esa ECOSPHERE

Suitability of Laurentian Great Lakes for invasive species based on global species distribution models and local habitat

Andrew M. Kramer,[1,†] Gust Annis,[2] Marion E. Wittmann,[3,4] William L. Chadderton,[2]
Edward S. Rutherford,[5] David M. Lodge,[6,7] Lacey Mason,[8] Dmitry Beletsky,[9]
Catherine Riseng,[8] and John M. Drake[1]

[1]*Odum School of Ecology, University of Georgia, Athens, Georgia 30602 USA*
[2]*The Nature Conservancy, Lansing, Michigan 48906 USA*
[3]*Department of Biological Sciences, University of Notre Dame, Notre Dame, Indiana 46556 USA*
[4]*Natural Reserve System, University of California, Santa Barbara, California 93106 USA*
[5]*NOAA Great Lakes Environmental Research Laboratory, Ann Arbor, Michigan 48108 USA*
[6]*Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York 14853 USA*
[7]*Environmental Change Initiative, University of Notre Dame, Notre Dame, Indiana 46556 USA*
[8]*School of Natural Resources and Environment, University of Michigan, Ann Arbor, Michigan 48109 USA*
[9]*School for Environment and Sustainability, Cooperative Institute for Great Lakes Research,*
University of Michigan, Ann Arbor, Michigan 48108 USA

Citation: Kramer, A. M., G. Annis, M. E. Wittmann, W. L. Chadderton, E. S. Rutherford, D. M. Lodge, L. Mason, D. Beletsky, C. Riseng, and J. M. Drake. 2017. Suitability of Laurentian Great Lakes for invasive species based on global species distribution models and local habitat. Ecosphere 8(7):e01883. 10.1002/ecs2.1883

Abstract. Efficient management and prevention of species invasions requires accurate prediction of where species of concern can arrive and persist. Species distribution models provide one way to identify potentially suitable habitat by developing the relationship between climate variables and species occurrence data. However, these models when applied to freshwater invasions are complicated by two factors. The first is that the range expansions that typically occur as part of the invasion process violate standard species distribution model assumptions of data stationarity. Second, predicting potential range of freshwater aquatic species is complicated by the reliance on terrestrial climate measurements to develop occurrence relationships for species that occur in aquatic environments. To overcome these obstacles, we combined a recently developed algorithm for species distribution modeling—range bagging—with newly available aquatic habitat-specific information from the North American Great Lakes region to predict suitable habitat for three potential invasive species: golden mussel, killer shrimp, and northern snakehead. Range bagging may more accurately predict relative suitability than other methods because it focuses on the limits of the species environmental tolerances rather than central tendency or "typical" cases. Overlaying the species distribution model output with aquatic habitat-specific data then allowed for more specific predictions of areas with high suitability. Our results indicate there is suitable habitat for northern snakehead in the Great Lakes, particularly shallow coastal habitats in the lower four Great Lakes where literature suggests they will favor areas of wetland and submerged aquatic vegetation. These coastal areas also offer the highest suitability for golden mussel, but our models suggest they are marginal habitats. Globally, the Great Lakes provide the closest match to the currently invaded range of killer shrimp, but they appear to pose an intermediate risk to the region. Range bagging provided reliable predictions when assessed either by a standard test set or by tests for spatial transferability, with golden mussel being the most difficult to accurately predict. Our approach illustrates the strength of combining multiple sources of data, while reiterating the need for increased measurement of freshwater habitat at high spatial resolutions to improve the ability to predict potential invasive species.

Key words: environmental niche; golden mussel; habitat suitability; killer shrimp; nonindigenous species; northern snakehead.

Received 21 April 2017; accepted 25 May 2017. Corresponding Editor: Wyatt F. Cross.

† **E-mail:** kramera3@uga.edu

INTRODUCTION

Aquatic invasive species (AIS) have imposed substantial ecological damage on freshwater ecosystems (Ricciardi and MacIsaac 2000, Cucherousset and Olden 2011), prompting a more proactive, holistic approach to invasive species management (Leung et al. 2002, Pagnucco et al. 2015). The identification of high-risk species, transport pathways (e.g., Ricciardi and Rasmussen 1998, Keller et al. 2009, Gantz et al. 2015), surveillance sites, and opportunities for implementation of slow-the-spread strategies all rely upon an accurate prediction of locations suitable for nonindigenous species to establish and persist (Gormley et al. 2011, Jiménez-Valverde et al. 2011, Gallien et al. 2012, Václavík et al. 2012).

Species distribution models (SDMs) estimate the statistical relationship between species occurrence and environmental conditions (Elith and Leathwick 2009), and applications of these models have been used to identify suitable habitat outside of the current range (Barve et al. 2011), predict range shifts in response to climate change (Austin and Van Niel 2011, VanDerWal et al. 2013), and predict the spread of invasive species (Kulhanek et al. 2011). However, these applications involve violation of a key assumption of SDM methods, namely stationarity in species occurrence (Barve et al. 2011, Pagel and Schurr 2012, Václavík and Meentemeyer 2012). A spreading species is not in equilibrium with environmental conditions and has not had previous opportunity to sample novel environments in which it may thrive. The result is limited information on the suitability of novel combinations of environmental conditions (Veloz et al. 2012). For actively invading species, using data from the invaded and native ranges provides the strongest basis for extrapolation and is the most practical approach given that physiological information needed for a mechanistic model is generally lacking (Araújo and Peterson 2012). Nevertheless, there is still a risk of underestimating the extent of suitable habitat.

