

FORUM

Modelling the future distribution of the amphibian chytrid fungus: the influence of climate and human-associated factors

Jason R. Rohr*, Neal T. Halstead and Thomas R. Raffel

University of South Florida, Department of Integrative Biology, Tampa, FL 33620, USA

Summary

1. Many of the global losses of amphibians are believed to be caused by the chytrid fungus, *Batrachochytrium dendrobatidis* (*Bd*). Hence, determining its present and future environmental suitability should help to inform management and surveillance of this pathogen and curtail the amphibian biodiversity crisis.
2. In this issue of *Journal of Applied Ecology*, Murray *et al.* (2011) offer an important step in this direction by providing a species distribution model that projects the environmental suitability of *Bd* across Australia and predicts locations of chytridiomycosis and amphibian declines. *Batrachochytrium dendrobatidis* presence was predicted by diurnal temperature range (a measure of temperature variability) and mean precipitation. Human population density, a positive predictor of *Bd*, accounted for the most variation when removed from the statistical model.
3. This work represents an invaluable case study and has great potential for managing chytridiomycosis and associated amphibian declines, but its value in practice will depend on how well managers understand the limitations of species distribution models.
4. *Synthesis and applications.* To improve the management of chytridiomycosis, amphibian-chytrid research should attempt to understand how humans may affect the distribution of *Bd*, how climatic means and variances affect *Bd* transmission, how much variation in the distribution of *Bd* is unique to and shared among climate, human, and other factors, whether human-related factors and climate statistically interact, and how these potentially correlated factors and any interactions affect the predictability of species distribution models. In response to the swift spread of *Bd* and our rapidly changing planet, we encourage the application of *Bd* distribution models to other regions of the globe and predictions of *Bd*'s distribution under future climate change scenarios.

Key-words: *Batrachochytrium dendrobatidis*, bioclimatic envelope models, biotic interactions, chytridiomycosis, climate change, disease, dispersal, diurnal temperature range, management, species distribution models

Introduction

Alarmingly, almost a third of amphibian species are considered threatened and more than 43% are experiencing some form of population decline (Stuart *et al.* 2004). Many of these amphibian losses are believed to be driven by the disease chytridiomycosis, caused by the pathogenic chytrid fungus *Batrachochytrium dendrobatidis* (*Bd*; Wake & Vredenburg 2008). Given that *Bd* may be spreading and/or emerging (Rohr *et al.* 2008; James *et al.* 2009) and that climate is changing, one of

the priorities for managing this devastating pathogen is to determine its present and future environmental limitations at global and local scales. If this can be done accurately, it might help to predict the future distribution of *Bd*, identify where *Bd* poses the greatest future threats, and facilitate prioritization of species and locations for monitoring and management given scarce conservation funds. In this issue of *Journal of Applied Ecology*, Murray *et al.* (2011) offer an important step in this direction by providing a species distribution model that projects the environmental suitability for *Bd* across the entire continent of Australia.

Murray *et al.* (2011) base their models on an impressive spatiotemporal database consisting of 821 sites in Australia where

*Correspondence author. E-mail: jasonrohr@gmail.com
Conflicts of interest: No conflicts declared

115 amphibian species and 10 183 individuals were tested for *Bd* from 1956–2007. Previous large-scale databases associated with *Bd*-related declines have proven to be useful in understanding the biology of this pathogen (Lips *et al.* 2008; Rohr *et al.* 2008; Rohr & Raffel 2010), and there is little question that this new database will also be valuable for addressing the amphibian biodiversity crisis and questions of disease ecology in general. From 19 climatic variables, as well as information on distance to water, vegetation type, and human population density, Murray *et al.* (2011) identified annual precipitation and diurnal temperature range (a measure of temperature variation) as important predictors of *Bd* presence. Moisture has been well established as a crucial factor for *Bd* persistence (Johnson *et al.* 2003; Berger *et al.* 2004). Evidence for the importance of diurnal temperature range is interesting in light of a recent study that revealed that temperature variability, in general, and diurnal temperature range specifically, might drive amphibian declines putatively caused by chytridiomycosis (Rohr & Raffel 2010).

