

RESEARCH ARTICLE

Exploring the Distribution of the Spreading Lethal Salamander Chytrid Fungus in Its Invasive Range in Europe – A Macroecological Approach

Stephan Feldmeier¹, Lukas Schefczyk², Norman Wagner¹, Günther Heinemann², Michael Veith¹, Stefan Lötters^{1*}

1 Department of Biogeography, Trier University, Trier, Germany, **2** Department of Environmental Meteorology, Trier University, Trier, Germany

* loetters@uni-trier.de



OPEN ACCESS

Citation: Feldmeier S, Schefczyk L, Wagner N, Heinemann G, Veith M, Lötters S (2016) Exploring the Distribution of the Spreading Lethal Salamander Chytrid Fungus in Its Invasive Range in Europe – A Macroecological Approach. PLoS ONE 11(10): e0165682. doi:10.1371/journal.pone.0165682

Editor: Brian Gratwicke, National Zoological Park, UNITED STATES

Received: September 12, 2016

Accepted: October 14, 2016

Published: October 31, 2016

Copyright: © 2016 Feldmeier et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: Relevant data are within the paper and its Supporting Information files.

Funding: S.F. and L.S. are funded by the Trier Centre for Sustainable Systems (TriCSS). Our *Bsal* research benefits from funds by the Deutsche Gesellschaft für Herpetologie und Terrarienkunde (DGHT), Nikolaus Koch Stiftung, Stiftung Artenschutz, Verband der Zoologischen Gärten and Zoo Landau. The funders had no role in study

Abstract

The chytrid fungus *Batrachochytrium salamandrivorans* (*Bsal*) is a dangerous pathogen to salamanders and newts. Apparently native to Asia, it has recently been detected in Western Europe where it is expected to spread and to have dramatic effects on naïve hosts. Since 2010, *Bsal* has led to some catastrophic population declines of urodeles in the Netherlands and Belgium. More recently, it has been discovered in additional, more distant sites including sites in Germany. With the purpose to contribute to a better understanding of *Bsal*, we modelled its potential distribution in its invasive European range to gain insights about the factors driving this distribution. We computed *Bsal* Maxent models for two predictor sets, which represent different temporal resolutions, using three different background extents to account for different invasion stage scenarios. Beside ‘classical’ bioclimate, we employed weather data, which allowed us to emphasize predictors in accordance with the known pathogen’s biology. The most important predictors as well as spatial predictions varied between invasion scenarios and predictor sets. The most reasonable model was based on weather data and the scenario of a recent pathogen introduction. It identified temperature predictors, which represent optimal growing conditions and heat limiting conditions, as the most explaining drivers of the current distribution. This model also predicted large areas in the study region as suitable for *Bsal*. The other models predicted considerably less, but shared some areas which we interpreted as most likely high risk zones. Our results indicate that growth relevant temperatures measured under laboratory conditions might also be relevant on a macroecological scale, if predictors with a high temporal resolution and relevance are used. Additionally, the conditions in our study area support the possibility of a further *Bsal* spread, especially when considering that our models might tend to underestimate the potential distribution of *Bsal*.

design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

Introduction

Worldwide, biological diversity is alarmingly declining [1], and it has been proposed that we are witnessing a sixth mass extinction in Earth's history [2]. Among the various reasons responsible for species and population declines and extinctions are emerging infectious diseases. There has been a remarkable pathogen-related increase in species declines during the last decades [3]. As pointed out by Daszak *et al.* (2000) [4], mediation by humans helps pathogens to cross evolutionary and ecological boundaries. Such a 'pathogen pollution' has led to dramatic species declines and extinctions in various regions [5,6].

Amphibians belong to the globally most threatened of all vertebrates. More than one third of the ca. 7,500 species is threatened with extinction when applying IUCN Red List criteria [1]. Emerging infectious diseases play a key role in the world's 'amphibian crisis' and are seen as one main factor for the global amphibian decline [7]. The pandemic amphibian chytrid fungus (*Batrachochytrium dendrobatidis*, *Bd*) has significantly contributed to this crisis [8]. This pathogen is spreading and is already known from more than 400 host species in all three amphibian orders and on all continents where amphibians occur [8,9]. However, the effects of *Bd* infections depends on various factors, such as the *Bd* strain, the species, the population and regional climatic factors [8,9].

Recently, a congeneric chytrid fungus has been discovered in Europe [10]. *Batrachochytrium salamandrivorans* (*Bsal*) is lethal only to salamanders and newts, order Urodela. Under laboratory conditions, in many urodeles from outside Asia, *Bsal* infection led to 100% mortality within a few days [11]. Since this fungus has been found in wild Asian newts, it is expected that *Bsal* is native to Asia and has recently been introduced into Europe by humans [11]. Since 2010, observed Dutch populations of fire salamanders (*Salamandra salamandra*) have drastically declined due to *Bsal* infections, with sometimes less than one percent survival rate (the latter studied in one population only) [12,13]. In subsequent years, *Bsal* infections have been recorded in additional species and nearby sites (within a radius of about 100 km from first noted outbreaks) in Belgium and Germany, and it appears that *Bsal* is spreading in its invasive range [13]. According to these authors, to date *Bsal* infections in Europe in the wild are known in one salamander and two newt species at 14 sites. In addition, *Bsal* infections have recently been detected in captive salamanders and newts in the UK and Germany [14,15].

The emergence of *Bsal*, accompanied by massive amphibian diversity loss, is feared [11], especially in regions that are species-rich in salamanders and newts [16,17]. Biologists and conservationists are saying that *Bsal* mitigation strategies are necessary now. Recommendations for minimizing impacts of lethal emerging infectious diseases on wildlife, among others, include the reduction of local spread, habitat manipulation and host translocations [18]. Macroecological models forecasting the potential invasive range of pathogens are helpful in these steps [19]. Such 'spatial risk assessments' are available for the pandemic *Bd*, based on correlative species distribution models (SDMs). These use climatic information at pathogen presence records [20,21] to infer its environmental niche [22]. Until recently, the number of *Bsal* records was too few for SDM building. Aware of this circumstance, Yap *et al.* (2015) [23] provisionally used avatar species (i.e. records and random points inside the distribution of Asian urodeles that potentially can be *Bsal*-positive) to create a *Bsal* SDM for North America.

Besides using SDMs to predict distributions of species, they can be applied to gain insights about the environmental drivers of their distributions [24]. With this goal, we in this paper provide *Bsal* SDMs for the region where it is invasive in Europe. We use true observed presence records for SDM building. We create models with fine-scale weather data as well as 'classical' bioclimate data to explore the responses of *Bsal* with respect to different temporal resolutions, using predictors relevant to *Bsal* and adapted to known temperature limits [10]. A basic

assumption of SDMs is that a species and its environment are in equilibrium [25,26]. SDMs built in early invasion stages, as it is expected for *Bsal* [13], are in conflict with this assumption and tend to underpredict the potential distribution of a species [27]. On the other hand, with regard to the development of mitigation strategies, attempting to build a *Bsal* SDM might be a valuable contribution. Our models were fine-tuned to better meet equilibrium conditions with respect to different invasion stages and according to the small number of presences to minimize biases. We consider our study as an important step towards a better understanding of *Bsal*.

Materials and Methods

Climate predictors and *Bsal* presence data

The climate data used in this study were generated with the regional climate model COSMO-CLM (consortium for small-scale modelling—climate limited area modelling; [28]; <http://www.clm-community.eu>, version 5.0_clm6). It was forced with ERA-Interim data [29] and dynamically downscaled in a multi-nesting chain approach [30]. Hourly data of precipitation and surface temperature were modelled for the period from 1 January 2011 to 31 May 2014 at a horizontal resolution of ~ 1.3 km. We used the surface temperature because it is modelled with respect to seasonal vegetation cover, leaf area index, soil properties and others. As almost all *Bsal* records were located in forested areas, the surface temperature was supposed to reflect the conditions at ground level better than the standard 2 m air temperature. The climate data cover an area of 67,600 km² (40,000 grid cells) in Belgium, France, Germany and the Netherlands (Fig 1). The area has lowlands (< 100 m a.s.l.), such as the Rhine valley and low mountain ranges with most of the highest peaks < 800 m a.s.l., including the Ardennes, Eifel, Westermwald, Hunsrück and parts of the Black Forest. The climate time period and the modelling domain was restricted due to limited computational resources and because it was set in the context of a different project ('KlimLandRP'; <http://www.klimlandrp.de>). Despite these limitations, the application of this data is more appropriate than the use of standard Worldclim data [31], which strongly predates the *Bsal* presences and is not comparable in temporal resolution and quality.

