% of data for training and 20% for testing. Model hyperparameters, including the learning rate and variable interaction complexity, were optimized by fitting multiple hyperparameter combinations and finding the combination of parameters which gave the highest test AUC. We evaluated learning rates of 0.01, 0.005, 0.001 and 0.0001, and interaction depths of two through five. A learning rate of 0.001 and an interaction complexity of three were the optimal model parameters for our model. To account for the stochastic nature of model fitting, we bootstrap across five runs of our model, each time drawing a different subset of training data. We then calculate average model metrics, including variable importance, AUC, optimal trees and marginal effects. After initially bootstrapping the

model, we removed the variables determined from these metrics to have zero importance and reran the bootstrapping process to determine if model fit increased. Our final model excluded the variables with no importance. We separately bootstrapped a series of null models, shuffling species' *Bsal* labels and their corresponding weights to another random species to determine a corrected test AUC and evaluate if our model predicted better than random.

We generated predictions about *Bsal* susceptibility for each of the 619 species using a BRT model, with the optimal model hyperparameters and excluding variables with zero relative importance, trained on all labelled data. We binarized these predictions by categorizing species with at least 50% probability as susceptible to *Bsal*, and any species <50% probability as not susceptible. We evaluated our model at this stage by comparing the prediction for each species to its literature-derived *Bsal* test result and calculated the number of false positives, false negatives, true positives and true negatives (the confusion matrix). Using this assessment of prediction, we chose a data weighting scheme (see Appendix S1) to use in our final results that minimized false positives and negatives and maximized true positives and negatives.

2.2.3 | Spatial analysis

We mapped the fraction of salamanders predicted susceptible to *Bsal* relative to salamander richness in an area, based on salamander range maps for the United States (IUCN, 2020). Using a grid with a resolution of $\sim 100 \text{ km}^2$, we found the total number of ranges that overlapped each grid cell to calculate species richness. The same method of summation was used to calculate the total number of species predicted susceptible to *Bsal* in each grid cell. Finally, the fraction of salamanders susceptible to *Bsal* in each grid cell was the quotient of the number of species predicted susceptible divided by species richness.

2.3 | Risk analysis

The product of the fraction of salamanders susceptible to *Bsal* and the ENM suitability prediction gave a combined estimate of risk of salamanders to *Bsal* across the United States. We normalized the value for risk in every grid cell in the United States by dividing by the maximum predicted risk value in the United States. We identified areas most at risk from *Bsal* as those in the top quartile of combined risk values.

3 | RESULTS

3.1 | Ecological niche modelling

To develop an ENM to predict *Bsal* suitability in the United States, we fit a MaxEnt model on the native Asian range using a collection of independent variables we hypothesized to be important for determining *Bsal*'s environmental niche. After parameterization, we

fit our model using a regularization multiplier of 4.0 and the linear and quadratic feature classes. This model had good model fit using AUC, our threshold-independent evaluation statistic, showing 90% predictive accuracy (AUC = 0.90, Table 1). Omission rate, a metric of overfitting that measures the number of true positive points omitted by model predictions, showed low to marginal rates of model overfitting depending on the threshold chosen. Thresholds based on training presence point suitability scores typically showed lower omission rates and less signs of overfit (Table 1). Omission rate scores in the invaded range in Europe were similar or lower at all thresholds to those found in the native range in Asia (Table 1). Despite previously documented issues with determining the quality of presence-only models, TSS is another commonly reported metric of accuracy (Fourcade et al., 2018). TSS is defined as the sum of true positive and negative rates minus one, and for our model ranged from low to moderate depending on the threshold chosen (Table 1).

In the native range, the most important variables were mean diurnal temperature range (BIO-2), temperature seasonality (BIO-4), presence of evergreen deciduous needleleaf trees and presence of herbaceous vegetation (see Figure S2.1). Each of these variables was at least five times more important than any other variables and inversely related to the presence of *Bsal* (e.g. less variable temperatures across the year and throughout the day were associated with higher suitability of *Bsal*, see Figure S2.2).

In both the native and invasive range, the most suitable places predicted for *Bsal* tended to be close to coastlines or on islands (Figure 1). Coastlines with suitability above 0.75 can be found in Asia (Vietnam, Taiwan) and Europe (Norway). This trend extends to our model projection to the United States where similar regions, such as the Pacific Northwest, Florida, and the Gulf and Atlantic Coasts, have higher predicted suitability (Figure 1). The Appalachian Mountain region and portions of the eastern half of the country were also included in the top quarter of the most suitable areas for *Bsal* in the United States (Figure 2). Generally, our model predicted an overall less suitable environment for *Bsal* in the United States than in Europe and Asia (Figures 1 and 2).

