PROCEEDINGS OF THE ROYAL SOCIETY B

rspb.royalsocietypublishing.org

Research

Cite this article: Liu X, Rohr JR, Li Y. 2013 Climate, vegetation, introduced hosts and trade shape a global wildlife pandemic. Proc R Soc B 280: 20122506.
http://dx.doi.org/10.1098/rspb.2012.2506

Received: 21 October 2012
Accepted: 26 November 2012

Subject Areas:
ecology, health and disease and epidemiology, environmental science

Keywords:
global factors, emerging diseases, *Batrachochytrium dendrobatidis*, species distribution models, propagule pressure, trade

Author for correspondence:
Yiming Li
e-mail: liym@ioz.ac.cn

Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2012.2506 or via http://rspb.royalsocietypublishing.org.

Royal Society Publishing
Informing the science of the future

Climate, vegetation, introduced hosts and trade shape a global wildlife pandemic

Xuan Liu[1], Jason R. Rohr[2] and Yiming Li[1]

[1]Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, 1 Beichen West Road, Chaoyang, Beijing 100101, People's Republic of China
[2]Department of Integrative Biology, University of South Florida, Tampa, FL 33620, USA

Global factors, such as climate change, international trade and introductions of exotic species are often elicited as contributors to the unprecedented rate of disease emergence, but few studies have partitioned these factors for global pandemics. Although contemporary correlative species distribution models (SDMs) can be useful for predicting the spatial patterns of emerging diseases, they focus mainly on the fundamental niche (FN) predictors (i.e. abiotic climate and habitat factors), neglecting dispersal and propagule pressure predictors (PP, number of non-native individuals released into a region). Using a validated, predictive and global SDM, we show that both FN and PP accounted for significant, unique variation to the distribution of the chytrid fungus *Batrachochytrium dendrobatidis* (*Bd*), a pathogen implicated in the declines and extinctions of over 200 amphibian species worldwide. *Bd* was associated positively with vegetation, total trade and introduced amphibian hosts, nonlinearly with annual temperature range and non-significantly with amphibian leg trade or amphibian species richness. These findings provide a rare example where both FN and PP factors are predictive of a global pandemic. Our model should help guide management of this deadly pathogen and the development of other globally predictive models for species invasions and pathogen emergence influenced by FN and PP factors.

1. Introduction

Human and wildlife diseases are emerging at an unprecedented rate [1,2], posing major threats to human health and biodiversity. Understanding the factors that shape spatial patterns of disease emergence is critical for predicting risk and targeting management and conservation efforts. Global factors, such as climate change [3], international trade and global biotic homogenization (e.g. exotic species introductions) [4,5], are often evoked as contributors to disease emergence, but there are few predictive models that include these factors for emerging diseases at the global scale (but see [2,6]), especially for wildlife diseases.

Species distribution models (SDMs) have increasingly been used to predict the distribution of emerging pathogens and invasive species [7,8]. Most SDMs are based on climatic and habitat variables, stressing only the factors associated with fundamental niche (FN) [9], but neutral, metacommunity and invasion theories of ecology also emphasize the importance of other factors to species distributions, such as dispersal and propagule pressure (PP, the number of individuals released into a region to which they are not native) [10–12]. For instance, when PP is high, invasive species might be commonly found in suboptimal habitats and when it is low, they might be completely missing from optimal habitats. Global factors, such as international trade, exotic species introductions and human movement can facilitate the transmission of pathogens from reservoir to sympatric hosts and vice versa (spill-over and spill-back, respectively), or to completely new host species and areas (termed 'pathogen pollution') [1,5]. Such an increase in PP is likely to facilitate disease spread and sustain infectious diseases in suboptimal habitats or small patches where they might otherwise be extirpated (i.e. rescue effect). Therefore, to accurately predict the potential distributions of species, it is probable that SDMs must incorporate factors that can

© 2012 The Author(s) Published by the Royal Society. All rights reserved.

affect PP, such as estimates of human movement (e.g. trade) and exotic species introductions.

Here, we incorporate climate, habitat, host richness and factors that affect PP (e.g. trade, human population density and species introductions) into SDMs to identify variables important to the global distribution of the amphibian chytrid fungus *Batrachochytrium dendrobatidis* (*Bd*), one of the most deadly of emerging pathogens. *Bd* is widely considered one of the principal drivers of the global decline of amphibians [13], the most threatened vertebrate taxon on the Earth [14]. There have been several SDMs for *Bd* that use environmental predictors to explain *Bd* occurrence patterns [15–18]. Although these studies are useful for predicting *Bd* risk and making relevant management strategies, they mostly focus on FN predictors, or only limited PP factors, such as human population density at a continental scale [15]. Earlier studies have postulated that the distribution and abundance of *Bd* is affected by climate [15,17,19,20], elevation [21], vegetation [22,23], host species richness [22,24], exotic species introductions [25], frog leg trade [26], human movement [27] and the human footprint index [28]. Consequently, it is important to consider these plausible drivers concurrently because, if these factors are looked at independently, it could give the impression that particular factors are driving the distribution of *Bd* when in fact the causal driver might be another correlated factor.

Here we simultaneously consider all of these plausible drivers and quantify their unique, uncorrelated contribution to the global distribution of *Bd*. If PP accounts for a substantial portion of the variance in the distribution of *Bd*, then it would suggest that controlling human-assisted dispersal might be effective at limiting *Bd's* spread. Importantly, we evaluate the roles of FN and PP while controlling for both spatial autocorrelation and sampling bias by accounting for sampling efforts, the latter of which has never been controlled for in previous *Bd* SDMs. This is critical because evidence suggests that *Bd* sampling is generally biased towards hotspots of amphibian declines and easily accessed areas, such as urban or suburban locales and sites along highways (see the electronic supplementary material, figure S1), which would confound sampling effort with FN and PP [27,29].