Using recent advances in bioclimatic envelope modelling (Phillips, Anderson & Schapire 2006), Murray *et al.* (2011) estimated the range of environments suitable for *Bd* (its bioclimatic envelope) and then predicted its minimum potential geographic distribution across Australia. Importantly, sites with documented amphibian declines associated with severe chytridiomycosis had high *Bd* environmental suitability values, and environmental suitability values specific to each of Australia's 196 amphibian species were significant positive predictors of whether species experienced declines (even after controlling for species' range sizes). Hence, the developed species distribution model appears to be capable of predicting locations of high risk for both chytridiomycosis and amphibian losses. Some caution should be used interpreting these correlations, however, because sampling for *Bd* was likely biased towards locations where amphibians were in decline and/or showing signs of chytridiomycosis, so environmental suitability estimates might also be biased toward these locations. Finally, in an effort to facilitate and target management and monitoring, Murray *et al.* (2011) importantly identified amphibian species that have high environmental suitability scores for *Bd* and regions of Australia that have both high suitability scores and high amphibian species richness and endemism.

Although this work clearly has great potential for managing chytridiomycosis and associated amphibian declines, its value in practice will depend on how well managers understand the limitations of bioclimatic envelope models (BEMs) and how well the assumptions of these models were met by this study. BEMs are strictly correlational and do not directly model abiotic and biotic interactions, dispersal, or evolution, all of which can be important for predicting the effects of climate change on biodiversity (Davis *et al.* 1998; Rohr & Madison 2003; Araujo & Luoto 2007; Harmon, Moran & Ives 2009). Further, BEMs often have considerable uncertainty despite systematically overestimating model fits during model validation (Hampe 2004). The over-fitting occurs because BEMs generally do not account for spatial autocorrelation

among their data (a pseudoreplication issue; Segurado, Araujo & Kunin 2006). Finally, the results of BEMs can be quite sensitive to the model parameterization and model selection procedures that were implemented (Araujo & Guisan 2006). Ideally, several parameterization and selection procedures should be used to evaluate the robustness of the BEM results. Nevertheless, BEMs provide a useful first approximation and working hypothesis when identifying a species' future distribution (Pearson & Dawson 2003). These approximations should be improved upon with additional data and adaptive management approaches, as advocated by Murray *et al.* (2011).

Murray *et al.* (2011) also offer some important insights into how their model might be improved upon. Intriguingly, Murray *et al.* (2011) discovered that human population density (HPD) was a positive predictor of the presence of *Bd*, with *Bd* almost exclusively being found near port cities and the highways connecting them (their Fig. S1). Furthermore, the removal of HPD from their statistical model resulted in the greatest change in variation relative to all other predictors (their Fig. S8), indicating that HPD accounted for the greatest unique variation in the distribution of *Bd*. While it is possible that the correlation is driven by humans and *Bd* simply preferring the same climate, this seems unlikely given that the effect of humans was still evident after accounting for variation due to the climatic factors. Hence, the relationship between HPD and *Bd* presence suggests that, in addition to climate, human-associated factors might affect the distribution of this pathogen. This is not surprising given that humans are believed to be a major dispersal agent for *Bd* (Skerratt *et al.* 2007), a hypothesis that received support from two molecular studies concluding that the distribution of *Bd* was consistent with human-assisted migration (Morgan *et al.* 2007; James *et al.* 2009), and from a survey in Oregon and Northern California revealing that detectability of *Bd* increased markedly with human influence on the landscape (Adams *et al.* 2010).