Predicting suitable habitat for freshwater aquatic species using SDMs faces an additional challenge. Species distribution models are typically fit to measured or interpolated climate or environmental measurements of the terrestrial environment. This is because the most reliably available climate variables come from global datasets (Hijmans et al. 2005, Tyberghein et al. 2012) or remote sensing (Cord and Rödder 2011, Bisrat et al. 2012) that primarily measures terrestrial climate variables. These data are often only an indirect indicator of freshwater environmental conditions, and several physical characteristics of water bodies can strongly influence the correlation between atmospheric and aquatic conditions (Mohseni and Stefan 1999). For example, bottom waters of deep, seasonally stratified lakes are to a large extent decoupled from lake surface (and adjacent atmosphere) for a substantial portion of the year due to the presence of a thermocline (Boyce et al. 1989). Moreover, aquatic species predictions are also sensitive to aquatic environment-specific conditions such as hydrological and substrate stability, wave action or flow, water chemistry or clarity (Leathwick et al. 2005, 2011, Snelder et al. 2006, Brenden et al. 2008, McKenna and Castiglione 2010).

Identifying which nonindigenous species are most likely to be introduced, establish, and to result in negative impacts is a complex endeavor that complicates management of biological invasions. This not only requires knowledge about the pathways of introduction and propagule pressure, but also the suitability of the receiving environment and likelihood of establishment (Leung et al. 2012). One reliable predictor that a non-native species will cause environmental damage is invasiveness in other locations (Kolar and Lodge 2001). In addition, species that have high rates of introduction or are established in adjacent regions are also more likely to become established (Lockwood et al. 2005). For some species with known invasion histories and observations of widespread impact, information may exist on life history, environmental tolerance, and persistence outside the native range. The ability to assess invasion risk can be increased by combining SDMs with this existing information, even when widespread measurements are not available to create mechanistic predictions from laboratory-measured environmental tolerances.

We performed a two-part evaluation of the potential range of three nonindigenous species that could invade the North American Great Lakes: golden mussel (*Limnoperna fortunei*), killer shrimp (*Dikerogammarus villosus*), and northern snakehead (*Channa argus*). These species have been identified by the United States Aquatic Nuisance Species Task Force (USACE 2011) as species of concern to U.S. waters and have been predicted as probable future invaders of the Great Lakes (Ricciardi and Rasmussen 1998, Council of Great Lakes Governors 2013). First, we estimated the habitat suitability throughout the Great Lakes for each species using a novel SDM algorithm called "range bagging" (Drake 2015). This algorithm was designed to estimate species range limits based on climate variables measured at all precisely known occurrences worldwide. To assess ecosystem-specific suitable habitat, these model predictions were then merged with high-resolution spatially explicit data representing the localized aquatic environment in terms of established species tolerances (Wittmann et al. 2017). The results provide species range predictions for a set of molluscan, crustacean, and vertebrate nonindigenous aquatic species, illustrating the value of the two-part evaluation and showing that inclusion of measurements of aquatic conditions (or more reliable terrestrial surrogates) is key to providing models for the potential ranges of invasive aquatic species that are most relevant to management decisions (Kilroy et al. 2008, US Environmental Protection Agency 2008).

METHODS

Species

Three species were chosen for this analysis based on their likelihood of invasion and concern from scientists and the regional management agencies. The golden mussel (*Limnoperna fortunei;* Dunker, 1857) is an epifaunal bivalve, native to mainland China. Since the mid-1960s, golden mussel has been unintentionally dispersed across the globe through fouling of shipping vessels and established populations are now present in Hong Kong, Taiwan, Japan, Brazil, Paraguay, Uruguay, Bolivia, and Argentina (Ricciardi 1998). Spawning occurs at temperatures between 16° and 28°C (Xu et al. 2013), and after external fertilization, a free-living straight-hinged larva develops, subsequently evolving into an actively swimming veliger larva capable of survival in a wide variety of habitats (Karatayev et al. 2007). Golden mussel are thought to have life histories and habitat preferences similar to dreissenid mussels, which have a widespread distribution and ecological impacts in the Great Lakes watershed (Karatayev et al. 2007, Fahnenstiel et al. 2010, Kerfoot et al. 2010, Vanderploeg et al. 2010).