The mobility-oriented parity (MOP) surfaces analysis identified the United States and European areas of complete model extrapolation (combinations of environmental conditions not found anywhere

in the Asian range), which included the southern Appalachian region, northeastern coast, and parts of the Southwest in the United States and parts of the United Kingdom, France, Sweden and Finland in the European range (Figure 1).

3.2 | Trait-based modelling

To predict the susceptibility of salamander species to *Bsal* infection, we created a BRT model that correlated life history traits with susceptibility. Our BRT model performed with very high accuracy, with a training AUC of 0.99, a testing AUC of 0.90 and a corrected AUC of 0.85. Predictions from this model showed high levels of concordance with literature reports of confirmed species susceptibility to *Bsal*. There were fewer than 10 mismatched results, corresponding to a prediction accuracy greater than 91% (Table 2). Maximum longevity and mean body size were both at least twice as influential for prediction than the other variables in the model (Figure 3). Both of these variables predict a maximum susceptibility around their median values (Figures 4 and S2.3). Susceptibility to *Bsal* also increased with maximum clutch size (Figures 4 and S2.3). Finally, inclusion in the family Salamandridae, indicating increased susceptibility to *Bsal* (Figures 4 and S2.3), is more than twice as important as a predictor variable than inclusion in any other Caudata group (Figure 3).

The highest number of predicted susceptible salamanders within the United States occurs in the southern Appalachian region, while moderate numbers occur throughout the states east of the Plains region and the northern Pacific coast. These areas roughly correspond with hotspots of salamander species richness in the country (Figure 5). There are a total of 12 salamander species in the United States that our model predicts are susceptible to *Bsal* infection, four of which do not have observed infections to date (see Table S3.1). The product of the percent predicted susceptible species and pathogen suitability shows that the Gulf Coast of Texas and Louisiana, the Pacific Northwest, and Florida appear to have the highest risk for infection of *Bsal* (Figure 5), with additional states east of the Plains region, such as eastern Texas, Oklahoma, and states north and east of Louisiana, showing some risk of susceptible species (Figure 5). There are 31 states represented in the area covered by the top quartile of risk scores (Figure 6).

TABLE 1 Model evaluation metrics for the ecological niche model (ENM) in the native and invasive ranges, Asia and Europe, respectively. Note that area under the curve (AUC) is a threshold-independent evaluation statistic and does not vary across defined thresholds.

Threshold	Model evaluation metric			
	Native range			Invasive range
	AUC	True skills statistic (TSS)	Omission rate	Omission rate
Minimum presence	0.90	0.38	0.03	0.05
Lowest 10% of presence		0.52	0.12	0.11
Maximum specificity and sensitivity		0.69	0.18	0.05