However, if humans are regularly introducing *Bd* into areas of low environmental suitability, this could violate the underlying assumption of the BEM, that the climatic conditions where *Bd* is presently found will either match the conditions of its future range or at least be adequate surrogates for the factors that dictate its future distribution (Pearson & Dawson 2003). Research on source-sink dynamics and metapopulations, and more recently neutral theory, has shown that organisms can often appear in suboptimal habitats when immigration is high (Davis *et al.* 1998; Hanski 1998; Hubbell 2005). The fact that *Bd* is predominantly found in and around coastal cities might further exacerbate this concern because the coastline essentially functions as a giant drift fence, forcing dispersal along and away from the coast. If there are multiple introductions at nearby port cities and crossing waves of dispersal along the coast, then BEMs will provide greater weight to these coastal regions, even if they do not represent optimal *Bd* conditions. It remains to be seen how much of a concern this is to the reliability of Murray *et al.*'s (2011) predictions, but the potential influence of dispersal and human-associated factors point to some major challenges for future BEMs and amphibian-chytrid work.

Future research on BEMs should evaluate whether accounting for spatial autocorrelation using traditional approaches adequately accounts for dispersal barriers and limitations and spread from known or presumed introduction sites. This is particularly important given that the goal of BEMs, in many cases, is to model invasive species, which are often introduced at locations of high human population density, such as at cities with ports and airports. Amphibian-chytrid research should attempt to understand how humans affect the distribution of *Bd*; how much variation in the distribution of *Bd* is unique to and shared among climate, human, and other factors; whether human-related factors and climate interact statistically; and how these correlated factors and any interactions affect the predictability of BEMs. Finally, amphibian-chytrid research should better validate BEMs by determining how accurately they predict the spread of *Bd*.

Despite their limitations, BEMs represent an important tool for predicting the future distributions of species and Murray *et al.* (2011) provide an invaluable case study that should guide others in applying these tools worldwide. Undoubtedly, the reliability of these models for predicting the distribution of *Bd* will improve with a better understanding of the factors that dictate the persistence and transmission of this pathogen. In response to the swift spread of *Bd* (Skerratt *et al.* 2007; Rohr *et al.* 2008) and our rapidly changing planet, we encourage the application of BEMs to other regions of the globe and the use of BEMs and ensemble climate models to predict the distribution of *Bd* under future climate change scenarios (e.g. Lawler *et al.* 2009). Global climate change is creating a climatically more variable world (Raisanen 2002) and thus research must consider how changes to both the mean and variance of climatic variables affect *Bd*-amphibian interactions and species interactions, in general (Raffel *et al.* 2006; Rohr & Raffel 2010). These proposed efforts should help inform management and surveillance, and will hopefully curtail our amphibian biodiversity crisis.

Acknowledgements

We thank Marc Cadotte for providing us with the opportunity to write this commentary and for discussing with us the reviewers' praise and comments on this paper. Funds were provided by a National Science Foundation (DEB 0516227) grant to J.R.R., US Department of Agriculture (NRI 2006-01370, 2009-35102-05043) grants to J.R.R., and a US Environmental Protection Agency STAR grant to J.R.R. and T.R.R. (R833835).

References

- Adams, M.J., Chelgren, N.D., Reintz, D., Cole, R.A., Rachowicz, L.J., Galvan, S., McCreary, B., Pearl, C.A., Bailey, L.L., Bettaso, J., Bull, E.L. & Leu, M. (2010) Using occupancy models to understand the distribution of an amphibian pathogen, *Batrachochytrium dendrobatidis*. *Ecological Applications*, **20**, 289–302.
- Araujo, M.B. & Guisan, A. (2006) Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, **33**, 1677–1688.
- Araujo, M.B. & Luoto, M. (2007) The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography*, **16**, 743–753.
- Berger, L., Speare, R., Hines, H.B., Marantelli, G., Hyatt, A.D., McDonald, K.R., Skerratt, L.F., Olsen, V., Clarke, J.M., Gillespie, G., Mahony, M., Sheppard, N., Williams, C. & Tyler, M.J. (2004) Effect of season and