We constructed our global SDM using the MaxEnt model, one of the highest performing methods for modelling species' distributions [30], which was widely used as a robust approach to explore *Bd* potential distributions [15–17]. We simultaneously evaluated 22 variables probably affecting the FN of *Bd* and five variables that probably affected PP (see the electronic supplementary material, table S1) and their independent relative contributions of FN and PP to the global distribution of *Bd*. We then created a global risk map for *Bd* to facilitate targeting monitoring, conservation and management efforts. We hypothesize that (i) models based on the FN and PP should generate better predictions for the distribution of *Bd* than those based on the FN alone and (ii) the distribution of *Bd* should be positively related to global factors such as international trade and presence of introduced hosts.

2. Material and methods

(a) Data collection

Bd precise geographical coordinates ($n = 1829$) were attained from a combination of three sources spanning 88 countries across every continent except Antarctica (see the electronic supplementary material, appendix S1). We collected 27 predictor variables (electronic supplementary material, table S1) from different publications and public databases (see the electronic supplementary material, appendix S2). These predictors can be grouped into seven categories: (i) 19 climatic variables and elevational data at a resolution of 2.5 arc-min [18], (ii) global land use, (iii) introduced hosts variable using all available records of the 28 most widely distributed introduced amphibian host species [25] (see the electronic supplementary material, appendix S3), (iv) global trade and frog leg trade data for each country, (v) the human footprint as an index of biome-type-corrected human influence on the surface of the Earth [28], (vi) the average (1982–2000) normalized difference vegetation index (NDVI) as a vegetation and habit metric, and (vii) amphibian species richness by overlaying GIS historical range maps of 6188 amphibian species from the IUCN Global Amphibian Assessment. All non-climatic variables were resampled to the 2.5 arc-min resolution to match the bioclimatic variables using a bilinear interpolation function, which is considered more realistic than the simpler nearest-neighbour method [31].

The country-level trade data are admittedly at a relative coarse resolution compared with the other predictors, but trade data at 2.5 arc-min are not available. To determine how much this larger spatial resolution for trade affected our results, we reconducted our analyses using state-level, territory-level and province-level total trade data for the USA, Australia and China, respectively. These were the only countries that had finer scale trade data. Nevertheless, with the exception of Europe, which, in general, has very small countries, the USA, Australia and China represent the majority of global *Bd* sampling effort. If the finer resolution does not affect the results or even strengthens the relationships, then it would suggest that the coarser scale used for trade relative to the other variables is not problematic.

(b) Species distribution model building and validation

Given the difficulty of confidently asserting that amphibians sampled at a location are free of *Bd*, we developed presence-only SDMs by applying the maximum entropy method using MaxEnt (3.3.3e; www.cs.princeton.edu/~schapire/maxent/, accessed 20 October 2011). MaxEnt minimizes the relative entropy between the probability density of presence data and that of the landscape in covariate space [32] and was the most suitable algorithm for our study because it outperforms other correlative algorithms, including other presence-only methods and traditional presence–absence methods [30].

To minimize the effect of *Bd* sampling bias, we applied the FactorBiasOut method and a bias grid that weights the MaxEnt analysis by sampling effort [33] (see the electronic supplementary material, appendix S4). The FactorBiasOut method is an approach to ensure that the bias in the presence and pseudo-absence data are the same so that, under reasonable assumptions, they cancel one another out [33]. The bias grid approach more explicitly corrects for sampling bias by providing a grid of the total number of amphibians sampled in each cell as a proxy for sampling effort. This approach can be implemented for *Bd* because researchers generally reported sample sizes (the number of amphibian individuals examined) for *Bd* positive and negative samples.

We created our SDMs by first using a subset of the species presence data (training dataset) to examine the correlation structure of species presence and background pseudo-absences with a set of predictors and then used the remaining presence data (testing data) to validate the model [31,34]. We developed each model using linear, quadratic and hinge functions, which are considered the best combination of functions to avoid over-fitting [34]. For each model, we used 10-fold cross validations to give a more robust estimate of predictive performance [32]. For each

cross validation iteration, 75 per cent and 25 per cent of the presence data were randomly selected for use as training and testing datasets, respectively.

We used two competing models, the full and pruned models, to build our final predictive model in MaxEnt [15]. The full model, which included all predictors, might be oversized, overfitted and redundant [35]. We therefore created pruned models (subsets of the most important variables) using a jack-knife test that systematically excluded predictors one at a time and evaluated the resulting variation in model accuracy [35]. The importance of each predictor was evaluated according to their AUC (the area under curve of the Receiver Operating Characteristic) value in isolation and on the decline of AUC when predictors were omitted one at a time based on the jack-knife test [15,35]. We then ranked the importance of each variable. The top ranking variables, which together contributed *ca* 90 per cent of the information to a full model, were retained in the pruned model [15]. In order to evaluate whether taking into account PP variables improved model performance, we created the full models and the pruned models using FN variables alone and all 27 variables. Finally, we used the pruned MaxEnt models to generate a global risk map for *Bd* [15].

(c) The evaluation and validation of MaxEnt models

We used AUC and COR to depict the performance of the MaxEnt models [30,32]. The AUC is a standard statistical measure of the predictive accuracy of SDMs [36], and is considered a useful and sensible measure to evaluate the relative accuracy of different models under the same background dataset [37]. AUC measures the model performance at all possible thresholds and generally ranges from 0.5 (prediction no better than random) to 1 (perfect discrimination) [36]. COR, termed as point biserial correlation coefficient, measures the degree to which the MaxEnt prediction varies linearly with the observation (presence/background pseudo-absence data) [30,32]. Because the distribution of background data is not normal, we calculated the COR between observations and predictions using Spearman rank correlation tests.

