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Research

Physiology in ecological niche modeling: using zebra mussel's upper thermal tolerance to refine model predictions through Bayesian analysis

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Climate change and human-mediated dispersal are increasingly influencing species' geographic distributions. Ecological niche models (ENMs) are widely used in forecasting species' distributions, but are weak in extrapolation to novel environments because they rely on available distributional data and do not incorporate mechanistic information, such as species' physiological response to abiotic conditions. To improve accuracy of ENMs, we incorporated physiological knowledge through Bayesian analysis. In a case study of the zebra mussel *Dreissena polymorpha*, we used native and global occurrences to obtain native and global models representing narrower and broader understanding of zebra mussel' response to temperature. We also obtained thermal limit and survival information for zebra mussel from peer-reviewed literature and used the two types of information separately and jointly to calibrate native models. We showed that, compared to global models, native models predicted lower relative probability of presence along zebra mussel's upper thermal limit, suggesting the shortcoming of native models in predicting zebra mussel's response to warm temperature. We also found that native models showed improved prediction of relative probability of presence when thermal limit was used alone, and best approximated global models when both thermal limit and survival data were used. Our result suggests that integration of physiological knowledge enhances extrapolation of ENM in novel environments. Our modeling framework can be generalized for other species or other physiological limits and may incorporate evolutionary information (e.g. evolved thermal tolerance), thus has the potential to improve predictions of species' invasive potential and distributional response to climate change.

Keywords: Bayesian analysis, climate change, ecological niche model, Grinnellian niche, invasive species, physiological tolerance

Introduction

Species' geographic distributions are increasingly influenced by climate change and human-mediated dispersal (Walther et al. 2009, Keller et al. 2014, Gallardo et al. 2015,

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Wiens 2016). Organisms distribute in predictable patterns in geography and the relationship between species' distributions and abiotic conditions is explained by the ecological niche theory (i.e. fundamental niche or abiotic niche; Grinnell 1917, Hutchinson 1957, Soberón 2007). Ecological niche modeling (ENM), or species distribution modeling, has been used widely in studying species' abiotic niche and forecasting future distributions under global change (Franklin and Miller 2009, Peterson et al. 2011). To estimate potential distributions, transferring an ecological niche model through space and time is becoming a norm in the discipline (Peterson et al. 2007, Murray et al. 2009, Wenger and Olden 2012, Moreno-Amat et al. 2015, Duque-Lazo et al. 2016), but the underlying uncertainties of model transfers warrant our attention (Murray et al. 2011, Sequeira et al. 2016). The accuracy of ecological niche models (ENMs) relies on the completeness of knowledge of the abiotic niche, but species' occurrences, used in model calibration, rarely represent the abiotic niche adequately due to species' dispersal, biotic interactions and the unequal representation of environmental space in geographic space (Soberón and Peterson 2005, Soberón and Nakamura 2009, Veloz et al. 2012). For example, occurrences from the species' native range may be inadequate in explaining the relationship between the species and abiotic conditions in the introduced range; same concern applies to the adequacy of use of species' present occurrences to predict species' future ranges when novel or no-analog climate conditions will emerge in the future (e.g. warmer temperature) (Veloz et al. 2012). In other words, the abiotic niche is rarely well represented geographically given a specified landscape and time, thus model transfers rely heavily on methodological assumptions instead of data (Gelman and Hill 2007). Without adequate data, model prediction in novel environmental conditions (beyond range of conditions used in model calibration) will experience extrapolation, which is problematic (Peterson et al. 2011, Owens et al. 2013, Qiao et al. 2019).

To reliably forecast species' distributions, we ideally need mechanistic information of how species respond to abiotic conditions, because such information is transferable to new geographic regions and future climates that have novel environmental conditions. Porter et al. (1994) developed a mechanistic approach (NicheMapper) to estimate species' distributions through modeling species' thermodynamic interactions with its environment, but this approach relies on many biophysical parameters that are unavailable for most species (Peterson et al. 2015). Physiological knowledge should provide a good approximation of the abiotic niche (Hutchinson 1957, Soberón and Arroyo-Peña 2017) and should be transferable to novel conditions. Hybrid modeling approaches that aim to synthesize information from both species' distribution and physiology exist in the literature. Martínez et al. (2015) combined post hoc the predictions of physiological and distribution models that were run separately. Feng and Papeş (2017a) used physiological information indirectly, to improve the quality of calibration presences and absences and obtained higher modeling accuracy when presences were refined or when absences approximated true absences. However, these hybrid approaches are limited by the rigid workflow of ENM and the fact that the two sources of information (distribution and physiology) are not fully integrated. Thus, we aimed to explore a direct integration approach that effectively incorporates information from both sources.

Integration of different sources of knowledge requires a flexible modeling framework. The candidate model should have an ecologically meaningful assumption of the underlying truth (i.e. species' response to abiotic conditions) that is independent of calibration data, such that the model will be refined but not determined by calibration data. Therefore, we used a plateau modeling framework (Brewer et al. 2016), in which the conceptualized abiotic niche or response curve has three connected segments: upslope, plateau, and downslope (Fig. 1), which are relatively independent from each other, e.g. the slope of the left segment (upslope) is not directly affected by the slope of the right segment (downslope).

The implementation of plateau model through a Bayesian analysis also provides flexibility of integrating external information (Brewer et al. 2016), such as knowledge of limiting abiotic conditions for species' distribution. A subjective prior distribution represents a prior supposition regarding the probability distribution of an unknown parameter. When the prior is influenced by external information, the effects of such information will be introduced into Bayesian analysis as if there were additional data (Press 2003). The prior supposition could be based on scientific knowledge and plays a crucial role in Bayesian analysis (Press 2003, Goldstein 2006, Robert 2007).