Killer shrimp (*Dikerogammarus villosus*) is an amphipod native to the Ponto-Caspian region of eastern Europe and Ukraine. Since the 1980s, it has spread to at least 17 European countries along the complex European canal–river systems (Pöckl 2009) and to the United Kingdom via maritime shipping (Gallardo and Aldridge 2012). Killer shrimp is expected to continue its spread in Europe and eventually to North America (Ricciardi and Rasmussen 1998). Many studies show that *D. villosus* can prey upon many macroinvertebrate species, including native and other non-native amphipods, as well as fish eggs and larvae (Dick and Platvoet 2000, Dick et al. 2002, Casellato et al. 2006). *Dikerogammarus villosus* range expansion is influenced by hydrological regime, temperature, salinity, water quality, substrate, and food availability (Bruijs et al. 2001, Devin et al. 2003, Josens et al. 2005, Boets et al. 2010, MacNeil et al. 2010).

Northern snakehead (*Channa argus*) is a fish native to China, Russia, and Korea (Courtenay and Williams 2004). It is established in regions of the eastern and central United States (Potomac River, Chesapeake Bay, Lower Mississippi River [Arkansas]), and individuals have been observed in California, New Jersey, New York, and in watersheds adjacent to the Great Lakes (http://nas.er.usgs.gov). This species is capable of surviving in poorly oxygenated waters and has been found inhabiting shallow (<2 m) ponds or swamps, canals, reservoirs, lakes, and rivers (Courtenay and Williams 2004). The presence of submersed aquatic vegetation can provide a benefit for its reproduction, but is not necessary. *Channa argus* has a wider latitudinal range and temperature tolerance (0° to >30°C) compared with other snakehead species (Courtenay and Williams 2004), and earlier SDMs using global climate data suggest much of North America is suitable (Herborg et al. 2007). It is an aggressive predator, with a broad diet including fish, invertebrate, and amphibian species (Courtenay and Williams 2004). Northern snakehead is listed as injurious wildlife under the U.S. Lacey Act (Lacey Act 1900).

Occurrence data

Worldwide occurrence records for each study species were obtained from the primary literature, the Global Biodiversity Information Facility (http://www.gbif.org/), FishBase (Froese and Pauly 2011), and USGS (http://nas.er.usgs.gov) databases. All records with position uncertainty >50 km were removed to ensure accurate match with the environmental data. All presence locations in both the native and introduced ranges were included in this analysis, yielding 81 unique locations for *L. fortunei* (22 native and 59 introduced; Appendix S1: Fig. S1), 233 unique locations for *D. villosus* (16 native and 217 introduced; Appendix S1: Fig. S2), and 198 unique locations for *C. argus* (47 native and 151 introduced; Appendix S1: Fig. S3).

Environmental data

Nineteen global climate surfaces were obtained at 5-min resolution from the WorldClim dataset (Hijmans et al. 2005; http://www.worldclim.org). These variables are derivations of monthly rainfall and climate data that have been interpolated from weather stations, and are designed to have increased relevance to species physiological limits (Hijmans et al. 2005, Graham and Hijmans 2006). To reduce bias and improve model stability, climate variables were rescaled and, in some cases, transformed. Variables BIO1–BIO11 and BIO15 were rescaled by subtracting the global mean and dividing by the global standard deviation. Variables BIO18 and BIO19 were rescaled similarly after log transformation to improve symmetry. Variables BIO12–BIO14, BIO16, and BIO17 were transformed via the empirical cumulative distribution function to obtain a uniform distribution as a normal distribution could not be approximated. (See archived R code for further details.) All climate variables were included in the analysis in order to estimate the best predictive model given the limited a priori understanding of the correlations between atmospheric and aquatic climate and of which variables are most influential for each species.

Data on the distribution of submerged aquatic vegetation (SAV) at 30-m resolution in the optically shallow areas of Lakes Huron, Michigan, Erie, and Ontario were obtained from the Michigan Tech Research Institute. These data were generated using an MTRI-developed depth-invariant algorithm and depend on Landsat satellite data collected during the vegetative growing season (Michigan Tech Research Institute 2012, Shuchman et al. 2013). Vegetative growing season and years varied by lake: Lake Erie, May–September 2006–2011; Lake Huron, March–September 2007–2011; Lake Michigan, April–May 2008–2011; and Lake Ontario, April–September 2008–2011. Some portions of these lakes could not be classified due to high turbidity. Submersed vegetation data did not exist for Lake Superior or Lake St. Clair. Data for the remaining four lakes were combined using the Mosaic to New Raster tool process in ArcGIS version 10.2 (ESRI 2014) with a cell size of 30 m. This study used classes 1 (light SAV) and 7 (dense SAV).

Data on the spatial distribution of wetlands were compiled by the Great Lakes Coastal Wetland Inventory (Great Lakes Coastal Wetland Consortium 2004). The inventory utilized the most comprehensive coastal wetlands data available for the Great Lakes and connecting channels and was derived from multiple sources. Coastal wetlands polygonal data were rasterized with a cell size of 30 m.