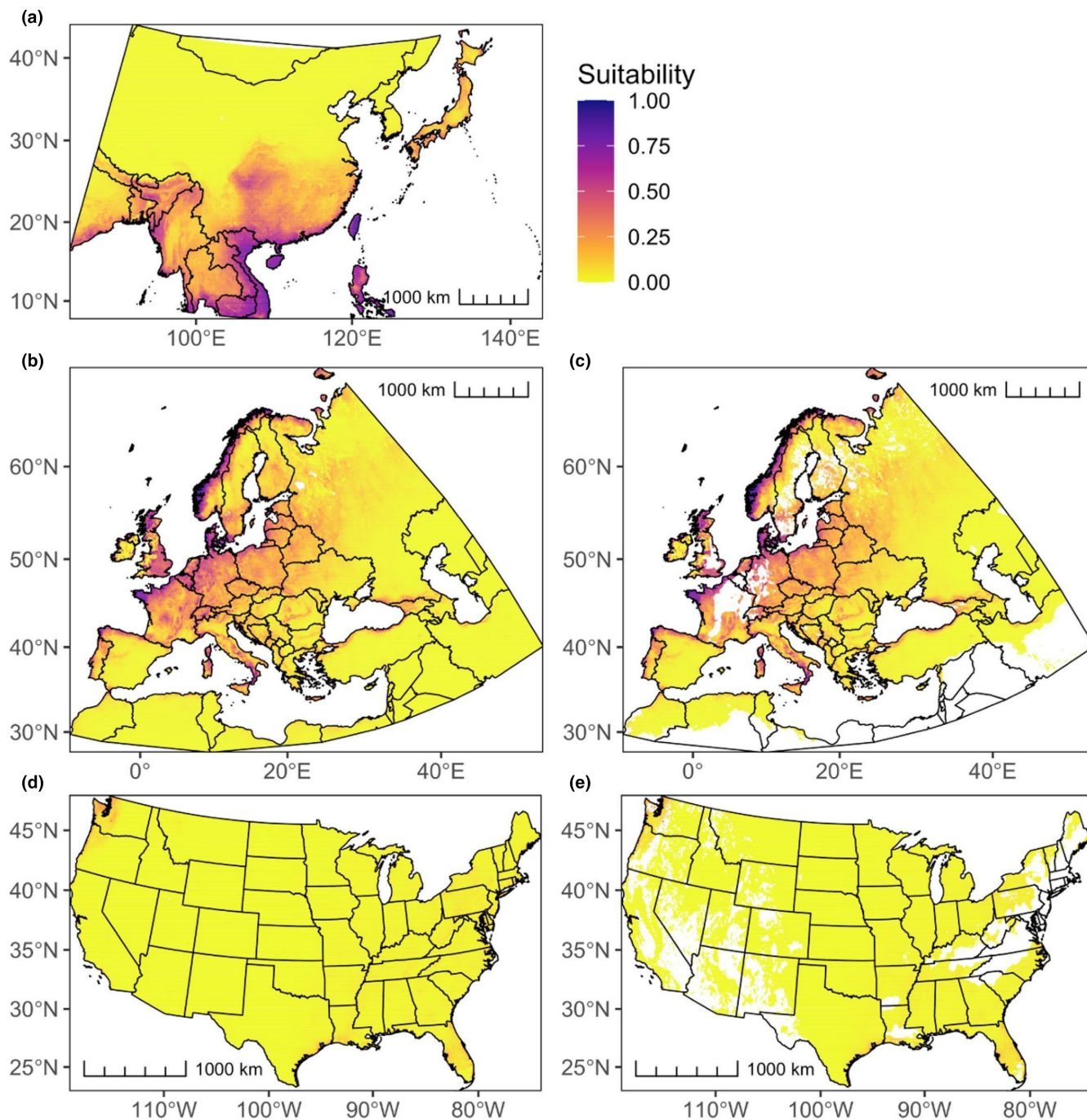


FIGURE 1 Spatial predictions for the probability of suitability of *Bsal* in its native Asian (a), invasive European (b) and potential US range (d), based on the environmental niche *Bsal* occupies in its native range as estimated using an environmental niche model (ENM). Maps on the right for the invasive (c) and US (e) ranges include areas with completely dissimilar environmental spaces from the native range, determined by mobility-oriented parity (MOP) surfaces analysis, and these areas have been removed from the prediction and appear white. Native and US range maps are projected using Albers equal area, and invasive range maps are projected using Lambert azimuthal equal area.

Our datasets are available online, including raster data for *Bsal* suitability, predictions for susceptibility of 619 species around the globe and their observed infection status, and final raster risk data (see Data Availability Statement), which may be used to generate tailored data visualizations most relevant to inform local conservation and research efforts.

4 | DISCUSSION

The United States has the highest biodiversity of salamanders on Earth (Yap et al., 2015), with numerous taxa apparently susceptible to *Bsal* infection (e.g. Carter et al., 2020; DiRenzo et al., 2021), raising the stakes if *Bsal* arrives in the United States after recently