A typical question in biogeography is what will be the distribution of a species introduced to a new landscape that has novel abiotic conditions? Addressing this question via traditional ENM requires new distributional data from the introduced landscape, but such data are not available until

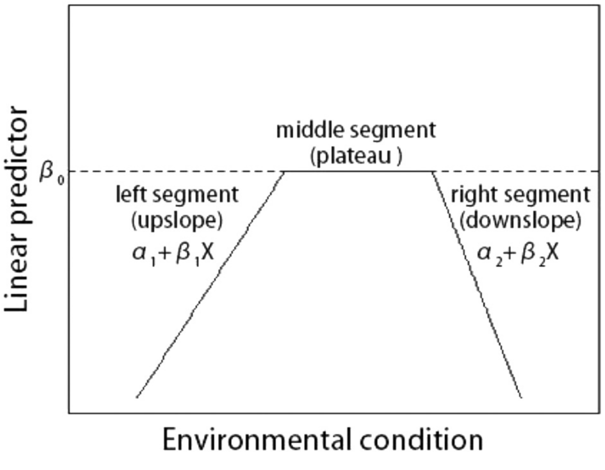

Figure 1. Illustration of a plateau model along an environmental variable.

new populations establish; otherwise model extrapolation in novel abiotic conditions will involve high uncertainties. To overcome this limitation, we propose to use physiological information to support model prediction in novel conditions (i.e. model extrapolation). The subjective prior in Bayesian analysis allows translating external knowledge (e.g. physiology) into information with quantified uncertainties for a focal problem (Goldstein 2006), which in our study represents species' response to environmental conditions.

The objective of this study was to integrate physiological data into ENM using a case study of a notorious invasive species in North America, the zebra mussel *Dreissena polymorpha* (U.S. Geological Survey 2016). We selected this species because its physiology and distribution are well studied, and its response to warm temperature represents a distributional limitation (Spidle et al. 1995, McMahon 1996, White et al. 2015). In the plateau framework, we quantified the relationship between physiological and distributional information based on the assumption of equivalence of abiotic conditions underlying species' physiology and geographic distribution. We designed two scenarios of narrower and broader knowledge of zebra mussel's distribution (i.e. native and global occurrences). We predicted that ENMs obtained with the native occurrences would underestimate the species' abiotic niche (lower predicted relative probability of presence) whereas ENMs based on the global occurrences would better approximate the abiotic niche. The distinction we made here between narrower and broader knowledge (native versus global distribution) is analogous to the incompleteness of current knowledge compared to unknown distribution of a species in the future. Additionally, we calibrated models based on native occurrences and physiology information. We expected that physiologically informed native models would have improved estimations of abiotic niche (increase in predicted relative probability of presence) compared to ENMs with native occurrences only.

Material and methods

The plateau model

Plateau is an ENM algorithm that emphasizes ecological realism (Brewer et al. 2016). In plateau, a species' response to an environmental condition (abiotic niche) is represented by three connected segments (Fig. 1), an ecologically rigid but experimentally flexible assumption. The ecological rigidity is given by the fact that no condition is continuously suitable for a species and that species have environmental limits, so the true response curve must have three segments. The flexibility is represented by three aspects: 1) a best fitted model may not necessarily have all three segments, 2) the left and right segments can have different slopes and 3) estimation of plateau parameters is achieved through Bayesian analysis, thus external information may be used for this purpose (Clark 2007, Brewer et al. 2016). For a single covariate (i.e. environmental condition), the conceptual plateau model can be implemented as:

$$Y_i \sim \text{Bernoulli}(p_i) \tag{1}$$

$$\text{logit}(p_i) = \log\left(\frac{p_i}{1-p_i}\right) = f(x_i) \tag{2}$$

$$f(x_i) = \min\{\alpha_1 + \beta_1 x_i, \beta_0, \alpha_2 + \beta_2 x_i\}, \quad \text{for } \beta_1 > 0 \text{ and } \beta_2 < 0 \tag{3}$$

In this model, *i* is a record from a species' distributional data; Y_i is a dichotomous response representing species' presence ($Y_i = 1$) or absence ($Y_i = 0$); and p_i is the probability of presence that is dependent on the environmental condition (x_i) and is determined through a logit link function, commonly used for binary data (Cramer 2003). The function *f*() has three connected linear segments, forming a plateau shape (Fig. 1). Parameters α_1 and α_2 are the intercepts of the left and right segments, β_1 and β_2 are the slopes of the left and right segments, respectively, and β_0 is the position of the plateau segment. The parameters of *f*() are estimated through the program BUGS (Lunn et al. 2000) with noninformative priors by default (Brewer et al. 2016), so the posterior distributions of parameters depend predominantly on data. However, the prior distributions of plateau parameters can be revised based on reasonable justifications, so it is possible to influence parameter estimations by introducing external information.

This implementation of the plateau model is similar to a logistic regression, except that the linear predictor function is constructed with three connected segments in plateau, compared to a single segment in logistic regressions. Since species' true absence data are rare (Mackenzie 2005, Mackenzie and Royle 2005), simulated absences are instead used in regression-based ENMs (Hirzel et al. 2001, Engler et al. 2004). A broadly applied method of simulating absences is random selection of the environmental profile of the study area, typically referred to as the background, which is compared to the environmental profile of known presence locations (Wintle et al. 2005, Elith et al. 2006, Barbet-Massin et al. 2012). If presences and random background points are used, the probability of presence should be interpreted as probability of presence relative to the study area (relative probability of presence or relative occurrence rate; Wintle et al. 2005, Elith et al. 2006, Merow et al. 2013). Studies from ecological and statistical perspectives suggest using a large sample of background points for an adequate representation of the environmental heterogeneity of the study area (Wintle et al. 2005, Phillips and Dudík 2008, Barbet-Massin et al. 2012, Renner et al. 2015). Given the similarity of plateau implementation and logistic regression, we used the same rationale to simulate background points for the plateau model.