We also validated the robustness of the MaxEnt-based model selection using Akaike information criterion (AIC) applied to a spatial generalized least-squares model (GLS) with a binomial error and logit link and controlling for sample spatial autocorrelation. As true absences of *Bd* are not available, particularly in those insufficiently surveyed or undetected localities, and GLS models are susceptible to false absence data [38], we included *Bd* presence and pseudo-absences as the response variable in GLS models [38] (see the electronic supplementary material, appendix S5). We used AIC to compare the full GLS models to the pruned models and to compare models with FN variables alone to models with FN and PP [39]. We performed the GLS model analyses using 'gls' function in 'nlme' package in R v. 2.13.1 [40].

(d) The predictive power of predictors

We identified the most important predictors for the pruned MaxEnt model using a jack-knife test based on main effects models only [32]. To confirm the predictive power of predictors in the pruned model, we also conducted model averaging based on the GLS model, including the variables in the pruned MaxEnt model. We performed the model averaging using the 'dredge' and 'model.avg.' functions in the 'MuMIn' package of R.

Because many of our predictors were collinear (see the electronic supplementary material, table S2), we used hierarchical partitioning (HP) analysis to evaluate the unique (unshared) and shared variance of each pruned variable and spatial variables in the GLS model [41]. The spatial variables from the best (lowest AIC) multiple logistic regression model with *Bd* presence and pseudo-absences as the dependent variable and the nine terms of a cubic polynomial model based on X and Y coordinates (X, Y, X^2, Y^2, XY, X^3, Y^3, X^2Y and XY^2) were chosen for HP analysis (XY and Y^3). We calculated the statistical significance of each variable's unique variance in the HP analysis as a pseudo Z-score using 100 randomizations [41]. These analyses were conducted using the 'hier.part' and 'rand.hp' functions in the R 'hier.part' package.

We are aware that not all of the predictors can be perfectly assigned to the FN or PP categories. Given the overlap of some variables between these categories, we used variance partitioning to quantify the unique and shared variance among FN, PP and spatial variable groups. The justification for grouping trade, introduced hosts and amphibian richness together as PP and others as FN was validated by a principal components analysis on all eight pruned predictors (see the electronic supplementary material, figure S2). Variance partitioning analyses derive the proportion of unshared deviance explained by each predictor group, the shared deviance among different groups, and total unexplained deviance (residual variations). We performed this variance partitioning analysis using the 'varpart' function in the 'vegan' package of R.

3. Results

None of our results or conclusions differed between analyses conducted with country-level or finer scale trade data. In fact, the variance explained by trade even increased with the finer scale trade data. These findings suggest that our results do not appear to be a function of the coarser scale at which trade was tested relative to the other predictors. Consequently, we only present the results for analyses that included the fine scale trade data.

(a) The building and validation of MaxEnt models

The pruned MaxEnt model based on the fundamental niche and propagule pressure (FNPP), included eight variables: temperature annual range (T_{range}), maximum temperature of warmest month (T_{max}), annual precipitation ($Prec_{an}$), vegetation (mean NDVI), precipitation of coldest quarter ($Prec_{cq}$), presence of introduced hosts, trade and amphibian species richness (see the electronic supplementary material, figure S3). Comparatively, the pruned model based on the FN alone contained nine variables: elevation, vegetation, $Prec_{an}$, $Prec_{cq}$, annual mean temperature (T_{annual}), mean temperature of coldest quarter (T_{cq}), T_{range}, T_{max} and minimum temperature of coldest month (T_{min}).

Average AUC scores and COR coefficients of the pruned models with FNPP were significantly higher than those of the full models with FNPP (Two-tailed Wilcoxon signed-rank test on the testing dataset, $Z = 3.152$, $p < 0.001$ for AUC; $Z = 2.488$, $p < 0.001$ for COR), the pruned models with FN ($Z = 4.239$, $p < 0.001$ for AUC; $Z = 3.025$, $p = 0.002$ for COR) and the full models with FN ($Z = 5.344$, $p < 0.001$ for AUC; $Z = 3.501$, $p < 0.001$ for COR), indicating that the pruned model with FNPP had better performance than other models.

The performance of pruned models with FNPP was also confirmed using the spatial GLS model. Indeed, the AIC value was smaller for FNPP (included the eight predictors from the pruned MaxEnt model) than for the full model (all predictors), the model including all FN variables and the model with the nine pruned FN variables (table 1).

(b) The predictive power of predictors

Jack-knife analyses revealed that in pruned FNPP MaxEnt models, the variables with the highest predictive power