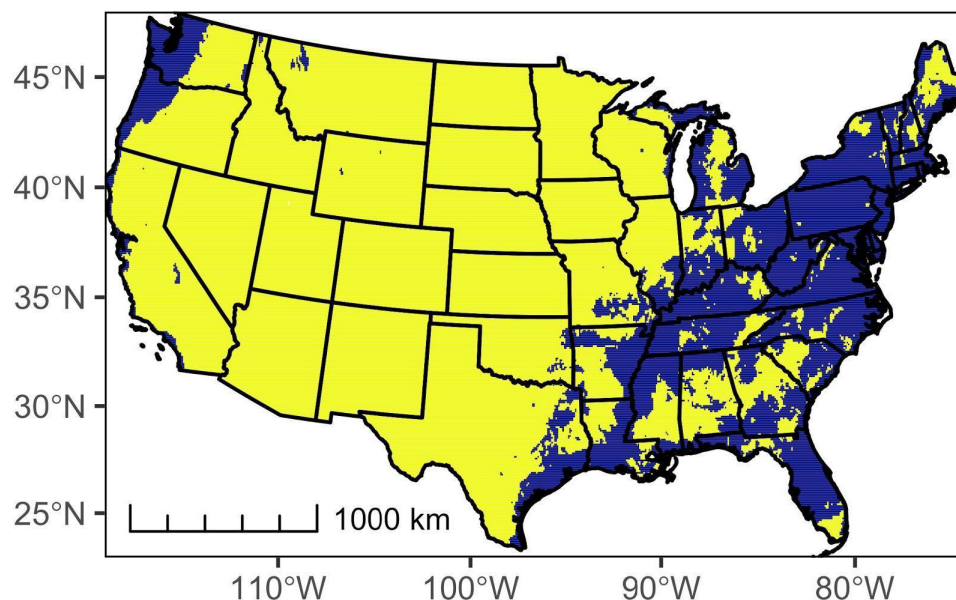


FIGURE 2 The areas of the United States that contain the top quartile of suitability scores for *Bsal*, coloured blue, based on an ecological niche model (ENM) trained in the native Asian range of the pathogen. The map is projected using Albers equal area.

TABLE 2 A summary of the prediction results of our boosted regression tree (BRT) model shown as a confusion matrix of observed and predicted susceptibility of salamander species to *Bsal*.

	Observed infection status	
	Positive	Negative
Predicted infection status		
Positive	40	6
Negative	2	47

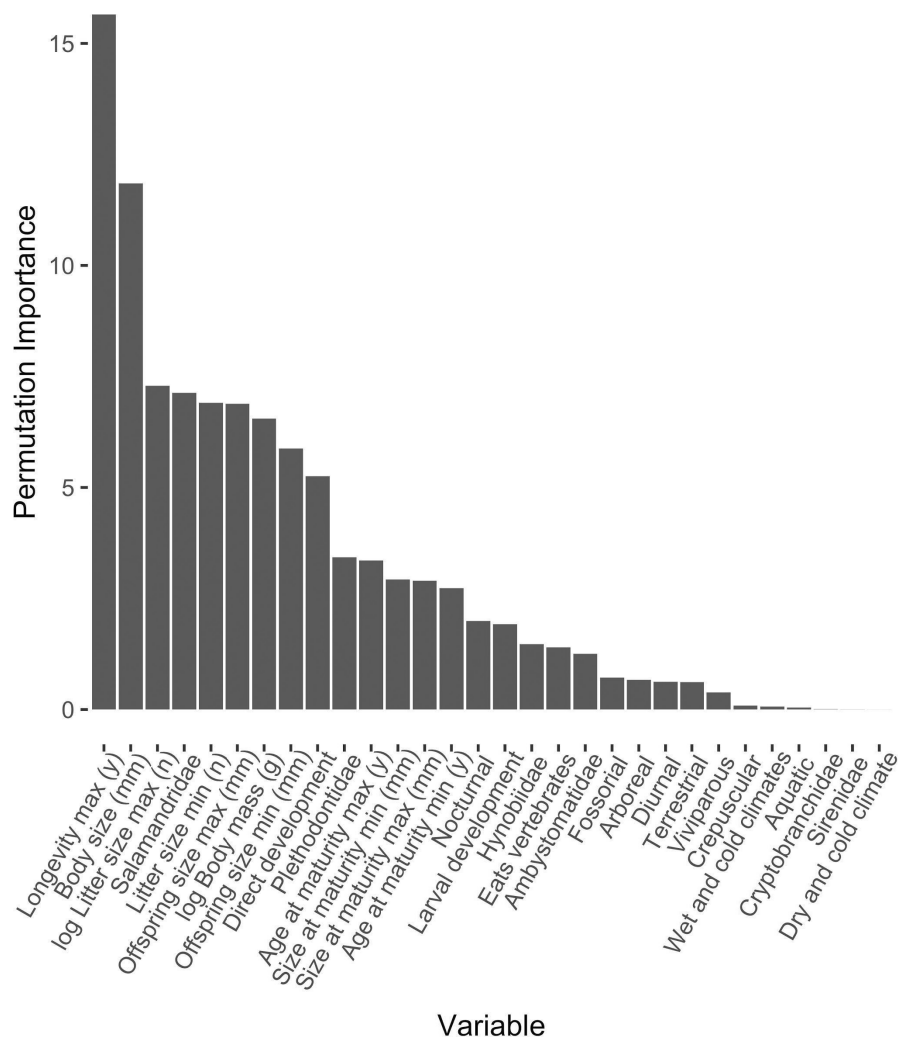
invading Europe and causing salamander population declines there. We combined an ENM to predict environmental suitability in the United States for the *Bsal* pathogen, together with a trait-based machine-learning model of host-species susceptibility to *Bsal* infection to estimate geographic and species-specific risk to salamanders across the country. Our models revealed overlap between areas with highest predicted *Bsal* suitability and areas with high diversity of salamander species predicted to be susceptible to infection, a finding that both demonstrates the need for and gives direction to future conservation actions. Despite varying methodologies, our risk assessment shows geographic agreement with previous models (e.g. Richgels et al., 2016; Yap et al., 2015), which reinforces our understanding about the risk of *Bsal* in particular areas of the United States. While previous studies estimated risk by estimating the total richness of salamander species that would be affected, our direct modelling of *Bsal* and salamander host traits corroborates the geographic predictions made by more coarse-scale predictions. Our approach further identifies salamander species of particular concern in these regions.