Out of these data, we generated two initial predictor sets for our *Bsal* modelling approach: (1) We calculated 25 indices of weather extremes (S1 Table) of the ECA project (European Climate Assessment; <http://www.eca.knmi.nl>), which are based on hourly and daily surface temperatures and precipitation data over the three and a half year climate period (i.e. no yearly averages). To better meet the *Bsal* ecology, indices were adapted in a way that they acknowledged temperature growth limits of *Bsal* [10]: that is 5–25°C, with an optimum growth at 10–15°C. (2) Monthly multi-year averages of the precipitation as well as the minimum and maximum surface temperatures were taken to calculate 19 BIOCLIM variables [31,32] (S2 Table). BIOCLIM variables are biologically meaningful predictors and are widely used in SDM building [33]. These variables have a lower temporal resolution than the ECA indices. Hence, they do not or less account for short term extreme events, while ECA indices do.

Of the so far 14 *Bsal*-positive sites reported [10,11,13], 12 fell into the study region (Fig 1). The addition of two yet unpublished *Bsal*-positive sites allowed us to employ 14 records in the modelling process (S3 Table).

Species distribution modelling

Model algorithm. The variety of algorithms available for correlative model computation can lead to markedly different SDM results. To account for this variation, it is generally recommended to employ distinct algorithms in SDM reconstructions [34–38]. On the other hand,

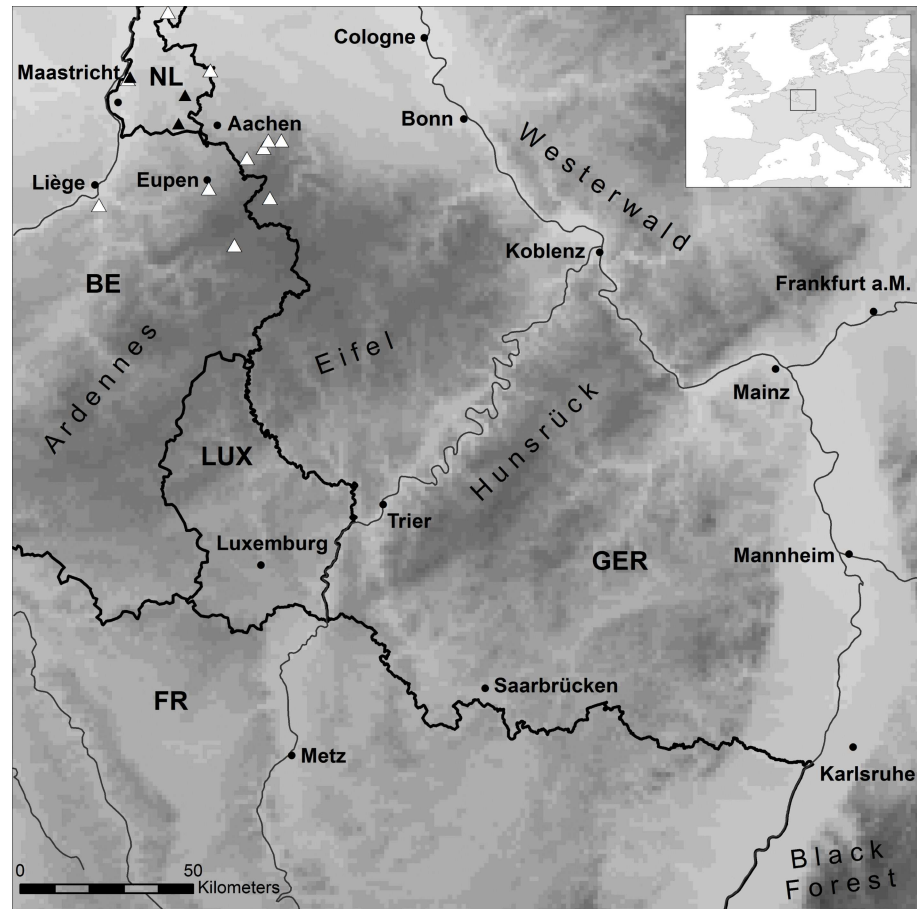


Fig 1. Western Europe study region. First noted *Bsal* outbreaks are indicated by black and subsequent records by white triangles. Elevational range (grey scales, light to dark: 28–1,050 m a.s.l.), borders (bold lines), rivers (thin lines), some major cities (normal font) and low mountain range names (sloped font) are shown.

doi:10.1371/journal.pone.0165682.g001

Warton & Aarts (2013) [39] highlighted, that for distinct algorithms when applied in a similar way (i.e. the same random points, predictors, type of model responses), differences will typically be small and can even lead to almost identical results. However, steering a single algorithm in different ways can reveal dramatic output alterations [39]. Therefore, it is important to select a method, which is suitable for the available data and a modelling approach, which is ecologically reasonable [39,40]. In this study, we used Maxent 3.3.3k [41] to generate models. Maxent is a machine-learning algorithm, following the principle of maximum entropy. Thereby, it uses environmental predictors (here, out of the ECA and BIOCLIM sets), species presence records and random background points (at which the presence of the target species is unknown). It contrasts the environmental conditions at species' presences against the conditions at the background points, to fit a function to estimate the relative habitat suitability [24,42,43].

We chose Maxent for our modelling approach for several reasons. We suggest that at the current state of knowledge a *Bsal* SDM should be based on presence-only information (i.e. applicable to Maxent). We reject the use of presence-absence, since a rigorous sampling for *Bsal* has just started in the invasive area [13]. For the same reason, we do not support the concept of pseudo-absence methods in this context. Besides, there is no clear strategy how to

generate pseudo-absence and this is still subject of ongoing research [44–47]. Also, in correlative SDMs, model quality and accuracy depends on the number of records available of the target species. When the number of records is low (as in *Bsal*), Maxent has been shown to build reliable models and it can be fine-tuned to maximize the utility of the available information [48–52]. Maxent produces response curves, which allow to assess the modelled responses in terms of ecological meaning. Furthermore, via background definitions, it allows us to account for different dispersal hypotheses (i.e. different invasion stages) across the landscape. We acknowledge that in recent years Maxent has been scrutinized by some studies, especially because of its uncritical use in the literature [24,53,54]. However, due to the considerations above, we conclude that Maxent is the most appropriate method here, which we navigated with highest care.

Predictor selection. To avoid both model overfitting and data collinearity and because our goal was the interpretation of the environmental drivers of the distribution of *Bsal*, we reduced the number of predictors in our two predictor sets. This procedure leads to more parsimonious and interpretable models [24,55,56]. For this purpose, we examined pairwise Pearson correlation coefficients between the predictors and eliminated correlated variables with absolute values higher than 0.8 [57,58], because a more restrictive threshold value would have resulted in considerably less predictors. Moreover, we selected variables according to their expected relevance to *Bsal* life history [59]. The hypotheses behind this selection were based on *Bsal* in vitro temperature responses [10] as well as some general ecological aspects of the hosts [60]. Too cold or too hot conditions, likewise to dry conditions, should be disadvantageous to *Bsal*, as both fungal parasites and amphibian hosts generally rely on humid conditions. We choose predictors that reflected optimal conditions and limitations of *Bsal* [10], with emphasis of the adapted temperature indices (ECA set). Out of the ECA set, we therefore favoured predictors with a consecutive character over counting predictors. While, for instance, thirty consecutive days that are too hot for *Bsal* growth can be a limiting factor, thirty hot days might not be limiting when regularly interrupted by cooler days. However, in our study region these consecutive predictors are correlated to some counting predictors and can therefore be seen as surrogates for them (S4 Table).

Similar to the ECA approach, we chose a set out of the available BIOCLIM predictors that represent extreme and favourable conditions to *Bsal* (similar to [20,23]). The predictor ‘bio 8’ (mean temperature of wettest quarter) was included to account for possible temperature relationships at expected beneficial humid conditions, and ‘bio 15’ (precipitation seasonality) was included to examine the importance of stable precipitation conditions over the year. The resulting final predictor sets are shown in Table 1, S1 and S2 Figs, for correlations between final predictor sets and between the final and the initial predictor sets see S4 Table.