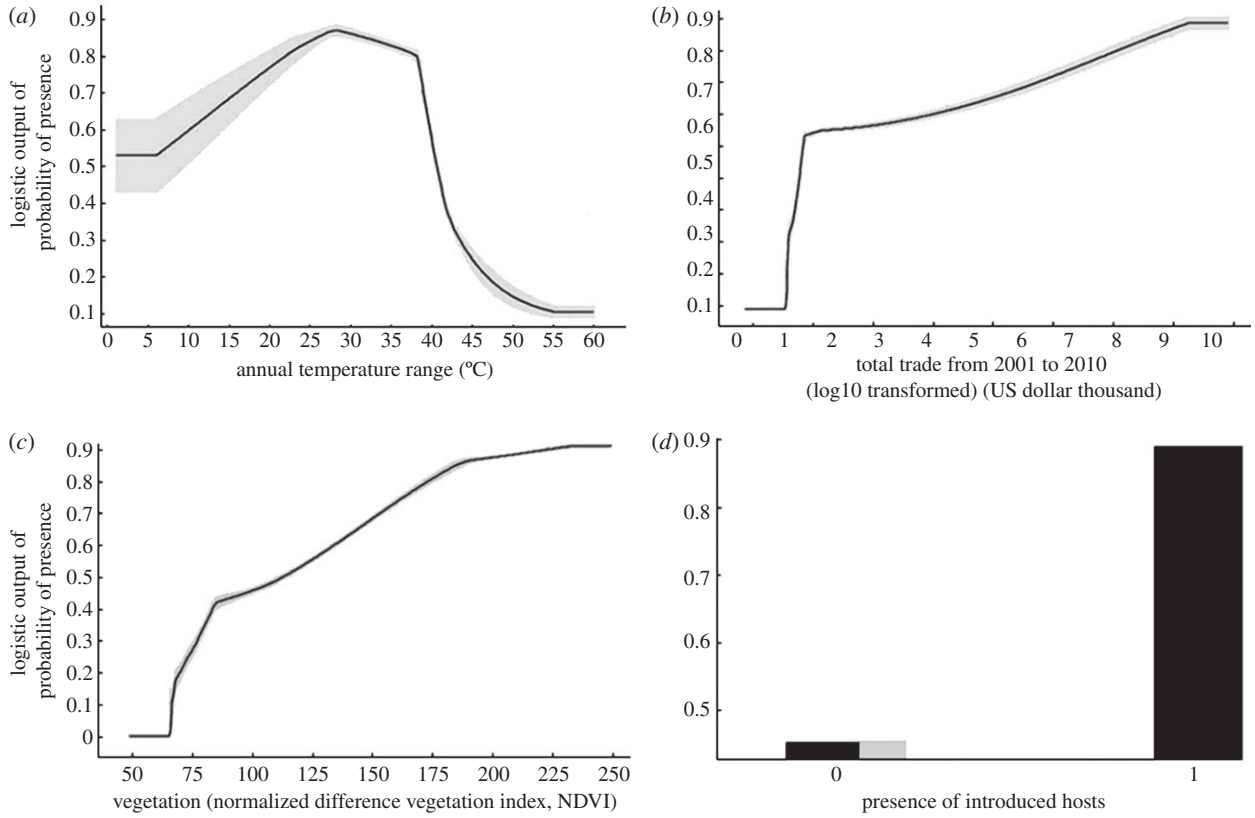

Figure 1. Relationships between the probability of *Bd* occurrence and the four most influential predictors in the pruned fundamental niche and propagule pressure (FNPP) MaxEnt model: (*a*) annual temperature range, (*b*) trade, (*c*) vegetation (mean NDVI), and (*d*) presence of introduced hosts. Grey margins are ±s.d. based on 10-fold cross-validation replicates.

Table 1. Relative performance of full and pruned FN alone and FNPP models for the global distribution of *Bd*. MaxEnt models were evaluated using AUC and COR values and spatial GLS models were evaluated using Akaike's information criterion (AIC).

	AUC	COR[b]	AIC
FN models			
full models (22 variables)	0.8120 ± 0.0258	0.48 ± 0.027	−6118.9
pruned models (nine variables)	0.8449 ± 0.0166	0.53 ± 0.032	−7002.2
FN and propagule pressure models			
full models (27 variables)	0.9032 ± 0.0214	0.61 ± 0.036	−7809.5
pruned models (eight variables)	0.9369 ± 0.0208	0.73 ± 0.021	−8147.2

[a]MaxEnt models were run after 10-fold cross validation and the AUC were shown as values ± s.e.
[b]COR was calculated between presence/background pseudo-absence and predictions using a Spearman rank correlation test.

when used in isolation were vegetation (AUC ± s.e. = 0.814 ± 0.0307), trade (AUC = 0.803 ± 0.0299), T_{range} (AUC = 0.764 ± 0.0198) and presence of introduced hosts (AUC = 0.729 ± 0.0302) (see the electronic supplementary material, figure S4). They were also the four predictor variables which significantly decreased AUC scores the most when omitted from the full model (vegetation: $Z = 5.908$, $p < 0.001$; trade: $Z = 6.133$, $p < 0.001$; T_{range}: $Z = 5.122$, $p < 0.001$; presence of introduced hosts: $Z = 6.319$, $p < 0.001$). Each of these variables was positively associated with *Bd* detection probability with the exception of T_{range} (figure 1*b*–*d*). At low levels, T_{range} was associated with increases in *Bd*, but at high levels it was associated with decreases in *Bd* (figure 1*a*).

The predictive power of T_{range}, vegetation, presence of introduced hosts and trade was also confirmed by model averaging based on the GLS model. Vegetation and trade had the greatest relative importance for the global distribution of *Bd* occurrence, followed by T_{range}, and presence of introduced hosts (table 2). The effect directions matched those in the MaxEnt model.

HP of the variables in the GLS model with FNPP (pruned eight predictors) revealed that vegetation (20%), trade (18%), introduced hosts (12%), T_{range} (14%) and Y^3 (9%) each accounted for significant independent variation in the distribution of *Bd* (table 2), whereas the remaining predictors were not significant.

The variance partitioning revealed that, despite their shared variation, FN (T_{range}, T_{max}, $Prec_{an}$, vegetation and $Prec_{cq}$), PP (presence of introduced hosts, trade and amphibian species richness) and spatial factors (XY, Y^3) accounted for significant unshared variation in the distribution of *Bd*, with 17 per cent, 15 per cent and 9 per cent of the deviance

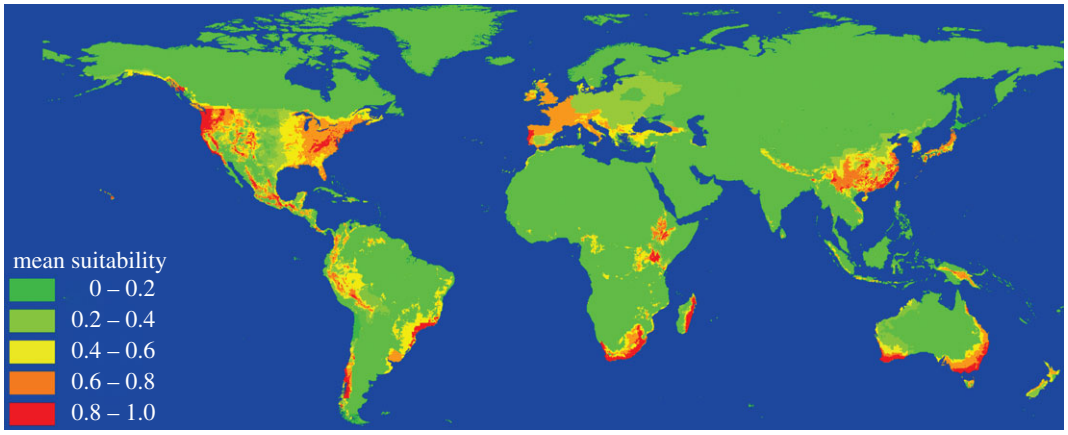

Figure 2. Average 'suitability' map (based on 10-fold cross-validation replicates) for *Bd* based on the pruned model that included FNPP variables (i.e. all eight pruned variables; table 2).