4.1 | Ecological niche model

The performance of our ENM in identifying the environmental suitability for *Bsal* in Asia (historic *Bsal* range) and Europe (invasive range) supported the predictive use of the model in the United States (potential future range). In the native range, the presence of *Bsal* is associated with environments along the coastlines with more seasonally stable weather, locations which have low mean diurnal range and temperature seasonality. Similarly, stable environments in the United States and Europe are found along coastlines, which manifested in the high predicted suitability of *Bsal* along coastlines in these study regions (Figure 1). In Europe, field-recorded presence points of *Bsal* validate the high predicted suitability in these areas, demonstrated by the low omission rate of the model.

The two major issues when fitting ENM models and predicting suitability into an invasive range are first, shifts in the species' niche during invasion, due to either niche expansion in the invasive range or partial filling of their niche in the native range; and second, uncertainty in extrapolating a model from the native range into a novel environmental outside the native range (Beukema et al., 2018; Owens et al., 2013; Pili et al., 2020). We address these issues of model transference by measuring model performance on an existing invasive range, Europe, for which there are *Bsal* occurrence records, similar to Basanta et al. (2019). Low omission rates of occurrence points in the invasive range in Europe show that *Bsal* has likely not expanded its niche during invasion, in accordance with the finding of Beukema et al. (2018) that *Bsal* in Europe only occupies a subset of the natively occupied environmental space. Across multiple thresholds of suitability values in the invasive range, our model excluded occurrence points at a similar or lower rate as in the native range. As

FIGURE 3 The importance of each variable used to predict the susceptibility of a salamander species to *Bsal* in a boosted regression tree (BRT) analysis.



a result of this strong model performance, we can be confident in our predictions for *Bsal* suitability in Europe, with the exception of areas with high environmental dissimilarity to the native range (e.g. northern France, inland United Kingdom and parts of Sweden).

To further assess how well ENM predictions are likely to transfer from the native range to the United States and Europe, we evaluated to what extent the environmental spaces in the United States and Europe overlap that of the native range. Our ENM predictions may not be interpretable for <25% of each study range due to dissimilarity with the native range to which our model was fitted. *Bsal* may be able to occur in these areas of environmental dissimilarity to the native range, but reliable predictions of *Bsal* suitability cannot be made in these areas due to known problems with ENM extrapolation into novel environmental space (Qiao et al., 2019). For example, some occurrences of *Bsal* in the invaded range fall inside uninterpretable areas of the ENM in Belgium, the Netherlands and Germany. Unfortunately, these uninterpretable regions overlap with some areas of high salamander diversity in the United States, such as at the intersection of Virginia, North Carolina and Tennessee. Therefore, conservation decisions for salamanders in these areas may need to rely on other indicators of infection risk such as predicted species susceptibility, based on our trait-based model, or the

presence of salamander trade (Richgels et al., 2016; Yap et al., 2015). Nevertheless, given strong model performance in the invasive range and our ability to identify regions with uninterpretable predictions, we conclude that our suitability predictions in the United States are likely biologically reasonable results for those areas that do have overlapping environmental conditions to the native range.

In general, our ENM predicted overall low suitability for *Bsal* in the United States, and moderate suitability in some coastal areas. The two main drivers of *Bsal* occurrence in the ENM, temperature seasonality and mean diurnal range, are divergent between southeast Asia and the United States (Fick & Hijmans, 2017). Both bioclimatic variables tend to be relatively low in the native range and high across most of the United States, except for at the coasts. One mechanism for this difference in bioclimatic variables may be the proximity to coastal areas where the ocean influences low temperature seasonality and mean diurnal range, and most *Bsal* occurrences in the native range are close to the Pacific Ocean. Likewise, the most suitable areas for *Bsal* in the United States are close to the coastlines. The same is generally true in the invasive range, especially where the coast of Norway shows high suitability for *Bsal*. Past studies found similar trends for coastal areas with high suitability for *Bsal* predicted for the southern Gulf coast