Model fine-tuning and evaluation. We ran Maxent with the model complexity specifications described by Shcheglovitova & Anderson (2013) [51] for models with small sample sizes (only hinge features, regularization multiplier of 2). These authors found that models with more complex feature classes (which can lead to model overfitting) and with higher regularizations (which results in simpler models) outperform models with standard settings for small sample sizes (simple feature class with lower regularization). As Maxent assumes that a species is equally likely to be anywhere in the background extent, the latter is often restricted to areas that are accessible via dispersal, while modifying this extent is equivalent to changing the a priori expectation of a species’ distribution [24]. As it is presumed that *Bsal* is in an early invasion stage, regions in the south-western part of our study region may be far beyond the invasion front. As it is not clear if *Bsal* is really a recently introduced pathogen, as there are indications that *Bsal* has been introduced to Europe more than 10 years ago (authors’ unpubl. data), we defined three background extents to account for different hypothetical invasion scenarios

Table 1. Final predictor sets used for the *Bsal* SDMs.

Set	Code	Definition	Unit
ECA	csu 5	largest number of consecutive days where $T_{max} > 5^{\circ}C$	days
	csu 25	largest number of consecutive days where $T_{max} > 25^{\circ}C$	days
	su 10–15	number of days where $10^{\circ}C < T_{max} < 15^{\circ}C$	days
	tr 10–15	number of days where $10^{\circ}C < T_{min} < 15^{\circ}C$	days
	cddn	number of consecutive dry day (cdd) periods with ≥ 5 cdd per period	number
	cwdn	number of consecutive wet day (cwd) periods with ≥ 5 cwd per period	number
	r 10	number of days with precipitation < 10 mm	days
BIO	bio 8	mean temperature of wettest quarter	$^{\circ}C$
	bio 10	mean temperature of warmest quarter	$^{\circ}C$
	bio 11	mean temperature of coldest quarter	$^{\circ}C$
	bio 15	precipitation seasonality (coefficient of variation)	-
	bio 16	precipitation of wettest quarter	mm
	bio 17	precipitation of driest quarter	mm

For additional information on ECA predictors, as explanations to codes, definitions of ‘dry’ or ‘wet’ days, see [S1 Table](#).

doi:10.1371/journal.pone.0165682.t001

(S3 Fig). We decided for an approach similar to Elith *et al.* (2010) [61] who compared a continent-wide background with a background restricted to a polygon in reachable distance around early invasion records. (1) As a conservative approach, we drew a minimum convex polygon (MCP) of 70 km distance (~ the known furthest distance of two *Bsal* records within the study region) around the presences to limit our background. This background represents the hypothesis of a recent arrival of *Bsal* in Europe and early invasive stage. (2) Additionally, we created a 150 km MCP (this distance accounts for the two presences outside our study region [13]) and (3) the full study area as alternative extents to account for the possibility of earlier unnoticed arrivals and a longer dispersal ability. Models, which were trained with a MCP background were again projected into the entire study area without ‘clamping’. When projecting a model into predictor conditions outside their training conditions, ‘no clamping’ results in continuing the response curve, while ‘clamping’ keeps the suitability constant at the limits of the training data [57]. We chose this setting because of the simple type of response curves. It seems reasonable to simply continue with them, as they are monotonic at their edges with no complex patterns. We present Multivariate Environmental Similarity Surfaces (MESS) maps [61] to identify areas outside of the training conditions of MCP-based models. In these areas, predictions could have poor support if the response curves are unrealistically extrapolated with respect to a species’ ecology [61].

Evaluating model performance for small sample sizes is a challenging task in SDM building for the lack of independent test data. To evaluate our models, we therefore employed a leave-one-out jackknife approach (in this case equal to a 14-fold cross-validation), which is applicable to small sample sizes [48,51]. Models were built for both predictor sets (ECA, BIO) and the three background extents (indexed ‘70’, ‘150’, ‘full’), respectively. We ran each model with 30 replicates to account for variance in the background data, using each time 10,000 different random background points. The area under the receiver operating characteristic curve (AUC) was calculated by Maxent as a measure of predictive accuracy, although we are aware that its use for presence-only data is controversially debated [54,62]. AUC values reflect the model’s ability to distinguish between presence and background points, giving information how general or restricted a distribution is along the range of the predictor variables in the study region [24,62].

AUC is considered useful to compare models built with the same data and background, which is not the case for the models in this study, as different background extents were used [24]. For this reason, we just state AUC as an indicator of how widespread the distribution of *Bsal* is predicted in our background area. Additionally, we present the omission of the test locality (test omission, proportion of misidentified test presences) with respect to the ‘minimum training presence’ (MTR) threshold, which is also calculated by Maxent [63]. For small sample sizes, this threshold rule represents a conservative approach, because it identifies the minimum predicted area, which keeps the omission error in the training data set at zero [48]. We also provide the predicted area for the binary maps with respect to the MTR threshold for each model type, calculated by Maxent. To identify the most important variables for each model, we used the analysis of variable contribution as incorporated in Maxent. We calculated for all measures the mean and standard deviation over all cross-validation folds and replicates. To compare the mean predictions of the different models we used Pearson correlation coefficients and Schoener’s D, a metric of niche overlap [64,65].

Additional information on software and data used

We used CDO 1.6.2 [66] to process the climate model output (netCDF format) and to calculate the ECA indices. The R 3.2.2 [67] packages RASTER [68] and DISMO [69] were employed for calculating BIOCLIM variables, raster correlations, niche overlap and boxplots. The PMCMR package [70] was used to apply the Kruskal-Wallis Nemenyi post-hoc test. ArcGIS 10.2.1 and SDMtoolbox 1.1b [71] were used to build the final predictor layers, check correlations between them and to create output maps and figures. Administrative boundary data was obtained from the GADM database 2.8 (<http://www.gadm.org>) and river data from the European Environment Agency, EEA (<http://www.eea.europa.eu>).

Results

ECA₇₀ performed best according to the test omission (Table 2). For both predictor sets the proportion of misidentified *Bsal* presence records increased with larger background extent, with the predicted area decreasing. Test AUC values mirrored the predicted area; less restricted predictions in the background extent (i.e. smaller AUC values) led to more widespread predictions over the entire study region. ECA₇₀ predicted the largest and BIO_{full} the most restricted distribution of *Bsal* (Fig 2).

The BIO models were almost identical to each other, independent from the background selection, which was reflected by high values of Pearson correlation coefficient and Schoener’s

Table 2. Test omission, test AUC and predicted area for the different *Bsal*/SDMs.

Model	Test omission	Test AUC	Predicted area
ECA ₇₀	0.079 ± 0.038 a	0.817 ± 0.004	0.436 ± 0.04 a
ECA ₁₅₀	0.290 ± 0.082 b	0.896 ± 0.006	0.141 ± 0.01 bc
ECA _{full}	0.271 ± 0.081 b	0.920 ± 0.006	0.125 ± 0.02 bd
BIO ₇₀	0.143 ± 0.000 c	0.871 ± 0.001	0.275 ± 0.00 ac
BIO ₁₅₀	0.143 ± 0.000 c	0.941 ± 0.002	0.114 ± 0.00 de
BIO _{full}	0.214 ± 0.000 b	0.952 ± 0.002	0.084 ± 0.00 e

Values are mean ± one SD. Test omission and predicted area were calculated with respect to the ‘minimum training presence’ threshold. Value pairs with no letter in common are significantly different (Kruskal-Wallis test, Nemenyi post-hoc, p < 0.05). As AUC values are not comparable between models, no statistical test was applied.