Benthic temperature data acquired from the National Oceanic and Atmospheric Administration Great Lakes Coastal Forecasting System (GLCFS) nowcasts were summarized by the Great Lakes Aquatic Habitat Framework. The GLCFS uses a 3D hydrodynamic model (Schwab and Bedford 1994, Chu et al. 2011, Beletsky et al. 2013) with a horizontal resolution ranging from 2 km (Lakes Erie, Huron, and Michigan) to 5 km (Lake Ontario) and 10 km (Lake Superior) to nowcast lake temperatures (among other physical variables) at 20 vertical levels in all lakes except Lake Erie (that has 21 levels). Averages of August monthly data from the years 2006 to 2012 were used and were combined for individual lakes using a mosaic process with an output cell size of 2000 m (ESRI 2014).

Modeling potential distribution

To determine the habitat suitability in novel environments, we applied SDMs using the range bagging algorithm (Drake 2015). This algorithm estimates species range limits in multi-dimensional climate space using bootstrap aggregation. Range bagging has comparable accuracy to the widely used MaxEnt approach on high-quality validation datasets (Drake 2015) and also performs similarly to widely used SDMs for traditional approaches (J. M. Drake and R. Richards, *unpublished data*) and invasive species (Wittmann et al. 2017; R. C. Cope, J. V. Ross, J. M. Drake et al., *unpublished data*) including the three species considered here (A. M. Kramer, M. E. Wittmann, and J. M. Drake, *unpublished data*). Range bagging was chosen over some more commonly used algorithms (e.g., MaxEnt) for two primary reasons. First, range bagging estimates the environmental limits of species habitat, giving it an ecologically relevant interpretation (Drake 2015; R. C. Cope, J. V. Ross, J. M. Drake et al., *unpublished data*). This quantity more closely matches the concept of the ecological niche advanced by Hutchinson (Hutchinson 1957). Consideration of environmental tolerances—rather than the central tendency—may offer a more conservative (i.e., larger) estimate of the ecological niche relevant to invasive species risk assessment. Further, range bagging uses only presence points, removing the need for selecting a suitable area from which to sample background points, as this choice has recently been shown to have substantial effects on model reliability (Barve et al. 2011; A. M. Kramer, M. E. Wittmann, and J. M. Drake, *unpublished data*).

Range bagging models were constructed by fitting convex hulls to 256 random combinations of two environmental variables from the global climate surfaces (Drake 2015). We specified the parameter identifying the proportion of points sampled in each bootstrapped combination to be 1. While smaller subsets may give better performance on the hold-out test points if presences are sampled from sink habitat (Drake 2015), such limitations could be restrictive relative to novel environmental conditions experienced by non-native species. Along with all approaches to species distribution modeling, range bagging models may still be biased due to the issues of non-stationarity and novel environmental combinations. For validation, therefore, models were fit to 80% of the data and performance (area under the receiver-operating curve, or AUC) was evaluated on a 20% hold-out test set (Appendix S1: Fig S4). For golden mussel, a 60–40 training test split was used due to fewer data points. The models fit to the training data are presented in the maps, such that performance on the 20% (or 40% for golden mussel) hold-out test set provides the measure of accuracy of the displayed models. As a second measure of performance, we estimated the continuous Boyce index (Hirzel et al. 2006, Petitpierre et al. 2012). The Boyce index was designed for presence-only data and was calculated with the R package "ecospat." The Boyce index varies from -1 to 1 with values greater than zero indicating agreement between the prediction and the presences in the test data (Hirzel et al. 2006). The AUC and the Boyce index were calculated with the same model output and data for each run of the model. Variance in model performance was assessed with 10-fold cross-validation on the training data (Appendix S1: Fig. S4). Additionally, we estimated the transferability of the model by performing fivefold cross-validation on data that were divided into longitudinal bins (Wenger and Olden 2012; Appendix S1: Fig. S4). This test measures the ability of the model to predict occurrence in distinct geographical areas, with longitudinal bins being appropriate for the occurrence of these species on multiple continents. Code used to fit models and display results is archived on Dryad (https://doi.org/10.5061/dryad.d4144).

The outcome of a range bagging model is an estimate of niche centrality for each species at each point on a map. After fitting the model, niche centrality was estimated for each grid cell in the global climate dataset and mapped. Niche centrality refers to the tendency of an environment to be centered within the environmental range of a species across multiple environmental variables. We also estimated variable importance for each species by permuting each predictor variable and measuring the reduction in accuracy on the withheld test set. Because data reflect only occurrence records, a set of random background points was necessarily selected to function as absence points in the AUC calculation (Elith and Leathwick 2009). These points were taken from a large buffer (2000 km surrounding the known occurrence records), consistent with the fact that these species are well known to be entrained in long-distance transport pathways and therefore not greatly limited by dispersal.

Aquatic habitat suitability

Species-specific information on environmental limits to occurrence, survival, and spawning was collected from extensive review of the primary literature, which included but was not limited to field-based and laboratory experiments, surveillance efforts, and review and synthesis publications. Published limits in any measured environmental variable, including temperature, substrate type, water chemistry, and aquatic vegetation, were recorded. Cases for which reliable Great Lakes-wide data were unavailable were discarded (primarily water quality data and zooplankton species composition). When sources differed in their reported limits, the extrema from the set of values were considered to be the limit. This resulted in surprisingly limited concrete knowledge about environmental limits to establishment and persistence for the three species considered here. These environmental conditions were then used to restrict the projected range bagging model to the suitable areas of the Great Lakes, treating the environmental limits as thresholds beyond which habitat was unsuitable for that aspect of species life history.