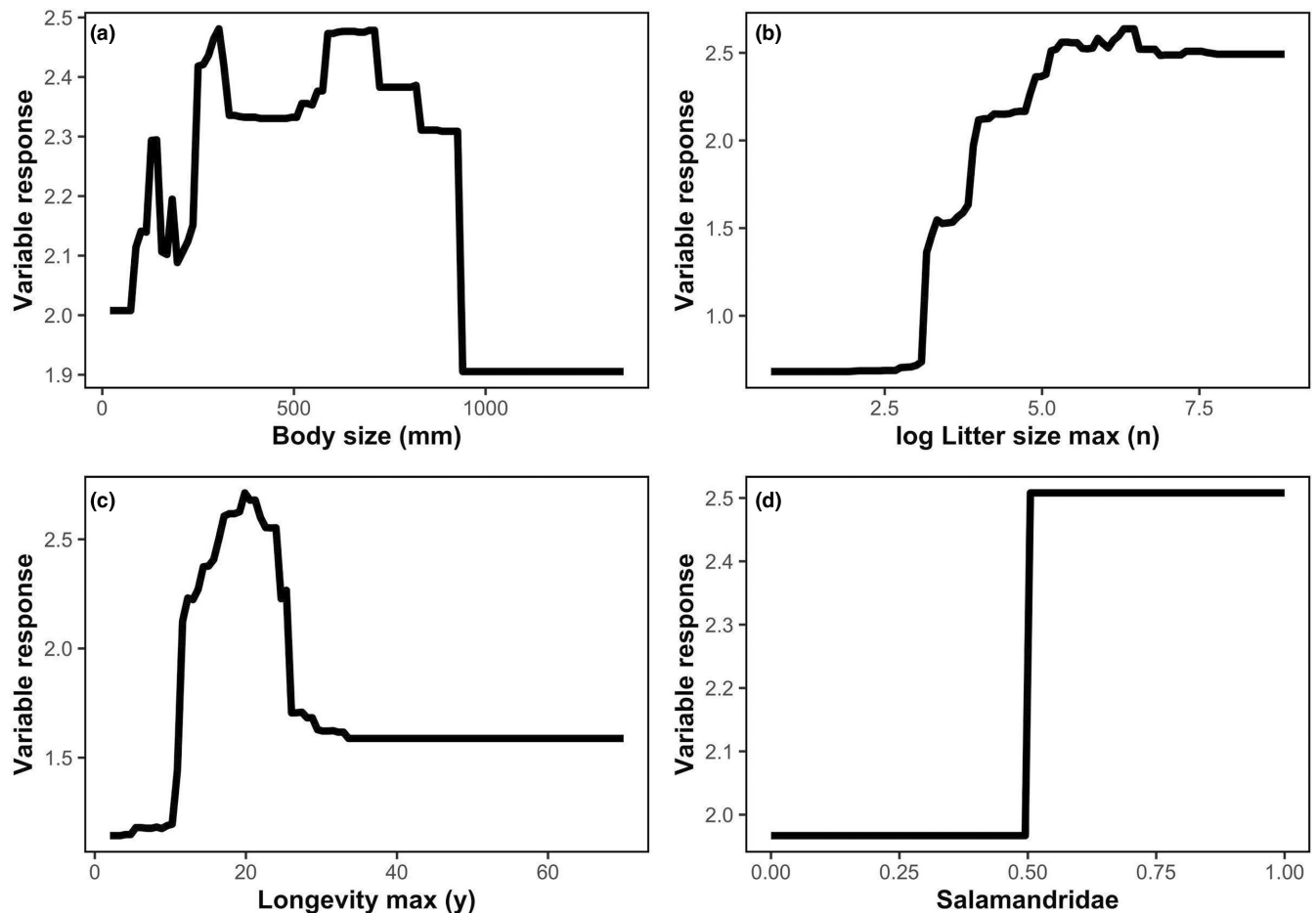


FIGURE 4 The effect of the four most important traits for the susceptibility prediction of each salamander species to *Bsal* with respect to the value of the predictor based on a boosted regression tree (BRT) model. For the effects of all traits used in the model, see Figure S2.3.

of Mexico (Basanta et al., 2019), northwestern coast of Europe (Beukema et al., 2018) and Costa Rica (Puschendorf et al., 2009). In fact, a widespread sampling across parts of the native range in China found no occurrences of *Bsal*, and those sampling locations were mostly inland (Zhu et al., 2014). Furthermore, Olson et al. (2013) found that the other chytrid fungus afflicting amphibians, *Bd*, occurred less with increasing temperature range, while Olson et al. (2021) showed that *Bd* occurrence decreased specifically at high temperature ranges. Both results align with our model results for *Bsal* in its native range. Therefore, the fact that *Bsal* suitability is generally limited to the coastlines of the United States may be due to its currently known preference for the environmental conditions of coastal areas, which are most similar to conditions where *Bsal* observations have been recorded.