Presences and background samples for model calibration

We used zebra mussel occurrences from Gallardo et al. (2013), representing zebra mussel's native and invasive distributions in Europe and North America. We updated the dataset by including recent occurrences and excluding sites with failed establishments in North America (U.S. Geological Survey 2016). Since zebra mussel is generally a freshwater species, we restricted our study to areas with freshwater (resampling Pekel et al. 2016 to 10 arc-min; hereafter water surface) and excluded occurrences not associated with water surface. We used a spatial window of 30 arc-min (approximately 55 km at equator) to reduce the spatial bias of the occurrence dataset (Boria et al. 2014, Fourcade et al. 2014). We retained 838 spatially unique occurrences, which were labeled as the global dataset (Fig. 2). Similarly, 61 occurrences from zebra mussel' native range (Son 2007, Gallardo et al. 2013) were labeled as the native dataset. We used the global and native datasets separately to construct the global and native ENMs.

We randomly selected background samples from a six decimal degree spatial buffer (approximately 660 km) on the water surface around native and global occurrences. In contrast to using either a country-wide or continent-wide background area, the buffered background is more likely to meet the assumption of distribution equilibrium (present in suitable conditions and absent from unsuitable conditions; Hutchinson 1957, Araújo and Pearson 2005) and to potentially avoid model overfitting (Anderson and Raza 2010). To actually assess the equilibrium status will require adequate presence and absence data, whereas in reality reliable absence data have been rare (Mackenzie 2005, Mackenzie and Royle 2005). Therefore, the assessments of equilibrium status have been mainly based on inferences (Araújo and Pearson 2005). One major factor that contributes to nonequilibrium status is limited dispersal capacity that prevents species from occupying suitable abiotic conditions (Peterson et al. 2011). However, the limitation of dispersal is less likely an issue for introduced species, whose distribution may have been expanded by humans. A recent study showed that introduced mollusks are mainly limited by climate rather than dispersal, suggesting a better approximation of the equilibrium status with abiotic conditions (Capinha et al. 2015). This conclusion should also hold for zebra mussel in our study, because zebra mussel is a well-known notorious species and its distribution has been broadly expanded by human activities in the past 30 yr (McMahon 1996). By restricting the background samples to water surface, we also better approximated the area that the species may access (Soberón and Peterson 2005). We selected 34% of all pixels (6000) from the native buffer and all pixels (82 634) from the global buffer for model training. We did not use the same number of background samples, rather we chose the number of background samples to ensure the same ratio of presences/background samples for native and global models, thus maintaining similar magnitudes of relative probability of presence (Papeş et al. 2016). The occurrences are archived on <https://github.com/shandongfx/paper_physiology_ENM_2019>.

The environmental profile of the background points can also have a strong effect on the model estimation (Elith et al. 2010, Merow et al. 2013). This effect can be problematic in case of model extrapolation (such as clamping in Maxent) when environmental conditions at the limits of the training data are not well sampled (Guevara and León-Paniagua 2019). This effect is less of an issue for our study, given that the environmental conditions from the background points are well beyond those of occurrences (Supplementary material Appendix 1 Fig. A1, A2) and the model extrapolation is restricted to a few degrees Celsius above zebra mussel's upper thermal tolerance.

Classic ENM to estimate species' response to the environment

To test whether plateau model estimations are similar to established ENM techniques, we included four commonly used ENM algorithms: boosted regression tree (BRT; Friedman et al. 2000, Leathwick et al. 2006), generalized linear model (GLM; McCullagh 1984, Wintle et al. 2005), generalized additive model (GAM; Hastie and Tibshirani 1990, Lehmann et al. 2002) and maximum entropy (Maxent; Phillips et al. 2004, Elith et al. 2006). GLM and GAM are representative of regression-based algorithms and BRT and Maxent are representative of machine learning algorithms. We followed the parameter settings from previous studies that have shown reliable performance (Supplementary

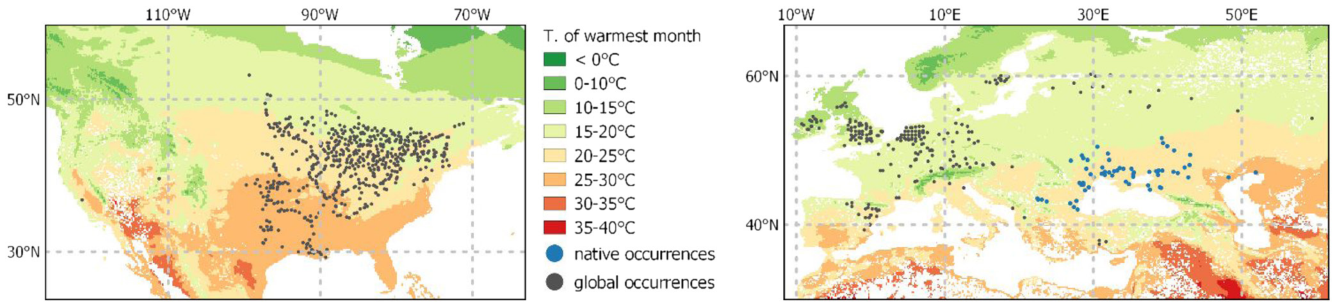

Figure 2. Global occurrences of zebra mussel. Occurrences in the native range are in blue and other occurrences are in gray. The background map represents mean temperature of the warmest month.

material Appendix 1; Feng and Papeş 2017a). We trained the five algorithms using native and global occurrence datasets separately, thus obtained five native models and five global models. We used the mean estimation of all five algorithms as benchmark to evaluate the improvement of physiologically informed plateau models (see below). We expected that the predictions of native models, compared with those of global models, will be lower in the warmer conditions (i.e. underestimate the relative probability of presence), and the predicted values will be higher through integrating physiological knowledge in the models.

Physiologically informed ENMs

Overview of physiological knowledge for zebra mussel

We used two types of physiological information from peer-reviewed literature. The first type suggests that 30°C is generally the upper thermal limit for zebra mussels at the time scale of a month (Iwanyzki and McCauley 1993, Aldridge et al. 1995, Spidle et al. 1995, McMahon 1996, White et al. 2015). The second type shows that the survival time (measured in hours) decreases exponentially as exposure temperature increases from 31°C to 37°C (Table 1 in McMahon et al. 1994). We integrated the two types of physiological information into the plateau model through three approaches: using the upper thermal limit of 30°C as an informative prior, using survival information as an informative prior, and using both as informative priors.