As spawning temperature >16°C is required for golden mussel reproduction (Xu et al. 2013), available benthic temperature data on the Great Lakes were used to delineate the potential spawning habitat. Constraints based solely on depth were not included, although it is thought that golden mussel may colonize the same habitats as dreissenid mussels in the Great Lakes (Ricciardi 1998). Further, the existing measured depth limits for golden mussel are constrained by sampling and their current largely riverine distribution.

Published field and laboratory studies of killer shrimp did not identify any useful environmental limitations that could be addressed with the Great Lakes dataset. The reported temperature range for survival is large (Bruijs et al. 2001, Wijnhoven et al. 2003, van der Velde et al. 2009), as is substrate usage (Boets et al. 2010) and dissolved oxygen (Gallardo and Aldridge 2012). Killer shrimp has only been reported at shallow depths (Lods-Crozet and Reymond 2006), but as with golden mussel this limit appears to depend on sampling, the limited depth range of colonized habitats, and other factors, rather than a well-understood biological limitation.

The minimum temperature requirement for northern snakehead spawning is 18°C (Amanov 1974), and survival has been observed at temperatures 0–30°C (Okada 1960, Courtenay and Williams 2004). *Channa argus* are known to survive long periods in low-oxygen environments (Frank 1970, Courtenay and Williams 2004) and prefer habitats with mud and aquatic vegetation (Okada 1960, Courtenay and Williams 2004). Thus, Great Lakes regions with wetlands and SAV are of particular concern, even though the fish is able to occur outside of these areas (Amanov 1974). To identify areas where population densities and ecological impacts may be highest, the snakehead niche map was restricted by the combination of coastal wetlands and SAV.

RESULTS

Golden mussel

There was relatively little climate overlap between the Great Lakes basin and native and current non-native golden mussel distribution (Fig. 1). Niche centrality was highest in Lake Erie, but never exceeded 0.39, indicating most of the marginal niche models did not include environmental conditions observed in the Great Lakes basin. At the global scale, several regions where golden mussel is not established had much higher relative suitability, including the southeast United States and eastern Australia (Fig. 2). Model AUC on a balanced set of withheld test points and random background points was 0.89 (Appendix S1: Fig. S5), and the Boyce index was 0.78. Random cross-validation showed a similar average AUC and slightly lower Boyce index (Appendix S1: Figs. S6, S7). The spatial cross-validation for golden mussel had much weaker performance, indicating the invaded and native ranges experience distinct climates (Appendix S1: Figs. S6, S7). The most influential variable for model performance was seasonality of precipitation (Appendix S1: Fig. S8); however, the loss of performance from permuting any single climate value was small and of similar magnitude, indicating redundancy due to high correlation among variables and/or a multivariate niche.

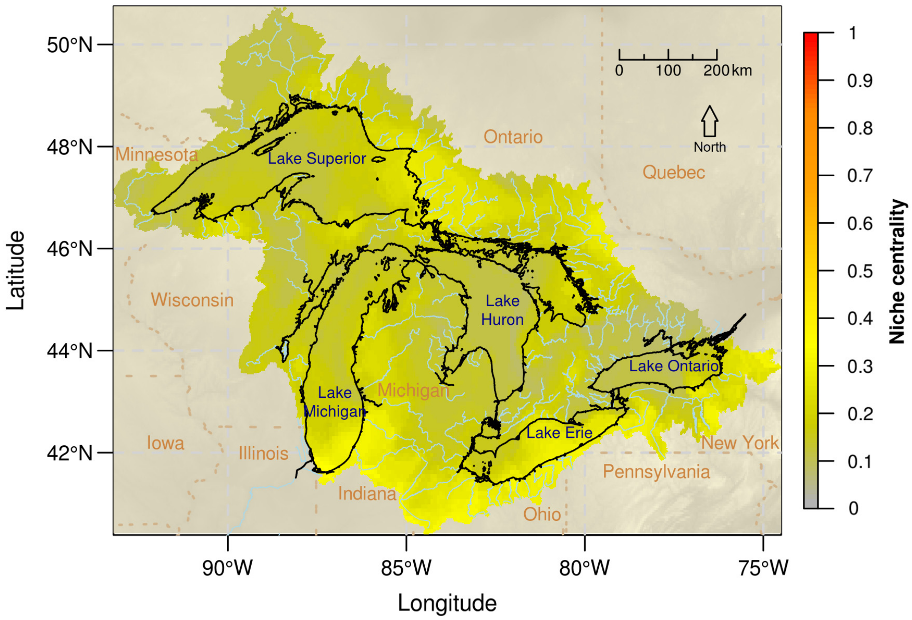

Fig. 1. Golden mussel niche centrality in the North American Great Lakes basin. Low values of niche centrality indicate climate conditions in the Great Lakes basin are often outside of the predicted niche.