4.2 | Trait-based susceptibility model

Although *Bsal* suitability is generally low across the United States, the quarter of the country that is most suitable for *Bsal* includes the Appalachian Mountains, the southeastern Gulf and Atlantic Coasts, and the Pacific Northwest. In order to discern appropriate

conservation actions in these regions, however, it is important to know if these areas are also inhabited by salamanders that are susceptible to *Bsal* infection. Our BRT model trained on life history traits showed that the most important variables influencing susceptibility were maximum longevity, body size and maximum clutch size. Compared to other salamander species, we found that *Bsal* salamander hosts tended to have intermediate body sizes and life spans while still achieving high fecundity. We postulate that species with intermediate body size and maximum longevity might be more susceptible owing to an accumulation of infectious contacts as body size and lifespan increase (Kuris et al., 1980) and less robust immune function compared to larger- or longer-lived individuals (Downs et al., 2020; Johnson et al., 2012). Similarly, species with larger clutch sizes tend to have lower investment in immune function (Johnson et al., 2012), and we show they are more likely to be susceptible to *Bsal*. These results are in accordance with trait-based modelling done for *Bd* susceptibility that showed species with large body sizes and clutch sizes are more susceptible to *Bd* infection (Bancroft et al., 2011). Species with larger clutches may spend more time in water during mating around multiple other breeding pairs increasing their contact with higher densities of infectious zoospores.

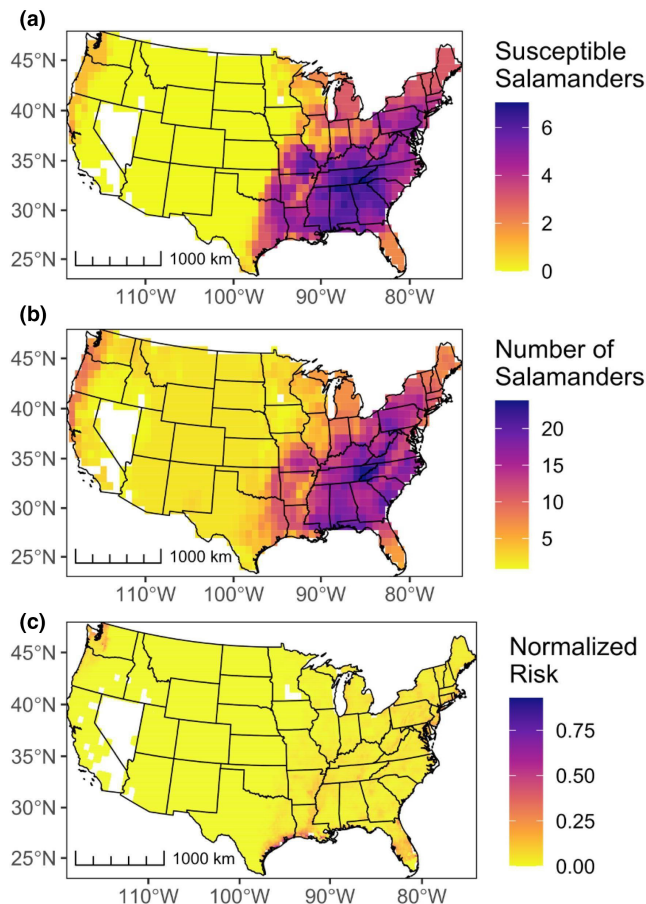


FIGURE 5 The location of salamanders predicted susceptible to *Bsal* by (a) a boosted regression tree (BRT) classification susceptibility based on species traits, (b) total species richness of salamanders and (c) risk of salamanders to *Bsal* based on the product of environmental suitability for the pathogen, from our ecological niche model (ENM), and species susceptibility based on traits. All maps are projected using Albers equal area.