Table 2. A summary of model averaging and hierarchical partitioning (HP) analyses for the global distribution of *Bd*. The relative importance of the eight pruned variables was calculated by summing the Akaike weights of each variable across all spatial GLS models based on model averaging. HP analysis provided the independent contributions of the eight pruned variables in the GLS model and two spatial variables to the deviance of the global distribution of *Bd*.

	model averaging controlling for spatial structure		HP
variables	relative importance	parameter estimate ± s.e.	independent deviance explained (%)
FN			
vegetation (average (1982–2000) NDVI)	0.7933	0.0197 ± 0.00191	19.75[a]
T_{range} (temperature annual range, °C)	0.7208	−0.1904 ± 0.00855	14.23[a]
T_{max} (max. temperature of warmest month, °C)	0.0251	−0.0031 ± 0.00727	2.73
$Prec_{ann}$ (annual precipitation, mm)	0.0069	0.0009 ± 0.00198	6.54
$Prec_{cq}$ (precipitation of coldest quarter, mm)	0.0405	0.0005 ± 0.00025	7.92
propagule pressure			
amphibian species richness	0.0411	0.0052 ± 0.00103	6.25
total trade from 2001 to 2010 (US Dollar thousand, $\log_{10}$ transformed)	0.7513	0.0306 ± 0.00208	18.33[a]
presence of introduced hosts	0.6344	0.0206 ± 0.00319	11.85[a]
spatial structure			
XY	—	—	3.81
Y^3	—	—	8.59[a]

[a]Statistically significant ($p \leq 0.05$) estimates of unique deviance determined using randomizations tests based on 95% CI (*Z*-scores > 1.65).

explained by each, respectively (see the electronic supplementary material, table S3).

(c) Global predicted distribution of *Batrachochytrium dendrobatidis*

The pruned MaxEnt model based on FNPP suggested that the most suitable habitat for *Bd* appeared to be in western Europe, most North America except central regions, Mexico, Central America, southeastern and western South America, some eastern and western Africa, South Africa, Madagascar, Japan, southwestern and southeastern China, South Korea, Indonesia, northern Philippines, southern India, Papua New Guinea, southern and southeastern Australian coastlines and New Zealand (figure 2).

4. Discussion

Here we provide support for our initial hypotheses, that the global distribution of the emerging amphibian chytrid fungus is a function of both its FN, such as climate and habitat (vegetation), and PP, such as international trade and non-native host introductions. Both the MaxEnt and GLS models that included FN and PP performed better at predicting the global distribution of *Bd* than models based on the FN alone. Furthermore, international trade and the presence of introduced hosts had positive effects on the distribution of *Bd* in both the MaxEnt and GLS models, and the HP analysis revealed that each of the FN and PP factors accounted for significant unique variation in the models.

Previous studies had detected *Bd* on imported amphibian species in markets [42] and provided molecular evidence

suggesting that *Bd* might be spread by amphibian trade [43,44], but before this study, there was little statistical evidence linking *Bd* distributional patterns to trade in general, even at regional scales [45]. This previous research prompted several researchers to propose that the trade of bullfrogs was a primary driver of the spread of *Bd* [43,44]. However, recent evidence suggests that crayfish are also hosts of *Bd* [46]. This, coupled with the fact that total trade was a stronger predictor of the global distribution of *Bd* than the combination of all introduced amphibian species, suggests that bullfrog trade might not be the primary contributor to the spread of *Bd*. It is possible that bullfrog trade could be correlated with overall trade giving the impression based on molecular evidence that bullfrogs are responsible for *Bd* introductions. Despite finding a positive relationship between *Bd* at the global scale and introduced hosts and total trade, we need more historical data and molecular analyses to discriminate between emergences versus introductions and between bullfrog trade and the trade of other *Bd* hosts as primary contributors to any *Bd* introductions. Additionally, although our analyses suggest that the difference in spatial resolution between trade and the other tested predictors is unlikely to account for our results, compiling finer-scale trade data to further explore the role of trade in shaping pathogen distributions at different spatial scales would be fruitful.

We found little evidence that the other three factors associated with PP, such as frog leg trade, human footprint and amphibian species richness, were significant predictors of *Bd*. Frog leg trade probably adds little variation, which is not accounted for by overall trade, and frog legs are typically skinned and frozen before shipment, which should remove and kill *Bd*, respectively [26]. Previous studies conducted at regional scales showed that *Bd* detectability was positively related to the human footprint index [28]. Human footprint was assumed to largely reflect human movement (e.g. road densities) that might facilitate *Bd* transmissions [28]. We found no unique effects of human footprint on *Bd's* distribution at the global scale, suggesting that it either plays little role in the distribution of *Bd* or that it is correlated with other variables that are more important predictors.