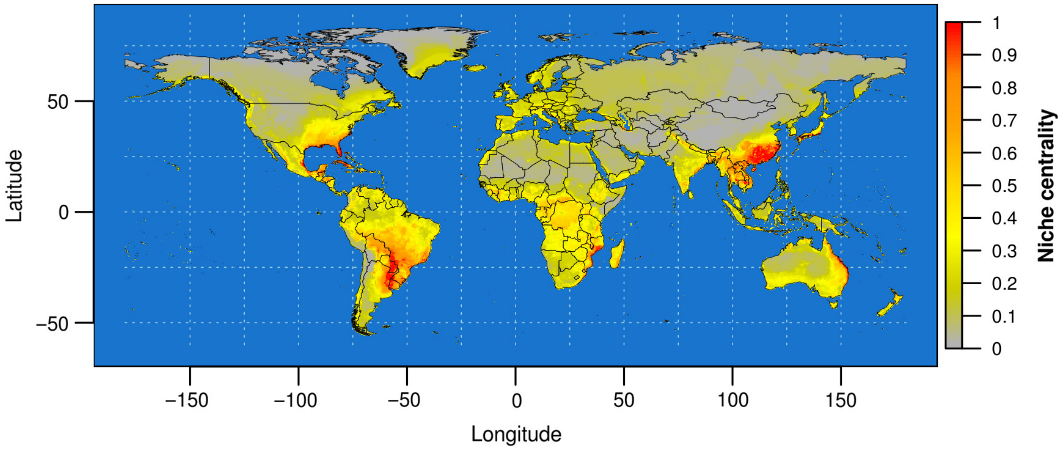

Fig. 2. Golden mussel global niche. Map of niche centrality values with higher values indicating climate conditions falling within the modeled niche.

The suitable niche for golden mussel was further restricted when limitations on reproduction were taken into account. Areas with average summer benthic temperatures warm enough to facilitate spawning were limited to Lake Erie, southern Lake Michigan, and shallow bays of all lakes (Fig. 3). The range bagging model and water temperature data indicated that Lake Superior and colder areas are unlikely to support viable populations.

Killer shrimp

Killer shrimp displayed variable, intermediate niche centrality across the Great Lakes basin, with the highest match with current occurrences occurring in the southern regions (Fig. 4). There were

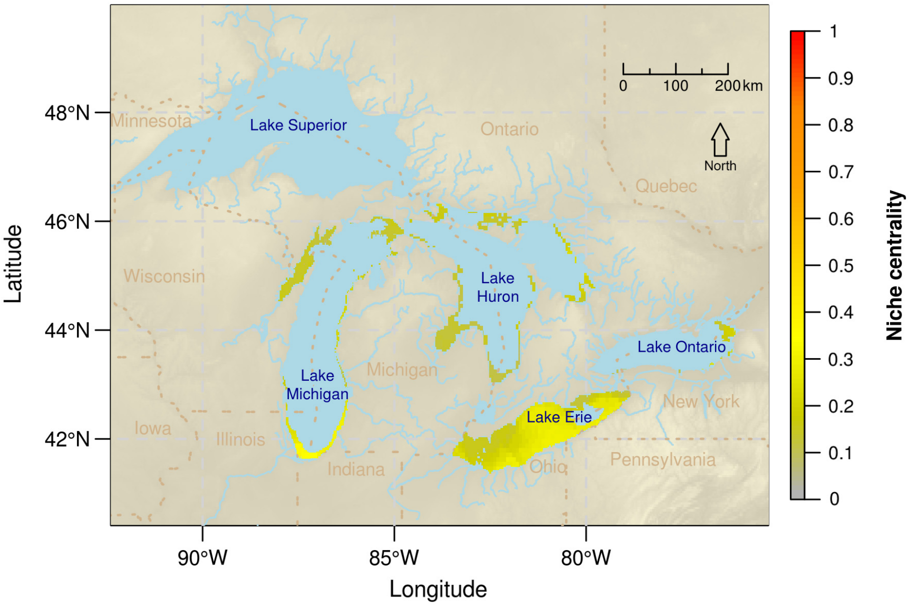

Fig. 3. Golden mussel habitat suitability restricted by spawning habitat. Visualization of the climate-based niche in areas of the Great Lakes warm enough for golden mussel spawning. Spawning can occur at benthic temperatures >16°C (Xu et al. 2013).