Approach 1: the upper thermal limit (30°C)

ENM estimates the probability of presence (p) that is dependent on environmental conditions (env_p); the physiological knowledge represents species' response (s) that is also dependent on environmental conditions (env_s) but that may be different from env_p. Linking ENM and physiological knowledge means quantifying the relationship between p and s, here with $D()$, and between env_p and env_s, here with $I()$:

$$p = D(s) \tag{4}$$

$$\text{env}_p = I(\text{env}_s) \tag{5}$$

Instead of estimating $I()$, we resorted to finding reciprocal approximations of env_p and env_s. Because physiological knowledge from literature is static (i.e. cannot be manipulated), we turned to constructing an env_p that approximates env_s. Since global data for water temperature do not exist (cf. distance weighted air temperature in Domisch et al. 2015), we used global air temperature. To match the physiological knowledge that zebra mussel tolerates 30°C for a month, we compiled a raster of mean air temperature of the warmest month (T_{warm}) from a global raster of monthly mean temperature representing the climate of 1950–2000, at the resolution of 10 arc-min (approximately 18 km) (WorldClim ver. 1.4; Hijmans et al. 2005) by searching for the maximum value over 12 months for each pixel using the raster package in R (Hijmans et al. 2016). In contrast with similar bioclimatic variables, e.g. maximum temperature of warmest month or warmest week (Hijmans et al. 2005, Kriticos et al. 2014), our T_{warm} variable represents warm temperature that lasts for a month, matching the time scale of upper thermal limit for zebra mussel. Water temperature may be influenced by other factors (Caissie 2006), but air temperature is directly associated with water temperature, especially over a longer time scale (Stefan and Preud'homme 1993), e.g. T_{warm} as we used here.

Quantifying the relationship between p and s seems difficult; an alternative solution is to find cases when the two responses share a similar ecological meaning under the same environmental condition. Because 30°C is considered the upper thermal limit of zebra mussel, it is reasonable to assume that a temperature ≤ 30°C is necessary for the species' presence. This interpretation was supported by the maximum T_{warm} (29.4°C) associated with zebra mussel's global occurrence dataset.

Continuous ENM predictions of relative probability of presence are transformed into binary maps (presence and absence) using a threshold. Minimum training presence (MTP) is a commonly used threshold that represents the lowest relative probability value associated with known presences (Pearson and Dawson 2003) and values of p higher than MTP are assumed to be as suitable as known presences. Since MPT and 30°C both represent the marginal condition for zebra mussel' presence, we reasoned that the value of relative probability of presence associated with MTP should be a more adequate estimation for 30°C than that obtained from the native model. We built the native plateau model first, based on the native occurrence dataset, and extracted the MTP value. Then, we built a model ($\text{Native}_{\text{point}}$) with the native presence dataset and a near-deterministic relationship (i.e. informative prior) for the right segment of the plateau model that directed the right segment through the point corresponding to 30°C and MTP value obtained from the first model. The near-deterministic relationship allows limited deviation from the physiological prior, roughly 0.5 at linear predictor scale, which corresponds to a variance of MTP/100 (Supplementary material Appendix 2). Mathematically, using the upper thermal limit, we imposed a constraint on the parameter space of the model, which would force the parameter estimates to reflect this marginal condition.

Approach 2: survival data (31–37°C)

We extracted survival data for zebra mussels from McMahon et al. (1994), specifically mean survival time at 30°C acclimation temperature and at exposure temperatures of 31–37°C. We chose the highest acclimation temperature (i.e. 30°C), which would minimize the difference between acclimation and exposure treatments, and assumed that this would better mimic the relatively slow change of ambient temperature in natural condition (Stefan and Preud'homme 1993). For simplification, we ignored the effects from acclimation and body size, which were over 16 times smaller than effects from exposure temperature (McMahon et al. 1994).

To link distributional data and survival data, we assumed that there is an unknown underlying environmental suitability that determines the relationship between the survival time and the exposure temperature, as well as the relationship between relative probability of presence and ambient temperature. Therefore, we reasoned that, within the range of 31–37°C, the internal relationship in survival data (i.e. the relative difference among survival times) also holds for the internal relationship in relative probability of presence, or at least better approximates the true relative probability of presence than that estimated from native occurrences. This relationship is essentially a linear decay function in which survival time or relative probability of presence decreases in response to increasing temperature. Based on this assumption, we first estimated the slope parameter of the survival model and used the estimated mean as an informative prior for the slope of the right segment in the plateau model, allowing limited deviation, roughly 0.2 at linear scale, corresponding to a variance of 1/100 of the calculated slope (Supplementary material Appendix 2). We constructed the survival model using a log linear relationship, which is common in survival analyses (Therneau and Grambsch 2000), including McMahon et al. (1994), which is the source of the survival dataset in our study.

We built the plateau model with the native presence dataset and an informative prior for β_2 (Eq. 3) (Supplementary material Appendix 2). The interpretation is that the slope from survival data is used to adjust the slope of right segment of the native plateau model that is suspected to be incorrect because of inadequate support from native presence dataset. We termed this model Native$_{\text{survival}}$.

Approach 3: combining upper temperature limit (30°C) and survival data (31–37°C)

We further integrated information of upper thermal limit from Approach 1 and survival data from Approach 2 in a plateau model with the native presence dataset while using upper temperature limit and survival information as informative priors to influence the right segment of the plateau model. The informative priors would direct the right segment through the point corresponding to 30°C and MTP value with a slope estimated from survival data (Supplementary material Appendix 2). We termed this model Native$_{\text{point-survival}}$.