- temperature on mortality in amphibians due to chytridiomycosis. *Australian Veterinary Journal*, **82**, 434–439.
- Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. & Wood, S. (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature*, **391**, 783–786.
- Hampe, A. (2004) Bioclimate envelope models: what they detect and what they hide. *Global Ecology and Biogeography*, **13**, 469–471.
- Hanski, I. (1998) Metapopulation dynamics. *Nature*, **396**, 41–49.
- Harmon, J.P., Moran, N.A. & Ives, A.R. (2009) Species response to environmental change: impacts of food web interactions and evolution. *Science*, **323**, 1347–1350.
- Hubbell, S.P. (2005) Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional Ecology*, **19**, 166–172.
- James, T.Y., Litvintseva, A.P., Vilgalys, R., Morgan, J.A.T., Taylor, J.W., Fisher, M.C., Berger, L., Weldon, C., du Preez, L. & Longcore, J.E. (2009) Rapid global expansion of the fungal disease chytridiomycosis into declining and healthy amphibian populations. *PLoS Pathogens*, **5**, e1000458.
- Johnson, M.L., Berger, L., Philips, L. & Speare, R. (2003) Fungicidal effects of chemical disinfectants, UV light, desiccation and heat on the amphibian chytrid *Batrachochytrium dendrobatidis*. *Diseases of Aquatic Organisms*, **57**, 255–260.
- Lawler, J.J., Shafer, S.L., White, D., Kareiva, P., Maurer, E.P., Blaustein, A.R. & Bartlein, P.J. (2009) Projected climate-induced faunal change in the Western Hemisphere. *Ecology*, **90**, 588–597.
- Lips, K.R., Diffendorfer, J.E., Mendelson, J.R. & Sears, M.W. (2008) Riding the wave: reconciling the roles of disease and climate change in amphibian declines. *PLoS Biology*, **6**, 441–454.
- Morgan, J.A.T., Vredenburg, V.T., Rachowicz, L.J., Knapp, R.A., Stice, M.J., Tunstall, T., Bingham, R.E., Parker, J.M., Longcore, J.E., Moritz, C., Briggs, C.J. & Taylor, J.W. (2007) Population genetics of the frog-killing fungus *Batrachochytrium dendrobatidis*. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 13845–13850.
- Murray, K.A., Retallick, R.W.R., Puschendorf, R., Skerratt, L.F., Rosauer, D., McCallum, H.I., 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*. *Journal of Applied Ecology*, **48**, 163–173.
- Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.
- Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.
- Raffel, T.R., Rohr, J.R., Kiesecker, J.M. & Hudson, P.J. (2006) Negative effects of changing temperature on amphibian immunity under field conditions. *Functional Ecology*, **20**, 819–828.
- Raisanen, J. (2002) CO₂-induced changes in interannual temperature and precipitation variability in 19 CMIP2 experiments. *Journal of Climate*, **15**, 2395–2411.
- Rohr, J.R. & Madison, D.M. (2003) Dryness increases predation risk in efts: support for an amphibian decline hypothesis. *Oecologia*, **135**, 657–664.
- Rohr, J.R. & Raffel, T.R. (2010) Linking global climate and temperature variability to widespread amphibian declines putatively caused by disease. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 8269–8274.
- Rohr, J.R., Raffel, T.R., Romansch, J.M., McCallum, H. & Hudson, P.J. (2008) Evaluating the links between climate, disease spread, and amphibian declines. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 17436–17441.
- Segurado, P., Araujo, M.B. & Kunin, W.E. (2006) Consequences of spatial autocorrelation for niche-based models. *Journal of Applied Ecology*, **43**, 433–444.
- Skerratt, L.F., Berger, L., Speare, R., Cashins, S., McDonald, K.R., Phillott, A.D., Hines, H.B. & Kenyon, N. (2007) Spread of chytridiomycosis has caused the rapid global decline and extinction of frogs. *EcoHealth*, **4**, 125–134.
- Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L. & Waller, R.W. (2004) Status and trends of amphibian declines and extinctions worldwide. *Science*, **306**, 1783–1786.
- Wake, D.B. & Vredenburg, V.T. (2008) Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 11466–11473.

Received 10 September 2010; accepted 29 September 2010
Handling Editor: Marc Cadotte