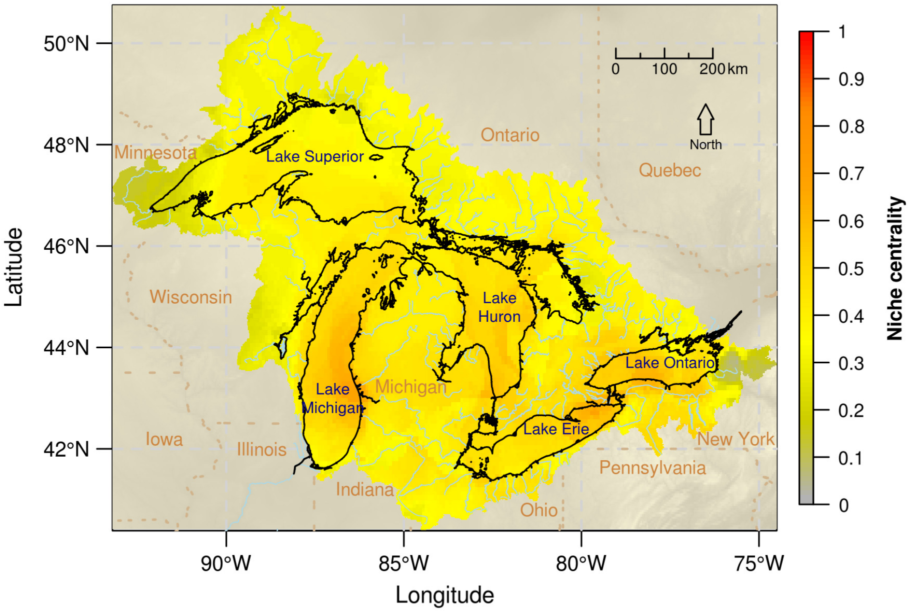

Fig. 4. Killer shrimp niche centrality in the North American Great Lakes basin. Intermediate values of niche centrality indicate climate conditions in the Great Lakes basin often, but not completely, overlap the predicted niche.

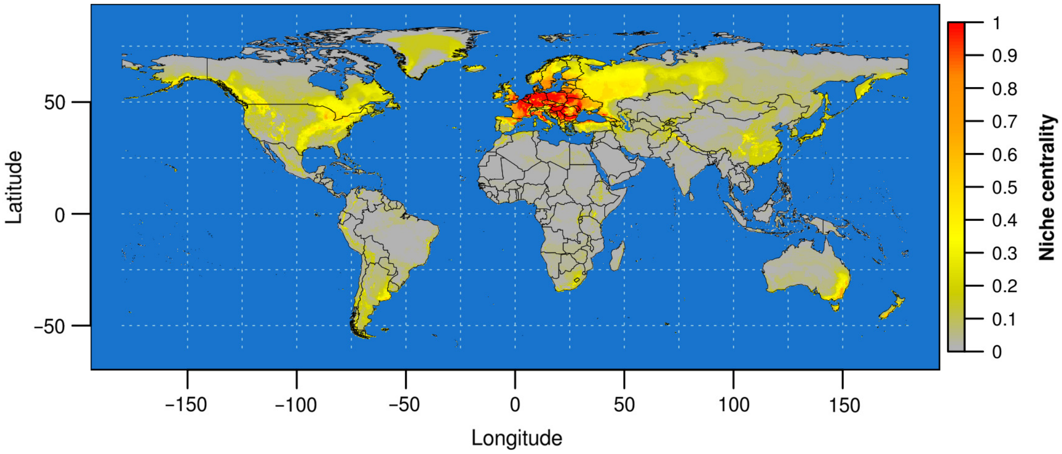

Fig. 5. Killer shrimp global niche. Map of niche centrality values with higher values indicating climate conditions falling within the modeled niche.

no areas fully within the climate envelope of known killer shrimp populations. Indeed, viewed at the global scale, the climate niche only estimates high niche overlap for the native and currently invaded areas in the Ponto-Caspian region and Europe (Fig. 5). Model AUC was high at 0.96 (Appendix S1: Fig. S9) with the most influential variables including the amount of precipitation in the wettest month and the wettest quarter (Appendix S1: Fig. S10). The Boyce index was 0.56, with comparable performance for both random and spatial cross-validation (Appendix S1: Figs. S6, S7). Alternative models using only temperature covariates had lower (killer shrimp and snakehead) or equivalent performance (golden mussel) for these species and did not provide increased ability to differentiate importance among the correlated climate predictors. As explained above, the few directly measured biotic limitations to killer shrimp persistence were so broad as to include the entirety of the Great Lakes.

Northern snakehead

The snakehead niche model estimated high climate overlap in the Great Lakes basin. The majority of Lake Erie, Lake Michigan, and Lake Ontario, as well as large areas of Lakes Huron and Superior, had niche centrality exceeding 0.8 (Fig. 6). This was unsurprising given the high niche centrality of much of eastern North America (consistent with the frequency of known persistent populations in this region; Appendix S1: Fig. S8). The model predicted a large area of Europe and part of South America as equally suitable environments for this species (Fig. 7). Model AUC was 0.93 (Appendix S1: Fig. S11) and Boyce index was 0.73. Cross-validation showed consistently positive AUC and Boyce indices (Appendix S1: Figs. S6, S7). Several climate variables were influential in model performance, including the temperature of the wettest quarter and the diurnal range in temperature (Appendix S1: Fig. S12).