doi:10.1371/journal.pone.0165682.t002

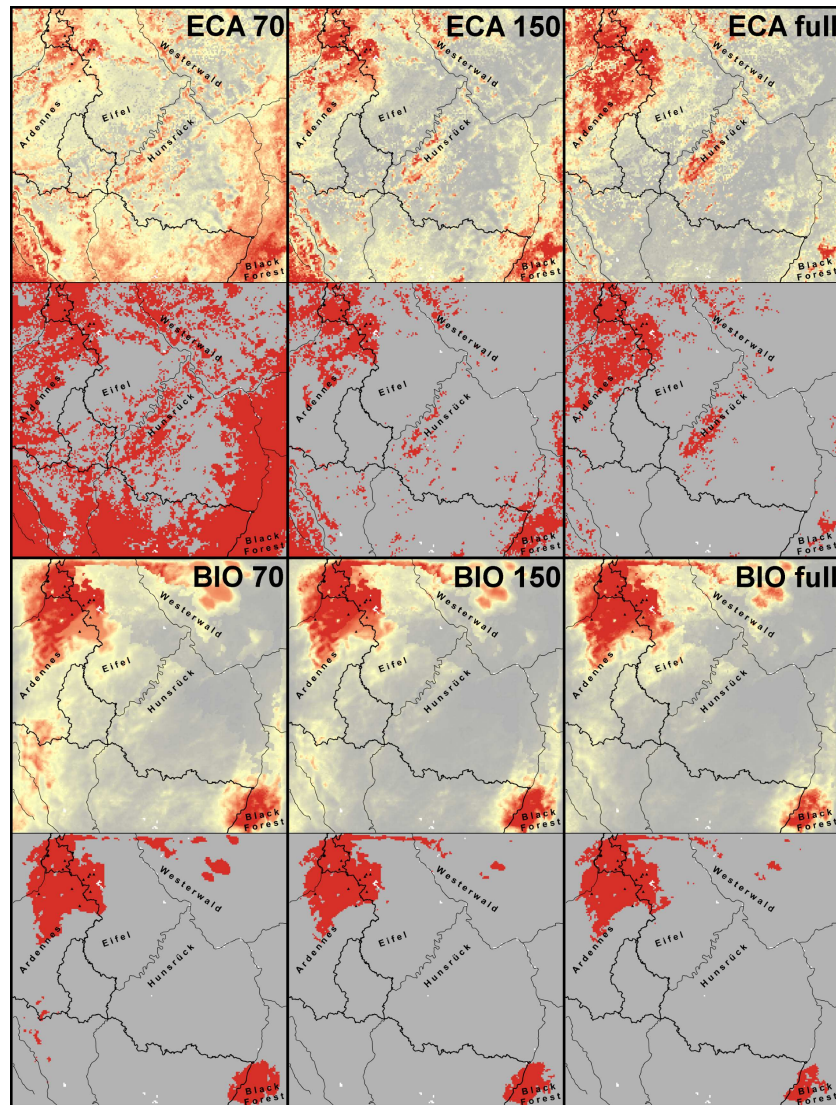


Fig 2. Predictions into the study region for the different *Bsal* SDMs. Predicted suitability maps (top) with corresponding presence-absence maps (below) for the different models. High suitability and presences are indicated in red, low suitability and absences in grey. *Bsal* presences are indicated by black triangles.

doi:10.1371/journal.pone.0165682.g002

D (Table 3). Suitable areas were mainly predicted in the region of the known *Bsal* presences, into small parts of the Westerwald and the northern portion of the Black Forest. On the contrary, ECA models differed more strongly from each other, most obvious between ECA_{70} and ECA_{full} (Fig 2, Table 3). ECA_{70} predicted suitable areas all over the study area, with larger areas

Table 3. Pairwise Pearson correlation coefficients r and Schoener's D (grey-shaded) for average ECA and BIO model predictions.

$r \setminus D$	ECA_{70}	ECA_{150}	ECA_{full}	$r \setminus D$	BIO_{70}	BIO_{150}	BIO_{full}
ECA_{70}	1	0.795	0.701	BIO_{70}	1	0.840	0.799
ECA_{150}	0.836	1	0.797	BIO_{150}	0.960	1	0.921
ECA_{full}	0.451	0.784	1	BIO_{full}	0.929	0.982	1

doi:10.1371/journal.pone.0165682.t003

Table 4. Relative variable contributions of the predictor variables to *Bsal* SDMs.

	ECA ₇₀		ECA ₁₅₀		ECA _{full}	
	pc	pi	pc	pi	pc	pi
csu 25	34.4	32.8	26.5	24.0	39.4	49.4
csu 5	0.0	0.0	6.4	4.1	18.8	20.8
su 10–15	0.0	0.0	5.9	0.3	6.5	1.7
tr 10–15	56.2	55.8	32.1	48.0	4.0	10.9
cddn	0.3	0.5	19.5	7.1	30.1	15.2
cwdn	0.8	1.4	2.7	4.6	0.5	0.7
r 10	8.3	9.5	7.0	11.8	0.7	1.3
	BIO ₇₀		BIO ₁₅₀		BIO _{full}	
	pc	pi	pc	pi	pc	pi
bio 8	21.6	8.4	9.2	6.0	8.1	7.0
bio 10	0.0	0.0	0.0	0.0	2.1	4.1
bio 11	35.8	50.2	37.3	46.3	26.7	43.8
bio 15	3.0	1.1	12.6	2.6	21.1	3.3
bio 16	0.0	0.0	0.0	0.0	0.0	0.0
bio 17	39.6	40.2	40.9	45.0	42.0	41.9

Variable contributions are shown as average percent contribution (pc) and permutation importance (pi) (for details see <https://www.cs.princeton.edu/~schapire/maxent/tutorial/tutorial.doc>). For each model the three highest values are in bold.

doi:10.1371/journal.pone.0165682.t004

of unsuitability only in the Eifel, Westerwald and area between the Hunsrück and the Black Forest. The other ECA models predicted considerably less suitable areas to *Bsal*. They identified similar suitable regions as did the BIO models, with some additional areas in the Hunsrück and the south-western portion of the study region.

For ECA₇₀ and ECA₁₅₀, the temperature-based predictors ‘tr 10–15’ (days with minimum temperatures between 10° and 15°C) and ‘csu 25’ (highest number of consecutive days warmer than 25°C) were the most contributing variables. The other predictors contributed noticeably less (Table 4). In ECA_{full} though, ‘tr 10–15’ lost importance and ‘csu 25’ became the most explaining variable, followed by ‘cddn’ (number of dry periods) and ‘csu 5’ (highest number of consecutive days warmer than 5°C). Among all BIO models, ‘bio 11’ and ‘bio 17’ clearly were the most important variables. Associated variable response curves are provided in S4 Fig, and MESS maps to assess response extrapolation in S5 Fig.

Discussion

Model performance

Since SDMs infer the environmental niche of a species from its presences as well as from environmental data [22], it can be problematic if the number of presence data is too small to cover all suitable conditions to describe a species’ niche. Because of the small number of known *Bsal* presences and the expected Asian origin of this pathogen [11], it has to be taken into account that our models do not reflect the entire niche of *Bsal*. In addition, it should be considered that occasionally niche shifts occur during biological invasions [72,73]. As a consequence, our *Bsal* SDMs more represent ‘conservative’ approaches, which likely underestimate the potential distribution of *Bsal* [27]. Thus, they emphasize the predicted suitable areas. Nevertheless, as our main goal was to shed some light into the driving factors of *Bsal* distribution, our modelling approach is appropriate.

Among our models, ECA₇₀ performed best. As ECA predictors were customised according to *Bsal* temperature physiology and as the restricted background presumably reflects a more realistic invasion scenario, we suggest this to be a reasonable result. However, some uncertainty is casted on this, because of the second best performing models, BIO₇₀ and BIO₁₅₀. They markedly differed in their predictions in geographic space, while performing only slightly less well with regard to test omission. Differences between the various background extents, especially with respect to the predicted area, are not surprising. As a larger background usually goes hand in hand with a wider range of predictor values, it is easier for a model to fit responses to contrast the presences against the background (compare predictor responses for the different backgrounds, S4 Fig). As a consequence, the predicted *Bsal* distribution is more restricted around the presences. In reverse, projections from smaller backgrounds into the full area are less restricted.