Model evaluation

We obtained five models with native occurrences, five with global occurrences, and three models based on native occurrences and physiological knowledge (plateau as implemented in examples 1–3). We projected all models on a set of temperature conditions, from 8 to 37°C, with an increment of 0.1°C. For easier comparison, we rescaled all model predictions to 0–1 using the following method:

$$p' = \frac{p - \min(p)}{\max(p) - \min(p)} \tag{6}$$

where p' is the normalized value of the original prediction (p) from a model. Differences in magnitude of predictions between native and global models, if any, would be less influential after the rescaling procedure.

We calculated the mean of normalized predictions of the five native models as a representation of narrower knowledge of relative probability of presence, termed Native$_{\text{mean}}$. Similarly, we calculated the mean of five global models as a benchmark for more complete understanding of relative probability of presence, termed Global$_{\text{mean}}$. We calculated the dissimilarity index (DS) of two models (a, b) using the following equation:

$$\mathrm{DS}_{a,b} = \sum_{x=T_{\min}}^{T_{\max}} \frac{\left(p'_{a,x} - p'_{b,x}\right)^2}{N} \tag{7}$$

where dissimilarity $\mathrm{DS}_{a,b}$ between model$_{\text{a}}$ and model$_{\text{b}}$ is the sum of squared differences of normalized predictions $p'_{a,x}$ and $p'_{b,x}$ along the simulated environments (x ranges from $T_{\min}$ to $T_{\max}$, in 0.1°C increments), standardized by number (N) of x. The value of DS ranges from 0 to 1, where 0 indicates that model predictions are identical and 1 indicates maximum dissimilarity between model predictions. Using Global$_{\text{mean}}$ as a reference, we calculated DS between the reference model and Native$_{\text{mean}}$, Native$_{\text{point}}$, Native$_{\text{survival}}$ and Native$_{\text{point-survival}}$ within the range of 23–37°C. The lowest x (23°C) was close to the peak temperature of zebra mussel's response curve and the highest x (37°C) was the maximum temperature in the survival data of zebra mussel. The comparison of the models with this temperature range allowed us to assess the differences in the predictions under warm temperatures. We also assessed the differences between the range of 29.1 and 37°C, where the predictions of native models were considered as extrapolation (or strict extrapolaiton in Owens et al. 2013).

Results

Global versus native datasets

The range of the environmental predictor (mean temperature of the warmest month) was narrower in the native buffer (7.4–29.1°C), compared to that in the global buffer (4.6–36.7°C) (Supplementary material Appendix 1 Fig. A1). In the zebra mussel occurrence datasets, the range of the environmental predictor was 15.8–26.1°C among native occurrences, which was narrower than the range for global occurrences, 10.8–29.4°C (Supplementary material Appendix 1 Fig. A2).

Plateau versus classic algorithms

The five ENM algorithms generated comparable response curves (Fig. 3). All response curves generally followed a unimodal shape (i.e. upslope and downslope); only curves generated by GLM were symmetric; curves generated by BRT, GAM and Maxent showed a closer fit to calibration data.