Host species richness might amplify or dilute disease depending on host competency [47]. For example, *Bd* occurrence was found to increase with amphibian species richness in Costa Rica and Australia [22]. Contrary to this observation, a recent experimental study revealed a negative relationship between the presence of *Bd* and host species richness [24]. These contradictory results may be because of the fact that the effects of host species richness on emerging infections are probably complicated by a number of factors, such as host population densities, encounter rates between infected and susceptible individuals, disease transmission rates, spatial scales and mortality or recovery rates of infected individuals [47]. We revealed no overall positive or negative effect of amphibian species richness on *Bd*. This, of course, does not mean that dilution and amplification processes are absent. In fact, we know that they must be occurring given our result that invasive host species amplify *Bd*, consistent with the notion that species composition often dictates whether disease is amplified or diluted [47]. Spatial scales might be an important factor affecting the detection of the dilution effect.

T_{range} was an important factor associated with *Bd*, similar to the finding that mean diurnal temperature range contributed significantly on *Bd* distributions in Australia [15], and consistent with the finding that temperature variability was predictive of *Bd*-related amphibian declines in Latin America [19]. T_{range} might assimilate both the monthly minimum and maximum temperatures affecting *Bd* suitability. At the global scale, T_{range} was positively correlated with T_{max} and negatively correlated with T_{min} (see the electronic supplementary material, table S2). Therefore, an increase in T_{max} or a decrease in T_{min} will not only increase T_{range} but will also increase the chances of exceeding *Bd's* critical maximum or minimum temperatures [15].

Bd was also positively associated with vegetation (mean NDVI), consistent with previous studies on *Bd* [22,23]. The NDVI is often a surrogate for the dynamics of ground moisture and temperature, which might affect the survival of many pathogens, including *Bd*, which is known to be sensitive to moisture and temperature [19]. Vegetation might increase moisture by reducing evaporation and might reduce temperature extremes preventing high-temperature clearance of *Bd* [23]. We did not find a significant contribution of precipitation or water habitat to the global distribution of *Bd*. It is unclear why precipitation or water habitat was not predictive of *Bd*, which is generally regarded as an aquatic fungus. A possible explanation is that vegetation might be a more reliable predictor of *Bd* because it integrates moisture and temperature variation at the microhabitat level.

Gaps in knowledge are inevitable when global analyses are being conducted, but imperfect data should not prevent us from addressing questions at a global scale. For instance, there are gaps in amphibian species given that new species are being described regularly. However, these gaps in our knowledge should, for the most part, be random in their distribution and thus they should not dramatically alter our conclusions. In fact, random error should only increase the probably of false negatives, and given the significance of several of our predictors, this seems unlikely to be an issue here. We laud all the field biologists whose data were used by our analyses and, as additional data are gathered, we encourage further ground-truthing (i.e. field data) to support or refute our conclusions.

Bd is among the most serious threats to amphibians along with land-use and climate change [48], and it is important to develop accurate predictive models for *Bd's* potential risk [27]. The SDM presented here has at least three important and novel contributions compared with previous SDMs for *Bd*. First, our SDM includes both FN and PP, whereas most previous models included FN only [16–18] or only included limited PP factors, such as human population density at the regional scale [15]. We incorporated more factors associated with globalization, such as international trade and the presence of introduced hosts, to more accurately capture PP factors that might be influencing the distributional pattern of *Bd* at the global scale. Second, we control for known *Bd* sampling bias by accounting for sampling effort differences among locations and thus can be more confident that our significant FN and PP variables are not confounded by this bias. Third, our models are based on a larger *Bd* sampling dataset that spans the globe and includes previously under-represented localities, such as in Asia, where several new datasets were only recently published [49,50]. Consequently, our SDM provides a slightly different picture of *Bd* suitability compared with previous global SDMs. For instance, our models predict a more restricted *Bd* distribution in Central America, Caribbean islands, central South America, Africa, southeastern Asia, central Europe and Australia, but more

suitable areas in eastern US and eastern Asia (see the electronic supplementary material, table S4). These differences might be partly because of the probable improved accuracy and precision of our models relative to previous SDMs. We recommend focusing monitoring efforts on regions where there are threatened amphibians and where *Bd* suitability is high but *Bd* is not known to be present and encourage adaptive management approaches to amphibian conservation.

In conclusion, we provide a unique example where both FN and PP were predictive of the distribution of a global pandemic. By integrating factors associated with both FN and PP, our study should offer more reliable recommendations for monitoring and management of amphibians than were previously available. Finally, owing to the rapid pace of anthropogenic homogenization of the Earth's biota, there is a growing need for globally predictive models of the future distribution of species that incorporate both climate and human movement patterns. We hope our model is not only useful for guiding amphibian conservation, but is also useful in guiding the development of these global models for other species invasions and pathogen emergences.

We thank Z. W. Ke, F. Xu, C. M. Bai, Y. Luo, S. P. Wang, W. Zhu, C. N. Jin, X. P. Li and Z. T. Liu for data collection. We are grateful to S. Phillips, R. Mateo, T. R. Raffel, N. Raes and L. B. Buckley for very helpful suggestions in model building and data analysis. We also thank K. Murray, P. Johnson and B. Sears for providing helpful comments on the manuscript. The editors and three anonymous reviewers supplied constructive comments which have greatly improved this manuscript. X.L. and Y.L. were supported by grants from the National Natural Science Foundation of China (31200416, 31172111) and the Chinese Academy of Sciences (kscx2-yw-z-1021). J.R.R. was supported by grants from the US Department of Agriculture (NRI 2006-01370, 2009-35102-05043) and the US Environmental Protection Agency (STAR R833835 and CAREER 83518801).