Since almost all *Bsal* presences are located in forested areas and as the known amphibian host species in our study area are ground-dwelling, we accentuated the surface temperature for the calculation of the temperature variables. Through the incorporation of the effect of vegetation cover, we expected that our temperature-based predictors well reflect the niche of *Bsal*. Additionally, the shapes of all response curves were reasonable and supported the hypotheses, which were considered during the process of variable selection. The response of 'bio 8' appears to be uncommon, but is sound when accounting for the fact that the wettest quarter is associated to cold temperatures in the study region. Therefore, too warm conditions in winter might correlate with too hot conditions in summer. As the predictor ranges in the full study region compared to the restricted background extent were pretty similar (see MESS maps, S5 Fig [61]), questionable extrapolations into new predictor conditions were not problematic.

Predictor importance

The temporal more coarse BIO models were mainly driven by 'bio 11' (mean temperature of coldest quarter) and 'bio 17' (precipitation of driest quarter), representing an approach that identifies regions according to the modelled lower limits of temperature and precipitation suitable to *Bsal*. These findings are in concordance with the known needs of *Bsal* under laboratory conditions, but depicted a rather simple model, as the expected upper temperature limit [10] was not found or reached by the mean monthly temperature. As hosts often die from *Bsal* within a few days after infection [11], short time weather events might be more relevant to *Bsal* survival and added valuable extra information to our models. Several studies have brought to light that SDMs benefit from the incorporation of weather extremes [74–77]. This was acknowledged by the ECA predictor set. ECA models with restricted background were mainly influenced by 'tr 10–15', i.e. the number of days where the minimum temperature lays in the optimal growth temperature range of *Bsal*. Opposed to the BIO models, the second most important variable was also temperature-related, namely 'csu 25', the maximum length of heat periods. Such temperature-based predictors seem plausible to explain the current distribution of *Bsal*, because in previous laboratory experiments colonization of hosts occurred at temperatures above 15°C, but the critical thermal maximum for *Bsal* was 25°C [10,78,79]. A precipitation-based predictor, 'cddn' (number of dry periods), became again more influent for ECA_{full}. These findings indicate that temperature conditions may play a more important role to *Bsal* than precipitation, at least in our study region. Furthermore, high temperatures might be a stern limiting factor to the fungus, even on a landscape scale. However, to identify these limiting temperatures, predictor variables may be needed with a high temporal resolution, rather than data based on monthly averages.

Assessing *Bsal* high risk zones

So far, *Bsal* is known from a limited number of records only, but is expected to spread [13]. The known host species in the pathogen's invasive European range are, when put together, distributed more or less evenly throughout our study region [80]. This implies that unlimited pathogen spread is a possible scenario, even when amphibians are the only *Bsal* vectors. Even worse, if additionally other spread pathways play a role, such as human-mediated long distance dispersal (as known in *Bd* [8]). For these reasons, an essential question is, where in our study region *Bsal* is able to cope with the abiotic environment. Even when we are unable to fully answer this question with the present SDMs, because of the fungus' cryptic niche as a result of its expected non-equilibrium stage, these SDMs help to gain knowledge on high risk zones of *Bsal* invasion. In conservation practice, this is an important first step when developing mitigation strategies [18] and justifies a *Bsal* SDM approach despite its presumed early invasion stage.

Certain areas within the study region were identified as highly suitable to *Bsal* by all modeling approaches (Fig 3). This included the north-western portion, i.e. parts of the Ardennes and the Eifel; likewise, parts of the Westerwald and the Black Forest. We suggest these to represent 'most likely high risk zones'. All ECA models additionally supported high suitability in the Hunsrück. Moreover, these models suggested patchily distributed high suitability in-between the areas mentioned. In ECA₇₀, which was considered as the best model (Table 2), this resulted in the largest extant of high suitability covering half of our study region (Fig 2), supporting the future scenario of further spread of the pathogen. As the ECA approach accounted for weather extremes, which might be informative in the case of *Bsal* (see above), we propose these areas to represent 'likely high risk zones'.

Conclusion

We identified the apparently most important predictors for the present distribution of the fungus for the lethal amphibian pathogen *Batrachochytrium salamandrivorans* in its invasive

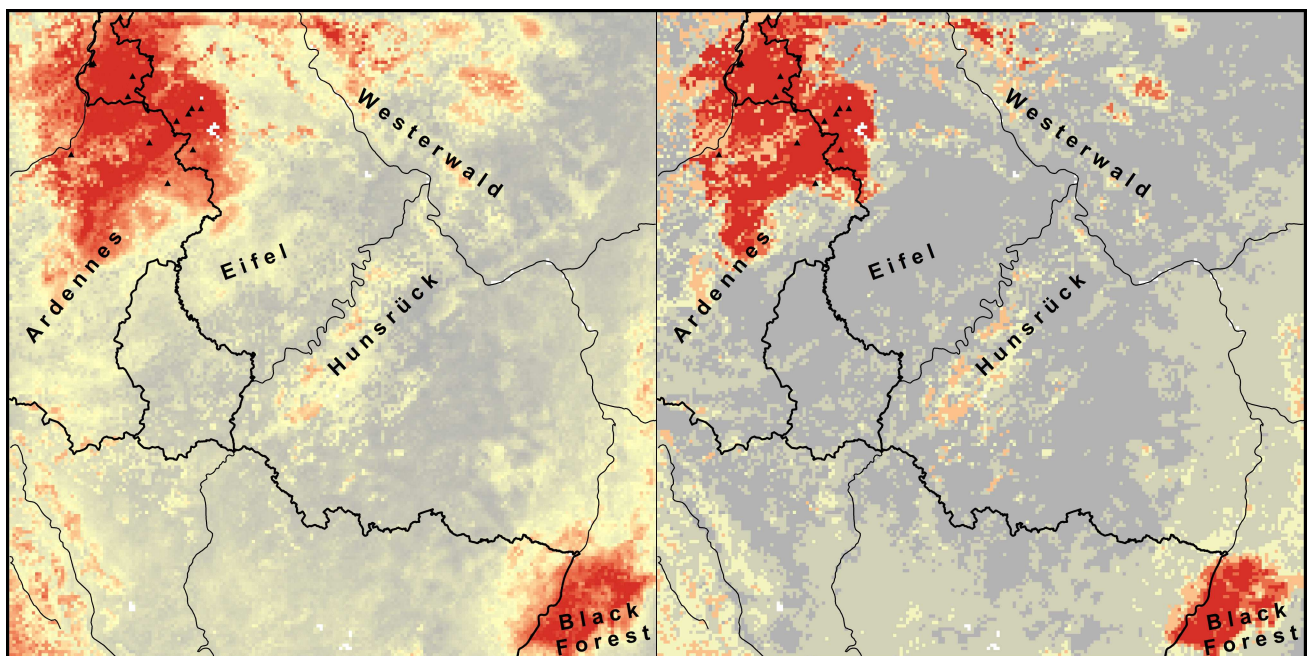


Fig 3. Average predictions of all *Bsal* SDMs. Average predicted suitability map (left) and presence-absence map (right) of all models. High values are indicated in red, low values in grey. *Bsal* presences are indicated by black triangles.

doi:10.1371/journal.pone.0165682.g003

range in Europe. Different SDMs with both bioclimate and fine-scale weather data helped us to further identify possible risk zones. The most important predictors of the best fitting model were temperature-based (number of days with minimum temperature $> 10^{\circ}\text{C}$ and $< 15^{\circ}\text{C}$ and the largest number of consecutive days where the maximum temperature was $> 25^{\circ}\text{C}$). This seems plausible with regard to the (still limited) information on the biology of this recently discovered pathogen and indicates that growth limiting temperature values of laboratory experiments are also relevant on a landscape scale. The best model predicted suitable areas all over the study area, with larger areas of unsuitability only in parts of the Eifel, Westerwald and the area between the Hunsrück and the Black Forest, indicating that a further *Bsal* spread is a possible scenario. Especially because it is known that niche shifts can occur during biological invasions and as we probably did not capture the entire niche of *Bsal*, our models may underpredict the potential distribution of this amphibian pathogen in Europe. Nevertheless, as our main goal was to shed some light into the driving factors of *Bsal* distribution, our modeling approach was reasonable and can be helpful for further *Bsal* exploration and SDMs.