4.3 | Future directions and conclusion

In this study, we define susceptibility based on whether a salamander becomes infected or not with the *Bsal* pathogen. However, among the salamanders that are susceptible to *Bsal* there are differences in the degree to which *Bsal* affects individuals and species. For example, some salamander species are asymptotically infected while others show clinical signs of infection but limited mortality (Martel et al., 2014). We recommend future work applying trait-based modelling to predicting salamander mortality and morbidity due to *Bsal* infection at a higher resolution across species and individuals. Such work would require more experimental data to be available, such as data that determines the level of susceptibility of some species (Carter et al., 2020; Martel et al., 2014; North American *Bsal* Task Force, 2022). An individual salamander's response to infection varies significantly across experimental conditions, such as temperature (Sauer et al., 2020), indicating the benefits of standardized experimental approaches across studies. After our analyses were completed, DiRenzo et al. (2021) demonstrated

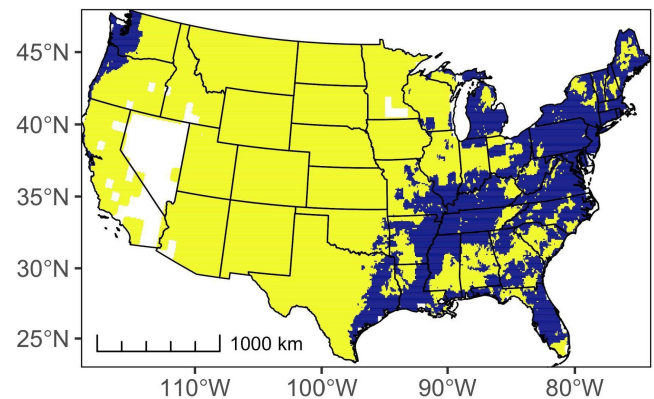


FIGURE 6 The areas of the United States with the top quartile of risk scores to *Bsal*, coloured blue, based on a combination of environmental suitability for the pathogen and the susceptibility of species to infection. The map is projected using Albers equal area.

susceptibility of numerous species through controlled laboratory inoculation experiments, providing an opportunity to validate the predictions of our model, and also to demonstrate how ours and similar predictive models could be updated in light of new findings. While we binarize our continuous predictions of infection susceptibility (see Data Availability Statement), in future work, continuous measures of susceptibility (e.g. DiRenzo et al., 2021) may better integrate the outcomes of new experimental data with model predictions, as experimental outcomes often generate degrees of infection and susceptibility (e.g. via quantitative PCR). Although the main conclusions of our model remained unchanged with the inclusion of these new data (Figure S2.4, Tables S3.2 and S3.3), these outcomes demonstrate a necessary but rare iteration between modelling and experimental studies whereby advances in either inform the other. Given the small number of land cover types we use in our ENM and their importance in our final predictions, future suitability modelling should further resolve diverse land cover types present across native and invasive geographical ranges. Incorporating laboratory-derived physiological constraints for *Bsal* could further reduce uncertainty in a future ENM by bounding environmental ranges by known limits for the pathogen. Additionally, climatic change over the coming decades will likely affect the geographic locations of *Bsal* suitability. Future work should examine to what extent the niche for *Bsal* expands, contracts or shifts to interact with different salamander species under varying climate scenarios, similar to work being done for *Bd* (e.g. Xie et al., 2016).

This study begins to elucidate which areas in the country are inhabited by species that are likely to be susceptible to *Bsal* infection. The areas with the most likely susceptible salamanders also correspond to areas of high salamander species richness, *Bsal* suitability and risk for *Bsal* infection, including the Appalachian Mountains, Gulf and southeastern Atlantic Coasts, and the Pacific Northwest. Our results, which include both species traits driving susceptibility and *Bsal* environmental suitability, largely agree with previous studies that focused on the impact of trade on *Bsal* spread (Richgels et al., 2016; Yap et al., 2015), with our study also identifying the

coast of California as a potential hotspot for *Bsal* risk. Given widespread agreement among multiple spatial and biological risk assessments of *Bsal*, our study contributes to a growing consensus pointing to the need for pre-emptive conservation efforts against *Bsal* that prioritize particular areas exhibiting high suitability for *Bsal*, high susceptibility of salamander species to *Bsal* infection, as well as a high invasion risk from trade.

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CONFLICT OF INTEREST

The authors state no conflicts of interest with the work presented herein.

DATA AVAILABILITY STATEMENT

All of the data used to support the results of this work are available on figshare at the following DOI: [10.6084/m9.figshare.17695382](https://doi.org/10.6084/m9.figshare.17695382) (Moubarak et al., 2021).

PEER REVIEW

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ORCID

Michael Moubarak  <https://orcid.org/0000-0003-4276-0609>

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BIOSKETCH

Michael Moubarak is an undergraduate student at Hamilton College and Columbia University and a Research Experience for Undergraduates program student at the Cary Institute of Ecosystem Studies. He is interested in bridging mathematics with ecology to model patterns of natural phenomena.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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