References

1. Daszak P, Cunningham AA, Hyatt AD. 2000 Wildlife ecology: emerging infectious diseases of wildlife—threats to biodiversity and human health. *Science* **287**, 443–449. (doi:10.1126/science.287.5452.443)
2. Jones KE, Patel NG, Levy MA, Storeygard A, Balk D, Gittleman JL, Daszak P. 2008 Global trends in emerging infectious diseases. *Nature* **451**, 990–994. (doi:10.1038/nature06536)
3. Rohr JR, Dobson AP, Johnson PTJ, Kilpatrick AM, Paull SH, Raffel TR, Ruiz-Moreno D, Thomas MB. 2011 Frontiers in climate change-disease research. *Trends Ecol. Evol.* **26**, 270–277. (doi:10.1016/j.tree.2011.03.002)
4. Olden JD, Poff NL, Douglas MR, Douglas ME, Fausch KD. 2004 Ecological and evolutionary consequences of biotic homogenization. *Trends Ecol. Evol.* **19**, 18–24. (doi:10.1016/j.tree.2003.09.010)
5. Smith KF, Sax DF, Gaines SD, Guernier V, Guegan JF. 2007 Globalization of human infectious disease. *Ecology* **88**, 1903–1910. (doi:10.1890/06-1052.1)
6. Guernier V, Hochberg ME, Guegan JFO. 2004 Ecology drives the worldwide distribution of human diseases. *PLoS Biol.* **2**, 740–746. (doi:10.1371/journal.pbio.0020141)
7. Guisan A, Thuiller W. 2005 Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* **8**, 993–1009. (doi:10.1111/j.1461-0248.2005.00792.x)
8. Kearney M, Porter W. 2009 Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.* **12**, 334–350. (doi:10.1111/j.1461-0248.2008.01277.x)
9. Peterson AT. 2003 Predicting the geography of species' invasions via ecological niche modeling. *Q. Rev. Biol.* **78**, 419–433. (doi:10.1086/378926)
10. Hubbell SP. 2005 Neutral theory in community ecology and the hypothesis of functional equivalence. *Funct. Ecol.* **19**, 166–172. (doi:10.1111/j.0269-8463.2005.00965.x)
11. Leibold MA *et al*. 2004 The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* **7**, 601–613. (doi:10.1111/j.1461-0248.2004.00608.x)
12. Thuiller W, Richardson DM, Pysek P, Midgley GF, Hughes GO, Rouget M. 2005 Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biol.* **11**, 2234–2250. (doi:10.1111/j.1365-2486.2005.01018.x)
13. Cheng TL, Rovito SM, Wake DB, Vredenburg VT. 2011 Coincident mass extirpation of neotropical amphibians with the emergence of the infectious fungal pathogen *Batrachochytrium dendrobatidis*. *Proc. Natl Acad. Sci. USA* **108**, 9502–9507. (doi:10.1073/pnas.1105538108).
14. Stuart SN, Chanson JS, Cox NA, Young BE, Rodrigues ASL, Fischman DL, Waller RW. 2004 Status and trends of amphibian declines and extinctions worldwide. *Science* **306**, 1783–1786. (doi:10.1126/science.1103538)
15. Murray KA, Retallick RWR, Puschendorf R, Skerratt LF, Rosauer D, McCallum HI, Berger L, Speare R, VanDerWal J. 2011 Assessing spatial patterns of disease risk to biodiversity: implications for the management of the amphibian pathogen, *Batrachochytrium dendrobatidis*. *J. Appl. Ecol.* **4**, 163–173. (doi:10.1111/j.1365-2664.2010.01890.x)
16. Puschendorf R, Carnaval AC, VanDerWal J, Zumbado-Ulate H, Chaves G, Bolanos F, Alford RA. 2009 Distribution models for the amphibian chytrid *Batrachochytrium dendrobatidis* in Costa Rica: proposing climatic refuges as a conservation tool. *Divers. Distrib.* **15**, 401–408. (doi:10.1111/j.1472-4642.2008.00548.x)
17. Rödder D, Kielgast J, Lötters S. 2010 Future potential distribution of the emerging amphibian chytrid fungus under anthropogenic climate change. *Dis. Aquat. Organ.* **92**, 201–207. (doi:10.3354/dao02197)
18. Ron SR. 2005 Predicting the distribution of the amphibian pathogen *Batrachochytrium dendrobatidis* in the New World. *Biotropica* **37**, 209–221. (doi:10.1111/j.1744-7429.2005.00028.x)
19. Rohr JR, Raffel TR. 2010 Linking global climate and temperature variability to widespread amphibian declines putatively caused by disease. *Proc. Natl Acad. Sci. USA* **107**, 8269–8274. (doi:10.1073/pnas.0912883107)
20. Rohr JR, Raffel TR, Romansic JM, McCallum H, Hudson PJ. 2008 Evaluating the links between climate, disease spread, and amphibian declines. *Proc. Natl Acad. Sci. USA* **105**, 17 436–17 441. (doi:10.1073/pnas.0806368105)
21. Lips KR, Diffendorfer J, Mendelson JR, Sears MW. 2008 Riding the wave: Reconciling the roles of disease and climate change in amphibian declines. *PLoS Biol.* **6**, 441–454. (doi:10.1371/journal.pbio.0060072)
22. Becker CG, Zamudio KR. 2011 Tropical amphibian populations experience higher disease risk in natural habitats. *Proc. Natl Acad. Sci. USA* **108**, 9893–9898. (doi:10.1073/pnas.1014497108)
23. Raffel TR, Michel PJ, Sites EW, Rohr JR. 2011 What drives chytrid infections in newt populations? Associations with substrate, temperature, and shade. *EcoHealth* **7**, 526–536. (doi:10.1007/s10393-010-0358-2)
24. Searle CL, Biga LM, Spatafora JW, Blaustein AR. 2011 A dilution effect in the emerging amphibian pathogen *Batrachochytrium dendrobatidis*. *Proc. Natl Acad. Sci. USA* **108**, 16 322–16 326. (doi:10.1073/pnas.1108490108)
25. Fisher M, Garner T. 2007 The relationship between the emergence of *Batrachochytrium dendrobatidis*, the international trade in amphibians and introduced amphibian species. *Fungal Biol. Rev.* **21**, 2–9. (doi:10.1016/j.fbr.2007.02.002)
26. Gratwicke B, Evans MJ, Jenkins PT, Kusrini MD, Moore RD, Sevin J, Wildt DE. 2010 Is the international frog legs trade a potential vector for deadly amphibian pathogens? *Front. Ecol. Environ.* **8**, 438–442. (doi:10.1890/090111)
27. Rohr JR, Halstead NT, Raffel TR. 2011 Modelling the future distribution of the amphibian chytrid fungus:

the influence of climate and human-associated factors. *J. Appl. Ecol.* **48**, 174–176. (doi:10.1111/j.1365-2664.2010.01891.x)