Supporting Information

S1 Fig. Maps of the ECA predictor set.
(PDF)

S2 Fig. Maps of the BIO predictor set.
(PDF)

S3 Fig. Background restricting minimum convex polygons (MCPs).
(PDF)

S4 Fig. Model response curves.
(PDF)

S5 Fig. MESS maps.
(PDF)

S1 Table. ECA predictor variables.
(DOCX)

S2 Table. BIOCLIM predictor variables.
(DOCX)

S3 Table. *Bsal* presences.
(DOCX)

S4 Table. Predictor correlations.
(DOCX)

S1 ZIP Archive. ECA predictors (initial set, full extent).
(ZIP)

S2 ZIP Archive. BIOCLIM predictors (initial set, full extent).
(ZIP)

Acknowledgments

S.F. and L.S. are funded by the Trier Centre for Sustainable Systems (TriCSS). Our *Bsal* research benefits from funds by the Deutsche Gesellschaft für Herpetologie und Terrarienkunde (DGHT), Nikolaus Koch Stiftung, Stiftung Artenschutz, Verband der Zoologischen

Gärten and Zoo Landau. We thank the DKRZ (Deutsches Klimarechenzentrum, Hamburg) for providing the computational resources for running climate simulations. In addition, we are grateful to the Biologische Station Aachen and Biologische Station Düren for collaboration, and Annemarieke-Spitzen van der Sluijs (Amphibian & Fish Conservation Netherlands) for sharing ideas on the topic. We also thank three reviewers for valuable comments on an earlier manuscript version.

Author Contributions

Conceptualization: SL SF.

Data curation: SF LS.

Formal analysis: SF.

Investigation: SF.

Methodology: SF.

Resources: LS GH.

Supervision: SL.

Visualization: SF.

Writing – original draft: SF SL.

Writing – review & editing: SF LS NW GH MV SL.

References

1. Stuart SN, Hoffman M, Chanson JS, Cox NA, Berridge RJ, Ramani P, et al., editors. Threatened amphibians of the world. 1st ed. Barcelona: Lynx; 2008.
2. Barnosky AD, Matzke N, Tomiya S, Wogan GOU, Swartz B, Quental TB, et al. Has the Earth's sixth mass extinction already arrived. *Nature*. 2011; 471: 51–57. doi: [10.1038/nature09678](https://doi.org/10.1038/nature09678) PMID: [21368823](https://pubmed.ncbi.nlm.nih.gov/21368823/)
3. Smith KG, Lips KR, Chase JM. Selecting for extinction: nonrandom disease-associated extinction homogenizes amphibian biotas. *Ecol Lett*. 2009; 12: 1069–1078. doi: [10.1111/j.1461-0248.2009.01363.x](https://doi.org/10.1111/j.1461-0248.2009.01363.x) PMID: [19694784](https://pubmed.ncbi.nlm.nih.gov/19694784/)
4. Daszak P, Cunningham AA, Hyatt AD. Emerging Infectious Diseases of Wildlife—Threats to Biodiversity and Human Health. *Science*. 2000; 287: 443–449. doi: [10.1126/science.287.5452.443](https://doi.org/10.1126/science.287.5452.443) PMID: [10642539](https://pubmed.ncbi.nlm.nih.gov/10642539/)
5. Rahbek C. Disease ecology: the silence of the robins. *Nature*. 2007; 447: 652–653. doi: [10.1038/nature05889](https://doi.org/10.1038/nature05889) PMID: [17507926](https://pubmed.ncbi.nlm.nih.gov/17507926/)
6. Blehert DS, Hicks AC, Behr M, Meteyer CU, Berlowski-Zier BM, Buckles EL, et al. Bat white-nose syndrome: an emerging fungal pathogen. *Science*. 2009; 323: 227. doi: [10.1126/science.1163874](https://doi.org/10.1126/science.1163874) PMID: [18974316](https://pubmed.ncbi.nlm.nih.gov/18974316/)
7. Collins JP, Storfer A. Global amphibian declines: sorting the hypotheses. *Diversity and Distributions*. 2003; 9: 89–98.
8. Fisher MC, Garner TWJ, Walker SF. Global emergence of *Batrachochytrium dendrobatidis* and amphibian chytridiomycosis in space, time, and host. *Annu Rev Microbiol*. 2009; 63: 291–310. doi: [10.1146/annurev.micro.091208.073435](https://doi.org/10.1146/annurev.micro.091208.073435) PMID: [19575560](https://pubmed.ncbi.nlm.nih.gov/19575560/)
9. van Rooij P, Martel A, Haesebrouck F, Pasmans F. Amphibian chytridiomycosis. A review with focus on fungus-host interactions. *Vet Res*. 2015; 46: 9031. doi: [10.1186/s13567-015-0266-0](https://doi.org/10.1186/s13567-015-0266-0) PMID: [26607488](https://pubmed.ncbi.nlm.nih.gov/26607488/)
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; 110: 15325–15329. doi: [10.1073/pnas.1307356110](https://doi.org/10.1073/pnas.1307356110) PMID: [24003137](https://pubmed.ncbi.nlm.nih.gov/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: 630–631. doi: [10.1126/science.1258268](https://doi.org/10.1126/science.1258268) PMID: [25359973](https://pubmed.ncbi.nlm.nih.gov/25359973/)
12. Goverse E, Zeeuw MP de. Trends in aantallen NEM Meetnet Amfibieën 2014. *schubben & slijm*. 2015; 26: 12–14.
13. 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: 1286–1288. doi: [10.3201/eid2207.160109](https://doi.org/10.3201/eid2207.160109) PMID: [27070102](https://pubmed.ncbi.nlm.nih.gov/27070102/)
14. Cunningham AA, Beckmann K, Perkins M, Fitzpatrick L, Cromie R, Redbond J, et al. Emerging disease in UK amphibians. *Vet Rec*. 2015; 176: 468. doi: [10.1136/vr.h2264](https://doi.org/10.1136/vr.h2264) PMID: [25934745](https://pubmed.ncbi.nlm.nih.gov/25934745/)
15. Sabino-Pinto J, Bletz M, Hendrix R, Bina Perl RG, Martel A, Pasmans F, et al. First detection of the emerging fungal pathogen *Batrachochytrium salamandrivorans* in Germany. *Amphibia-Reptilia*. 2015; 36: 411–416.
16. 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: e1005251. doi: [10.1371/journal.ppat.1005251](https://doi.org/10.1371/journal.ppat.1005251) PMID: [26662103](https://pubmed.ncbi.nlm.nih.gov/26662103/)
17. Richgels KLD, 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: 150616. doi: [10.1098/rsos.150616](https://doi.org/10.1098/rsos.150616) PMID: [26998331](https://pubmed.ncbi.nlm.nih.gov/26998331/)
18. Langwig KE, Voyles J, Wilber MQ, Frick WF, Murray KA, Bolker BM, et al. Context-dependent conservation responses to emerging wildlife diseases. *Frontiers in Ecology and the Environment*. 2015; 13: 195–202. doi: [10.1890/140241](https://doi.org/10.1890/140241)
19. Jeschke JM, Strayer DL. Usefulness of bioclimatic models for studying climate change and invasive species. *Ann N Y Acad Sci*. 2008; 1134: 1–24. doi: [10.1196/annals.1439.002](https://doi.org/10.1196/annals.1439.002) PMID: [18566088](https://pubmed.ncbi.nlm.nih.gov/18566088/)
20. Rödder D, Kielgast J, Bielby J, Schmidlein S, Bosch J, Garner TWJ, et al. Global Amphibian Extinction Risk Assessment for the Panzootic Chytrid Fungus. *Diversity*. 2009; 1: 52–66. doi: [10.3390/d1010052](https://doi.org/10.3390/d1010052)
21. Hof C, Araújo MB, Jetz W, Rahbek C. Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature*. 2011. doi: [10.1038/nature10650](https://doi.org/10.1038/nature10650) PMID: [22089134](https://pubmed.ncbi.nlm.nih.gov/22089134/)
22. Peterson AT, Soberon J, Pearson RG, Anderson RP, Martinez-Meyer E, Nakamura M, et al. *Ecological Niches and Geographic Distributions*. Princeton: Princeton University Press; 2011.
23. Yap TA, Koo MS, Ambrose RF, Wake DB, Vredenburg VT. Averting a North American biodiversity crisis. *Science*. 2015; 349: 481–482. doi: [10.1126/science.aab1052](https://doi.org/10.1126/science.aab1052) PMID: [26228132](https://pubmed.ncbi.nlm.nih.gov/26228132/)
24. Merow C, Smith MJ, Silander JA. A practical guide to MaxEnt for modeling species' distributions. What it does, and why inputs and settings matter. *Ecography*. 2013; 36: 1058–1069. doi: [10.1111/j.1600-0587.2013.07872.x](https://doi.org/10.1111/j.1600-0587.2013.07872.x)
25. Guisan A, Zimmermann NE. Predictive habitat distribution models in ecology. *Ecological Modelling*. 2000; 135: 147–186. doi: [10.1016/S0304-3800\(00\)00354-9](https://doi.org/10.1016/S0304-3800(00)00354-9)
26. Guisan A, Thuiller W. Predicting species distribution. Offering more than simple habitat models. *Ecol Letters*. 2005; 8: 993–1009. doi: [10.1111/j.1461-0248.2005.00792.x](https://doi.org/10.1111/j.1461-0248.2005.00792.x)
27. Václavík T, Meentemeyer RK. Equilibrium or not. Modelling potential distribution of invasive species in different stages of invasion. *Diversity and Distributions*. 2012; 18: 73–83. doi: [10.1111/j.1472-4642.2011.00854.x](https://doi.org/10.1111/j.1472-4642.2011.00854.x)
28. Rockel B, Will A, Hense A. The Regional Climate Model COSMO-CLM (CCLM). *Meteorol. Z*. 2008; 17: 347–348. doi: [10.1127/0941-2948/2008/0309](https://doi.org/10.1127/0941-2948/2008/0309)
29. Dee DP, Uppala SM, Simmons AJ, Berrisford P, Poli P, Kobayashi S, et al. The ERA-Interim reanalysis. Configuration and performance of the data assimilation system. *Q.J.R. Meteorol. Soc*. 2011; 137: 553–597. doi: [10.1002/qj.828](https://doi.org/10.1002/qj.828)
30. Gutjahr O, Schefczyk L, Reiter P, Heinemann G. Impact of the horizontal resolution on the simulation of extremes in COSMO-CLM. *Meteorol. Z*. 2016. doi: [10.1127/metz/2016/0638](https://doi.org/10.1127/metz/2016/0638)
31. 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: 1965–1978. doi: [10.1002/joc.1276](https://doi.org/10.1002/joc.1276)
32. Nix HA. A biogeographic analysis of Australian elapid snakes. *Atlas of elapid snakes of Australia*. 1986; 7: 4–15.
33. Booth TH, Nix HA, Busby JR, Hutchinson MF, Franklin J. BIOCLIM. The first species distribution modeling package, its early applications and relevance to most current MaxEnt studies. *Diversity Distrib*. 2014; 20: 1–9. doi: [10.1111/ddi.12144](https://doi.org/10.1111/ddi.12144)