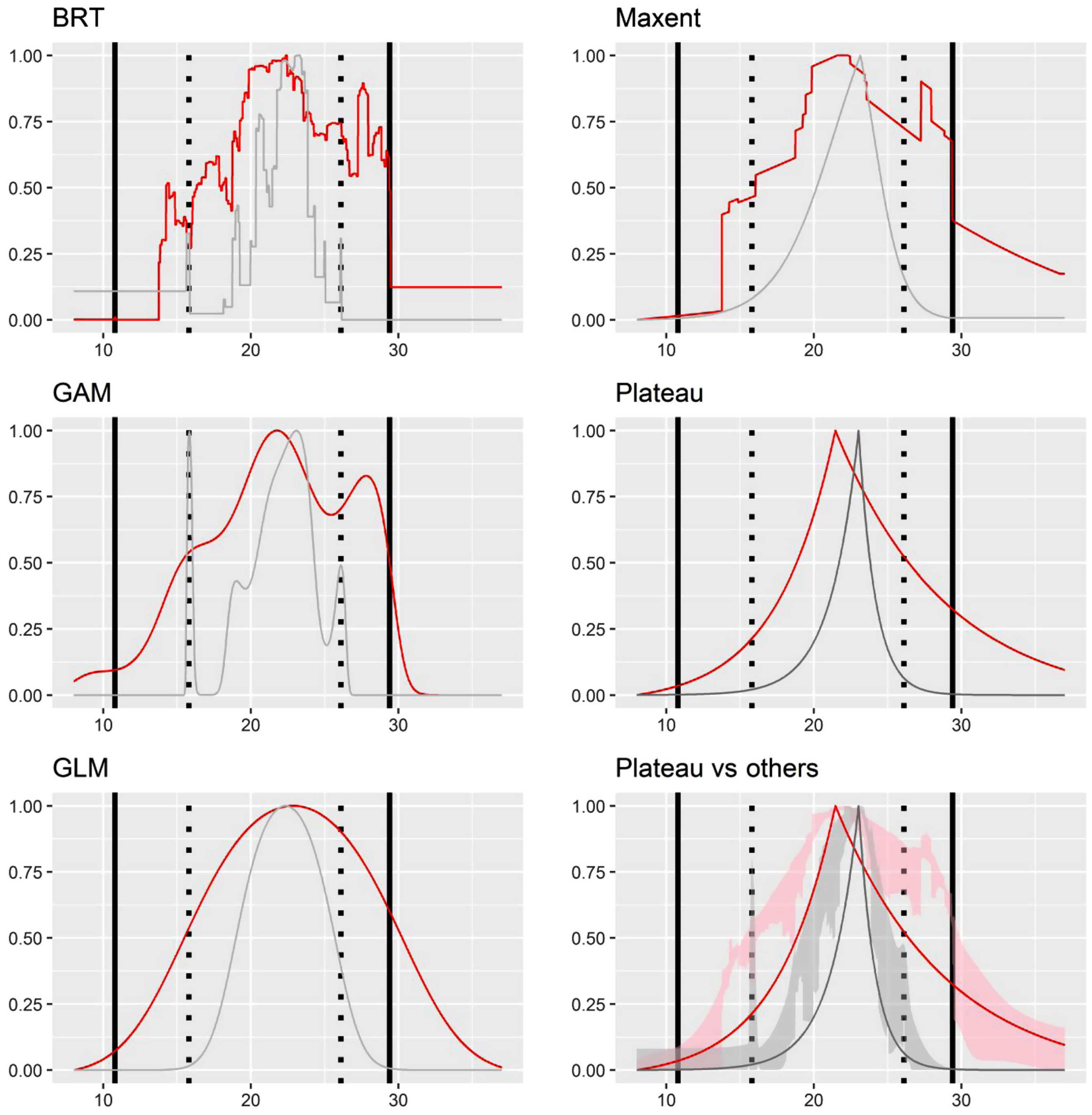

Figure 3. Response curves of native (gray) and global (red) models generated with five algorithms. The x-axis is the mean temperature of the warmest month (°C) and the y-axis is the normalized prediction of relative probability of presence. The shaded area in the bottom right panel represents the range (mean ± SD) of normalized predictions by BRT, GAM, GLM and Maxent models. The dotted vertical lines demarcate the range of climatic variable values associated with native occurrence dataset and the solid vertical lines the range of global occurrence dataset.

The difference between native plateau model and the mean of the other four native models was smaller than the difference between global plateau model and the mean of other four global models (Fig. 3). Compared to global models, all native models estimated lower relative probability of presence in the range of upper limits of native and global presences, suggesting insufficient knowledge of zebra mussel's thermal response.

Plateau models versus physiologically informed plateau models

The upslope (left) segment of $\text{Native}_{\text{point}}$ overlapped extensively with that of native plateau model, but the downslope (right) segment of $\text{Native}_{\text{point}}$ went through our assigned point (30°C, MTP) and had a gentler slope than that of native

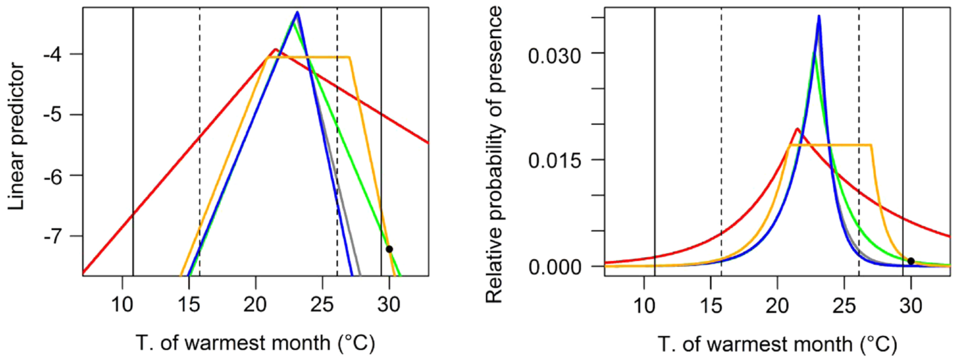

Figure 4. Response curves of plateau models. The x-axis is the mean temperature of warmest month and y-axis is model prediction at linear predictor scale (logit of relative probability of presence; left panel) and relative probability of presence scale (right panel). The gray curve represents native plateau model, red curve represents global plateau model, green curve represents Native$_{\text{point}}$, blue curve represents Native$_{\text{survival}}$, and orange curve represents Native$_{\text{point-survival}}$. The black dot represents the assigned point (30°C, MTP) to Native$_{\text{point}}$ and Native$_{\text{point-survival}}$, where MPT is the minimum training presence threshold, or the lowest value of probabilities associated with presences used in model calibration. The dotted vertical lines demarcate the range of climatic variable values associated with native occurrence dataset and the solid vertical lines the range of global occurrence dataset.

plateau model (Fig. 4). The left segment of Native$_{\text{survival}}$ also overlapped well with that of native plateau model, but the right segment had a steeper slope than that of native plateau model (Fig. 4). The right segment of Native$_{\text{point-survival}}$ also went through our assigned point (30°C, MTP) and had similar slope as that of Native$_{\text{survival}}$ (Fig. 4).

Physiologically informed plateau models versus native and global means

Compared to native models, physiologically informed models (Native$_{\text{point}}$ and Native$_{\text{point-survival}}$) predicted higher relative probability of presence in the range of upper temperature limits, with the exception of Native$_{\text{survival}}$ (Fig. 5). Among the three physiologically informed models, Native$_{\text{point-survival}}$ had the highest prediction at the upper thermal limits, but it exceeded the predictions of global models at the plateau segment. Around the upper thermal limit, predictions from Native$_{\text{point}}$ and Native$_{\text{point-survival}}$ were more similar (smaller DS values; Table 1) to the predictions of Global$_{\text{mean}}$, compared with predictions from Native$_{\text{mean}}$, while Native$_{\text{survival}}$ was less similar to Global$_{\text{mean}}$, compared with Native$_{\text{mean}}$. Among the three physiologically informed models, Native$_{\text{point-survival}}$ was most similar to Global$_{\text{mean}}$ and Native$_{\text{survival}}$ was least similar to Global$_{\text{mean}}$ (Table 1).

Discussion

In this study, we developed a modeling framework to integrate physiological knowledge and ENM. The physiological knowledge successfully integrated was zebra mussel's upper thermal limit (30°C) and a series of survival times around zebra mussel's upper thermal limit. Native models showed limited performance along zebra mussel's upper thermal limit, compared with global models. Including survival information alone did not improve the native model prediction for zebra mussel's response to warm temperature. However, including only the upper thermal limit improved the native model prediction, and the prediction was further improved by additionally integrating survival information. Such findings suggest that, with a proper integration approach, physiological knowledge can improve extrapolation ability of