28. Adams MJ *et al*. 2010 Using occupancy models to understand the distribution of an amphibian pathogen, *Batrachochytrium dendrobatidis*. *Ecol. Appl.* **20**, 289–302. (doi:10.1890/08-2319.1)
29. Murray KA, Retallick RWR, Puschendorf R, Skerratt LF, Rosauer D, McCallum HI, Berger L, Speare R, VanDerWal J. 2011 Issues with modelling the current and future distribution of invasive pathogens. *J. Appl. Ecol.* **48**, 177–180. (doi:10.1111/j.1365-2664.2010.01920.x)
30. Elith J *et al*. 2006 Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**, 129–151. (doi:10.1111/j.2006.0906-7590.04596.x)
31. Phillips SJ, Anderson RP, Schapire RE. 2006 Maximum entropy modeling of species geographic distributions. *Ecol. Model.* **190**, 231–259. (doi:10.1016/j.ecolmodel.2005.03.026)
32. Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ. 2011 A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.* **17**, 43–57. (doi:10.1111/j.1472-4642.2010.00725.x)
33. Dudík M, Schapire RE, Phillips SJ. 2005 Correcting sample selection bias in maximum entropy density estimation. In *Advances in Neural Information Processing Systems 18: Proceedings of the 2005 Conference*, pp. 323–330. Cambridge, MA: MIT Press.
34. Phillips SJ, Dudík M. 2008 Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* **31**, 161–175. (doi:10.1111/j.0906-7590.2008.5203.x)
35. Parolo G, Rossi G, Ferrarini A. 2008 Toward improved species niche modelling: Arnica montana in the Alps as a case study. *J. Appl. Ecol.* **45**, 1410–1418. (doi:10.1111/j.1365-2664.2008.01516.x)
36. Fielding AH, Bell JF. 1997 A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* **24**, 38–49. (doi:10.1017/S0376892997000088)
37. Duncan RP, Cassey P, Blackburn TM. 2009 Do climate envelope models transfer? A manipulative test using dung beetle introductions. *Proc. R. Soc. B* **276**, 1449–1457. (doi:10.1098/rspb.2008.1801)
38. Mateo RG, Croat TB, Felicisimo AM, Munoz J. 2010 Profile or group discriminative techniques? Generating reliable species distribution models using pseudo-absences and target-group absences from natural history collections. *Divers. Distrib.* **16**, 84–94. (doi:10.1111/j.1472-4642.2009.00617.x)
39. Burnham KP, Anderson DR. 2002 *Model selection and multimodel inference: a practical information-theoretic approach*. New York, NY: Springer.
40. R Development Core Team. 2011 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
41. Mac Nally R. 2002 Multiple regression and inference in ecology and conservation biology: further comments on identifying important predictor variables. *Biodivers. Conserv.* **11**, 1397–1401. (doi:10.1023/A:1016250716679)
42. Garner TWJ, Perkins MW, Govindarajulu P, Seglie D, Walker S, Cunningham AA, Fisher MC. 2006 The emerging amphibian pathogen *Batrachochytrium dendrobatidis* globally infects introduced populations of the North American bullfrog, *Rana catesbeiana*. *Biol. Lett.* **2**, 455–459. (doi:10.1098/rsbl.2006.0494)
43. Farrer RA *et al*. 2011 Multiple emergences of genetically diverse amphibian-infecting chytrids include a globalized hypervirulent recombinant lineage. *Proc. Natl Acad. Sci. USA* **104**, 13 845–13 850. (doi:10.1073/pnas.1111915108)
44. Schloegel LM *et al*. 2012 Novel, panzootic and hybrid genotypes of amphibian chytridiomycosis associated with the bullfrog trade. *Mol. Ecol.* **21**, 5162–5177. (doi:10.1111/j.1365-294X.2012.05710.x)
45. Kilpatrick AM, Briggs CJ, Daszak P. 2010 The ecology and impact of chytridiomycosis: an emerging disease of amphibians. *Trends Ecol. Evol.* **25**, 109–118. (doi:10.1016/j.tree.2009.07.011)
46. McMahon TA, Brannelly LA, Chatfield MWH, Johnson PTJ, Joseph MB, McKenzie VJ, Richards-Zawacki CL, Venesky MD, Rohr JR. In press. The chytrid fungus, *Batrachochytrium dendrobatidis*, has non-amphibian hosts and releases chemicals that cause pathology in the absence of infection. *Proc. Natl Acad. Sci. USA*.
47. Keesing F *et al*. 2010 Impacts of biodiversity on the emergence and transmission of infectious diseases. *Nature* **468**, 647–652. (doi:10.1038/Nature09575)
48. Hof C, Araújo MB, Jetz W, Rahbek C. 2011 Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature* **480**, 516–137. (doi:10.1038/Nature10650)
49. Bai CM, Liu X, Fisher MC, Garner TWJ, Li YM. 2012 Global and endemic Asian lineages of the emerging pathogenic fungus *Batrachochytrium dendrobatidis* widely infect amphibians in China. *Divers. Distrib.* **18**, 307–318. (doi:10.1111/j.1472-4642.2011.00878.x)
50. Swei A *et al*. 2011 Is chytridiomycosis an emerging infectious disease in Asia? *PLoS ONE* **6**, e23179. (doi:10.1371/journal.pone.0023179)