34. Elith J, Graham CH, Anderson RP, Dudík M, Ferrier S, Guisan A, et al. Novel methods improve prediction of species' distributions from occurrence data. *Ecography*. 2006; 29: 129–151. doi: [10.1111/j.2006.0906-7590.04596.x](https://doi.org/10.1111/j.2006.0906-7590.04596.x)
35. Franklin J. Mapping species distributions. Spatial inference and prediction. Cambridge, New York: Cambridge University Press; 2010.
36. Watling JI, Brandt LA, Bucklin DN, Fujisaki I, Mazzotti FJ, Romañach SS, et al. Performance metrics and variance partitioning reveal sources of uncertainty in species distribution models. *Ecological Modelling*. 2015; 309–310: 48–59. doi: [10.1016/j.ecolmodel.2015.03.017](https://doi.org/10.1016/j.ecolmodel.2015.03.017)
37. Pearson RG, Thuiller W, Araújo MB, Martinez-Meyer E, Brotons L, McClean C, et al. Model-based uncertainty in species range prediction. *J Biogeography*. 2006; 33: 1704–1711. doi: [10.1111/j.1365-2699.2006.01460.x](https://doi.org/10.1111/j.1365-2699.2006.01460.x)
38. Segurado P, Araújo MB. An evaluation of methods for modelling species distributions. *Journal of Biogeography*. 2004; 31: 1555–1568. doi: [10.1111/j.1365-2699.2004.01076.x](https://doi.org/10.1111/j.1365-2699.2004.01076.x)
39. Warton D, Aarts G. Advancing our thinking in presence-only and used-available analysis. *J Anim Ecol*. 2013; 82: 1125–1134. doi: [10.1111/1365-2656.12071](https://doi.org/10.1111/1365-2656.12071) PMID: [23488567](https://pubmed.ncbi.nlm.nih.gov/23488567/)
40. Austin M. Spatial prediction of species distribution. An interface between ecological theory and statistical modelling. *Ecological Modelling*. 2002; 157: 101–118. doi: [10.1016/S0304-3800\(02\)00205-3](https://doi.org/10.1016/S0304-3800(02)00205-3)
41. Phillips SJ, Anderson RP, Schapire RE. Maximum entropy modeling of species geographic distributions. *Ecological Modelling*. 2006; 190: 231–259. doi: [10.1016/j.ecolmodel.2005.03.026](https://doi.org/10.1016/j.ecolmodel.2005.03.026)
42. Phillips SJ, Dudík M. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*. 2008; 31: 161–175.
43. Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*. 2011; 17: 43–57. doi: [10.1111/j.1472-4642.2010.00725.x](https://doi.org/10.1111/j.1472-4642.2010.00725.x)
44. Hanberry BB, He HS, Palik BJ. Pseudoabsence generation strategies for species distribution models. *PLoS ONE*. 2012; 7: e44486. doi: [10.1371/journal.pone.0044486](https://doi.org/10.1371/journal.pone.0044486) PMID: [22952985](https://pubmed.ncbi.nlm.nih.gov/22952985/)
45. Barbet-Massin M, Jiguet F, Albert CH, Thuiller W. Selecting pseudo-absences for species distribution models. How, where and how many. *Methods in Ecology and Evolution*. 2012; 3: 327–338. doi: [10.1111/j.2041-210X.2011.00172.x](https://doi.org/10.1111/j.2041-210X.2011.00172.x)
46. Senay SD, Worner SP, Ikeda T. Novel three-step pseudo-absence selection technique for improved species distribution modelling. *PLoS ONE*. 2013; 8: e71218. doi: [10.1371/journal.pone.0071218](https://doi.org/10.1371/journal.pone.0071218) PMID: [23967167](https://pubmed.ncbi.nlm.nih.gov/23967167/)
47. Lobo JM, Jiménez-Valverde A, Hortal J. The uncertain nature of absences and their importance in species distribution modelling. *Ecography*. 2010; 33: 103–114. doi: [10.1111/j.1600-0587.2009.06039.x](https://doi.org/10.1111/j.1600-0587.2009.06039.x)
48. Pearson RG, Raxworthy CJ, Nakamura M, Townsend Peterson A. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography*. 2007; 34: 102–117. doi: [10.1111/j.1365-2699.2006.01594.x](https://doi.org/10.1111/j.1365-2699.2006.01594.x)
49. Wisz MS, Hijmans RJ, Li J, Peterson AT, Graham CH, Guisan A. Effects of sample size on the performance of species distribution models. *Diversity and Distributions*. 2008; 14: 763–773. doi: [10.1111/j.1472-4642.2008.00482.x](https://doi.org/10.1111/j.1472-4642.2008.00482.x)
50. van Proosdij André S. J., Sosef MSM, Wieringa JJ, Raes N. Minimum required number of specimen records to develop accurate species distribution models. *Ecography*. 2016; 39: 542–552. doi: [10.1111/ecog.01509](https://doi.org/10.1111/ecog.01509)
51. Shcheglovitova M, Anderson RP. Estimating optimal complexity for ecological niche models. A jack-knife approach for species with small sample sizes. *Ecological Modelling*. 2013; 269: 9–17. doi: [10.1016/j.ecolmodel.2013.08.011](https://doi.org/10.1016/j.ecolmodel.2013.08.011)
52. Hernandez PA, Graham CH, Master LL, Albert DL. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography*. 2006; 29: 773–785. doi: [10.1111/j.0906-7590.2006.04700.x](https://doi.org/10.1111/j.0906-7590.2006.04700.x)
53. Renner IW, Warton DI. Equivalence of MAXENT and Poisson point process models for species distribution modeling in ecology. *Biometrics*. 2013; 69: 274–281. doi: [10.1111/j.1541-0420.2012.01824.x](https://doi.org/10.1111/j.1541-0420.2012.01824.x) PMID: [23379623](https://pubmed.ncbi.nlm.nih.gov/23379623/)
54. Yackulic CB, Chandler R, Zipkin EF, Royle JA, Nichols JD, Campbell Grant EH, et al. Presence-only modelling using MAXENT. When can we trust the inferences? *Methods Ecol Evol*. 2013; 4: 236–243. doi: [10.1111/2041-210x.12004](https://doi.org/10.1111/2041-210x.12004)
55. Burnham KP, Anderson DR. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. 2nd ed.: Springer; 2002.

56. Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, et al. Collinearity. A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*. 2013; 36: 27–46. doi: [10.1111/j.1600-0587.2012.07348.x](https://doi.org/10.1111/j.1600-0587.2012.07348.x)
57. Webber BL, Yates CJ, Le Maitre DC, Scott JK, Kriticos DJ, Ota N, et al. Modelling horses for novel climate courses. Insights from projecting potential distributions of native and alien Australian acacias with correlative and mechanistic models. *Diversity and Distributions*. 2011; 17: 978–1000. doi: [10.1111/j.1472-4642.2011.00811.x](https://doi.org/10.1111/j.1472-4642.2011.00811.x)
58. Latinne A, Meynard CN, Herbretau V, Waengsothorn S, Morand S, Michaux JR. Influence of past and future climate changes on the distribution of three Southeast Asian murine rodents. *J. Biogeogr.* 2015; 42: 1714–1726. doi: [10.1111/jbi.12528](https://doi.org/10.1111/jbi.12528)
59. Rödder D, Schmidlein S, Veith M, Lötters S. Alien invasive slider turtle in unpredicted habitat: a matter of niche shift or of predictors studied. *PLoS ONE*. 2009; 4: e7843. doi: [10.1371/journal.pone.0007843](https://doi.org/10.1371/journal.pone.0007843) PMID: [19956684](https://pubmed.ncbi.nlm.nih.gov/19956684/)
60. Duellman WE, Trueb L. *Biology of amphibians*. Johns Hopkins Univ. Press; 1994.
61. Elith J, Kearney M, Phillips S. The art of modelling range-shifting species. *Methods in Ecology and Evolution*. 2010; 1: 330–342. doi: [10.1111/j.2041-210X.2010.00036.x](https://doi.org/10.1111/j.2041-210X.2010.00036.x)
62. Lobo JM, Jiménez-Valverde A, Real R. AUC. A misleading measure of the performance of predictive distribution models. *Global Ecol Biogeography*. 2008; 17: 145–151. doi: [10.1111/j.1466-8238.2007.00358.x](https://doi.org/10.1111/j.1466-8238.2007.00358.x)
63. Anderson RP. Real vs. artefactual absences in species distributions. Tests for *Oryzomys albigularis* (Rodentia: Muridae) in Venezuela. *Journal of Biogeography*. 2003; 30: 591–605. doi: [10.1046/j.1365-2699.2003.00867.x](https://doi.org/10.1046/j.1365-2699.2003.00867.x)
64. Warren DL, Glor RE, Turelli M. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution*. 2008; 62: 2868–2883. doi: [10.1111/j.1558-5646.2008.00482.x](https://doi.org/10.1111/j.1558-5646.2008.00482.x) PMID: [18752605](https://pubmed.ncbi.nlm.nih.gov/18752605/)
65. Rödder D, Engler JO. Quantitative metrics of overlaps in Grinnellian niches. *Advances and possible drawbacks*. *Global Ecology and Biogeography*. 2011; 20: 915–927. doi: [10.1111/j.1466-8238.2011.00659.x](https://doi.org/10.1111/j.1466-8238.2011.00659.x)
66. CDO. Climate Data Operators. 2015. <http://www.mpimet.mpg.de/cdo>.
67. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2015.
68. Hijmans RJ. raster: Geographic Data Analysis and Modeling. 2016. R package version 2.5–8. <https://cran.r-project.org/package=raster>.
69. Hijmans RJ, Phillips SJ, Leathwick JR, Elith J. dismo: Species Distribution Modeling. 2016. R package version 1.1–1. <https://cran.r-project.org/package=dismo>.
70. Pohlert T. The Pairwise Multiple Comparison of Mean Ranks Package (PMCMR). 2014. R package version 4.1. <https://cran.r-project.org/package=PMCMR>.
71. Brown JL. SDMtoolbox. A python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *Methods Ecol Evol*. 2014; 5: 694–700. doi: [10.1111/2041-210X.12200](https://doi.org/10.1111/2041-210X.12200)
72. Rödder D, Lötters S. Niche shift versus niche conservatism. Climatic characteristics of the native and invasive ranges of the Mediterranean house gecko (*Hemidactylus turcicus*). *Global Ecology and Biogeography*. 2009; 18: 674–687. doi: [10.1111/j.1466-8238.2009.00477.x](https://doi.org/10.1111/j.1466-8238.2009.00477.x)
73. Petitpierre B, Kueffer C, Broennimann O, Randin C, Daehler C, Guisan A. Climatic Niche Shifts Are Rare Among Terrestrial Plant Invaders. *Science*. 2012; 335: 1344–1348. doi: [10.1126/science.1215933](https://doi.org/10.1126/science.1215933) PMID: [22422981](https://pubmed.ncbi.nlm.nih.gov/22422981/)
74. Zimmermann NE, Yoccoz NG, Edwards TC, Meier ES, Thuiller W, Guisan A, et al. Climatic extremes improve predictions of spatial patterns of tree species. *Proc Natl Acad Sci U S A*. 2009; 106 Suppl 2: 19723–19728. doi: [10.1073/pnas.0901643106](https://doi.org/10.1073/pnas.0901643106) PMID: [19897732](https://pubmed.ncbi.nlm.nih.gov/19897732/)
75. Reside AE, Vanderwal JJ, Kutt AS, Perkins GC. Weather, not climate, defines distributions of vagile bird species. *PLoS ONE*. 2010; 5: e13569. doi: [10.1371/journal.pone.0013569](https://doi.org/10.1371/journal.pone.0013569) PMID: [21042575](https://pubmed.ncbi.nlm.nih.gov/21042575/)
76. Bateman BL, VanDerWal J, Johnson CN. Nice weather for bettings. Using weather events, not climate means, in species distribution models. *Ecography*. 2012; 35: 306–314. doi: [10.1111/j.1600-0587.2011.06871.x](https://doi.org/10.1111/j.1600-0587.2011.06871.x)
77. Rasztoivits E, Berki I, Mátyás C, Czimmer K, Pötzelberger E, Móczis N. The incorporation of extreme drought events improves models for beech persistence at its distribution limit. *Annals of Forest Science*. 2014; 71: 201–210. doi: [10.1007/s13595-013-0346-0](https://doi.org/10.1007/s13595-013-0346-0)

78. Blooi M, Martel A, Haesebrouck F, Vercammen F, Bonte D, Pasmans F. Treatment of urodelans based on temperature dependent infection dynamics of *Batrachochytrium salamandrivorans*. *Sci Rep*. 2015; 5: 8037. doi: [10.1038/srep08037](https://doi.org/10.1038/srep08037) PMID: [25623498](https://pubmed.ncbi.nlm.nih.gov/25623498/)
79. Blooi M, Pasmans F, Rouffaer L, Haesebrouck F, Vercammen F, Martel A. Successful treatment of *Batrachochytrium salamandrivorans* infections in salamanders requires synergy between voriconazole, polymyxin E and temperature. *Sci Rep*. 2015; 5: 11788. doi: [10.1038/srep11788](https://doi.org/10.1038/srep11788) PMID: [26123899](https://pubmed.ncbi.nlm.nih.gov/26123899/)
80. Sillero N, Campos J, Bonardi A, Corti C, Creemers R, Crochet P-A, et al. Updated distribution and biogeography of amphibians and reptiles of Europe. *Amphibia-Reptilia*. 2014; 35: 1–31. doi: [10.1163/15685381-00002935](https://doi.org/10.1163/15685381-00002935)