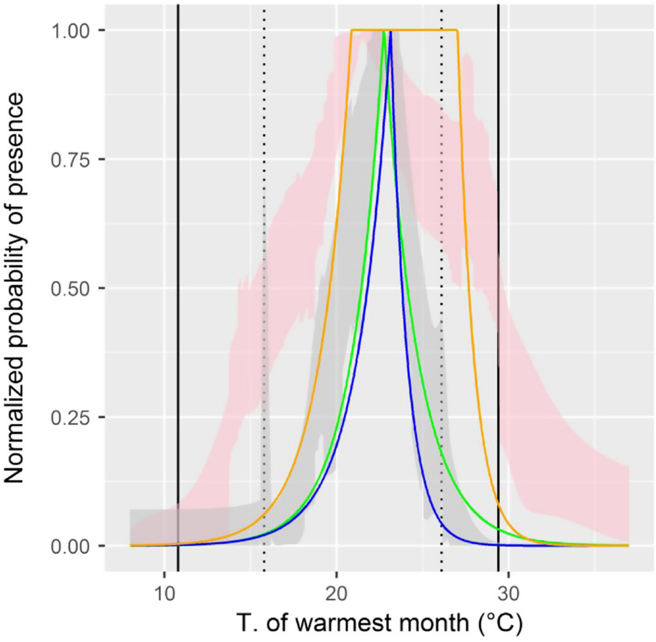

Figure 5. Response curves of native, global, and physiologically informed models. The red shaded area represents the range (mean ± SD) of the normalized predictions of five global models and the gray shaded area represents that of five native models. The green curve represents Native$_{\text{point}}$, blue curve represents Native$_{\text{survival}}$, and orange curve represents Native$_{\text{point-survival}}$. The dotted vertical lines demarcate the range of climatic variable values associated with native occurrence dataset and the solid vertical lines the range of global occurrence dataset.

Table 1. Dissimilarity index between plateau native models and the mean of global models, which are based on BRT, GAM, GLM, Maxent and Plateau algorithms. The mean of native models ($\text{Native}_{\text{mean}}$) is based on BRT, GAM, GLM, Maxent and Plateau algorithms without using physiological information. The physiological information is incorporated into the native plateau model in three ways: only using upper thermal limit ($\text{Native}_{\text{point}}$), only using survival data ($\text{Native}_{\text{survival}}$) and using both sources of information ($\text{Native}_{\text{point-survival}}$). The comparison is conducted in two ranges of temperatures: 23°C is close to the peak temperature of zebra mussel's response curve and 37°C is the maximum temperature in the survival data of zebra mussel; in the other range, 29.1°C is beyond the conditions used in the training of native models, thus the predictions of native models beyond 29.1°C will be considered as extrapolation.

Model name	DS (dissimilarity in the range of 23 and 37°C)	DS (dissimilarity in the range of 29.1 and 37°C)
$\text{Native}_{\text{mean}}$	0.1370	0.0447
$\text{Native}_{\text{point}}$	0.1297	0.0404
$\text{Native}_{\text{survival}}$	0.1791	0.0453
$\text{Native}_{\text{point-survival}}$	0.0562	0.0365

ENM, which will be valuable in predicting species' distribution under climate change.

Positive effects of physiological knowledge on model calibration

The environments associated with the native dataset were narrower than those of the global datasets, suggesting that both accessible and occupied conditions by zebra mussels in the native range were limited, compared to the global ones (Supplementary material Appendix 1 Fig. A1, A2). The native plateau model was less informative about the zebra mussel's abiotic niche than the global plateau model, shown by the deviated slope and position (or intercept) of the right segment, thus supporting our prediction of the difference between native and global models. We used zebra mussel's upper thermal limit to directly influence the slope of the right segment, which subsequently influenced the intercept. The largest improvement of native plateau model was achieved by adjusting both slope and position of the right segment through a close fit to the upper thermal limit and survival data. However, the prediction of $\text{Native}_{\text{point-survival}}$ overshot the prediction of global models inside the upper thermal limits, suggesting lack of proper knowledge of physiological information.

The model improvement also depends on the difference between native and global models, or how much less informative the native model is. On the other hand, even if the improvement in the response curve is limited, the effects may still be substantial in cases when a thresholding procedure is used, i.e. transforming raw prediction into binary maps (Peterson et al. 2011). In our study, the prediction at 30°C in $\text{Native}_{\text{point}}$ was raised to MTP threshold, thus if MTP is used in generating a potential distribution map, locations with 30°C or slightly lower will be considered as suitable for zebra mussel, which will contradict the native model.

The improvement of physiologically informed plateau models was based on the assumption that native occurrences only represented narrower knowledge of zebra mussel's distribution or abiotic niche. The limitation of native data could be attributed to dispersal or biotic interactions (Soberón and Peterson 2005); the difference in environments between native and global distributions is also termed niche unfilling (Guisan et al. 2014). In our zebra mussel study, the major reason could be that the human mediated dispersal has greatly expanded the accessible area to zebra mussel (Griffiths et al. 1991, Gallardo et al. 2015, De Ventura et al. 2016). Another reason for the relative narrowness of native occurrence data is adaptation of introduced populations to previously limiting conditions in the invaded range (Prentis et al. 2008, Moran and Alexander 2014). The thermal tolerances of zebra mussel used to be considered similar between North American (introduced) and European (native) populations (McMahon 1996) or among different geographic populations in North America (Elderkin and Klerks 2005), though new evidence strongly suggests the adaption of zebra mussel's upper thermal tolerance to higher water temperatures in southern US (southern Kansas) compared to that of individuals in northern US (New York) (Morse 2009a). However, the reason for the narrower range of native data does not affect the improvement in physiologically informed models, rather our conclusion is supported by incompleteness of native data and effectiveness of physiological information. Our modeling framework provides an opportunity to include external information (e.g. evolved thermal tolerance) in estimating species' response to environmental conditions.

The poor performance of the native model in the global context is analogous to decreased accuracy of a model calibrated with present climate data and projected to future climate data (Moreno-Amat et al. 2015, Fitzpatrick et al. 2018), since model extrapolation is involved in both scenarios (Qiao et al. 2019). Therefore, the improved model performance through integration of physiological information is also expected when projecting a model to climate change scenarios.

Comparison among algorithms

The flexibility of the plateau algorithm is the basis of our modeling framework. Nonparametric algorithms (e.g. GAM) and machine-learning algorithms (e.g. BRT and Maxent) are not appropriate for this purpose because 1) details of parameters are usually not provided or difficult to modify and 2) a parameter change in the algorithm (e.g. regularization multiplier in Maxent) may affect the estimated response curve as a whole, even in an intractable way, and thus a targeted modification to the response curve through external information becomes nearly impossible (but see Merow et al. 2017). GLM with quadratic function relies on a parabola curve that is simple and ecologically meaningful, but is limited by the rigid symmetric shape of the curve. The implementation of plateau through Bayesian analysis provides an avenue to introduce external information to influence parameter estimation. The framework with three segments of plateau provides an ecologically meaningful and mathematically flexible solution. Nevertheless, the drawback of a plateau model is longer computation time for parameter estimation to achieve convergence, which can range from hours to days, especially when the number of background samples is large. For example, the computation time of one hundred thousand iterations was about 1.6 h for the model with 6000 background points, and was about 42.6 h for the model with 82 634 background points in our study, using a desktop equipped with 4.20 GHz Intel Core i7.

Availability of physiological knowledge

Our proposed modeling framework relies on the availability of physiological knowledge. Physiology has been studied for decades (Scheer 1963), thus knowledge has been accumulated through time and should be abundant in literature. Recently, there have been many efforts to synthesize physiological information from literature (Sunday et al. 2011, Araújo et al. 2013, Hoffmann et al. 2013, Feng and Papeş 2017b) or compile such information into databases (Frimpong and Angermeier 2009, U.S. EPA 2012), such as GlobTherm, a database of thermal tolerances of aquatic and terrestrial organisms (Bennett et al. 2018). On the other hand, there are some biases in physiological knowledge in terms of species and type of physiological trait. Physiological knowledge is usually biased toward species that most interest the public and researchers (Sousa et al. 2014, Feng and Papeş 2017b). For the same species, the type of physiological traits is not evenly studied; for example, more studies of invasive bivalves in US focus on thermal physiology than salinity (Feng and Papeş 2017b). Even for the same trait, studies are also biased, as species of conservation concern are more often studied under optimal conditions (e.g. how to conserve endangered species; Thompson et al. 2017) while invasive species are more often studied under critical conditions (e.g. how to eradicate invasive species; Morse 2009b). When physiological knowledge is not available in the literature, the alternative is to carry out field surveys or laboratory experiments for focal species (Martínez et al. 2015), or infer the physiological trait based on that of other closely related species and phylogeny or geographic distributions (Grigg and Buckley 2013, Khaliq et al. 2015).

A quantitative link between species' physiology and geographic distribution

In our modeling framework, the critical step is linking physiological knowledge with ENM. The first challenge is the temporal scale that entails the duration of a condition and the species' response to such duration of condition. It is clear that species will have different responses to varied duration of experimental treatments, and it is also important to realize that species' occurrences are likewise time dependent (Feng and Papeş 2017b), though species' occurrences are usually assumed to represent long-term presence in many ENM applications because data to evaluate the species' presence status (e.g. population dynamics) are generally unavailable. The importance of temporal scale can also be understood through data availability. Laboratory experiments, a major source of physiological knowledge, are conducted over a limited time frame, e.g. days, weeks or months (McMahon et al. 1994, White et al. 2015); on the other hand, environmental layers used in ENM, especially at broader spatial scales, commonly characterize climate, thus represent longer time scales, e.g. monthly or yearly averages [(Hijmans et al. 2005, Kriticos et al. 2014), but see (PRISM Climate Group 2017)]. Therefore, an appropriate temporal scale also depends on data availability.

The second challenge is precise quantification of the relationship between laboratory-derived physiological knowledge and field conditions associated with species' distribution. Laboratory experiments are usually conducted under constant conditions (McMahon et al. 1994) or a simplified scenario of variations (McMahon and Ussery 1995). On the contrary, environmental conditions vary in complex or even unpredictable patterns in real world (Easterling et al. 2000). Therefore, assumptions of equivalence between field and lab settings or ignoring variance are necessary in the linkage. Even if a reasonable link between the two sources of conditions is available, building or compiling a relevant environmental variable across a broad landscape can still be problematic (e.g. calcium concentration in lakes; Papeş et al. 2011).

Lastly, quantifying the relationship between species' physiological response and distributional response is difficult. Ideally, the quantification should rely on a well-designed experiment that measures species' physiological and distributional responses under the same environmental conditions (cf. Hill et al. 2013); however, such data are rarely available. The alternative is to assume linkages that follow existing knowledge. The two assumptions we made were that 1) 30°C and MTP threshold had the same ecological meaning (marginal status) and 2) survival and distributional responses were determined by an underlying suitability function.

Looking forward

We exemplified direct integration of upper thermal tolerance and survival data with one climatic variable in modeling the abiotic niche of zebra mussel. Future studies may consider validating this approach with different physiological information, e.g. lower thermal tolerance, hygric or salinity tolerance, or further considering more environmental dimensions and interactions among them. Our approach may also be validated in the context of climate change, using species with well documented historical and current distributions (e.g. Grinnell resurvey project; Tingley and Beissinger 2009, Tingley et al. 2009) and relevant physiological knowledge.

In our modeling framework, we used physiological knowledge to inform parameters in correlative distribution models. Potentially, this framework can be extended hierarchically to include underlying evolutionary processes that influence physiological traits (Catullo et al. 2015, Bush et al. 2016) such as evolutionary potential and phenotypic plasticity. Given the potential of physiological information, ENM will make more informative predictions of species' distribution, thus better help invasive species management and conservation efforts under climate change.

Data availability statement

The BUGS codes are provided in Supplementary material Appendix 1–2. The occurrences are archived on <https://github.com/shandongfx/paper_physiology_ENM_2019>.

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Conflicts of interest – None.

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Supplementary material (available online as Appendix ecog-04627 at <www.ecography.org/appendix/ecog-04627). Appendix 1–2.