Areas with surface water temperatures suitable for northern snakehead spawning were relatively limited, but they occurred in all lakes other than Lake Superior (Fig. 8). Areas with existing SAV and wetlands comprised only 2% of the lake area, but constitute suitable habitat for this species (Fig. 9). In most cases, the spawning temperatures and aquatic vegetation coincide, indicating the potential for significant ecological impact if snakehead were to establish in the lakes.

DISCUSSION

Integrating habitat-specific information that characterizes the underwater environment with SDMs improved the delineation of potential suitable habitat for nonindigenous species. As a result, we were able to use an SDM with a range bagging algorithm to provide informative estimates of relative climate suitability for all three species at the regional scale. While these suitability estimates cannot directly predict the

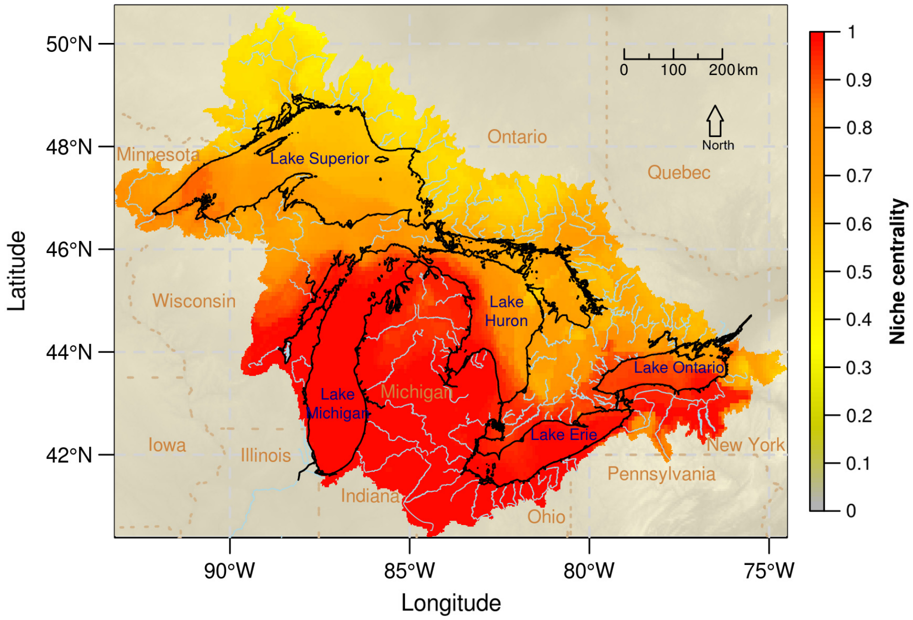

Fig. 6. Northern snakehead niche centrality in the North American Great Lakes basin. Map of niche centrality for northern snakehead in the Great Lakes basin. High values of niche centrality indicate climate conditions in the Great Lakes basin fall generally within the predicted niche.

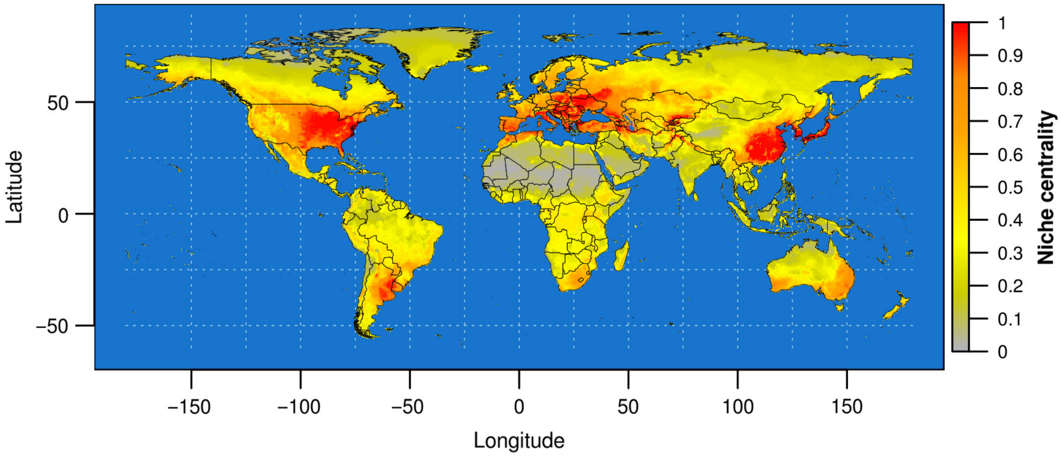

Fig. 7. Snakehead global niche. Map of niche centrality values with higher values indicating climate conditions falling within the modeled niche.

probability of persistence without additional information (Phillips and Elith 2013), the high AUC values indicated these models did successfully predict occurrence of the three species in their native and current introduced ranges. The broad temperature range of killer shrimp and lack of information on other habitat requirements precluded the production of a habitat-specific delineation for this species. However, high-resolution aquatic environmental data from within the Great Lakes enabled prediction at finer scale by identifying specific areas with highest chance of establishment and persistence for golden mussel and snakehead, as well as areas likely to

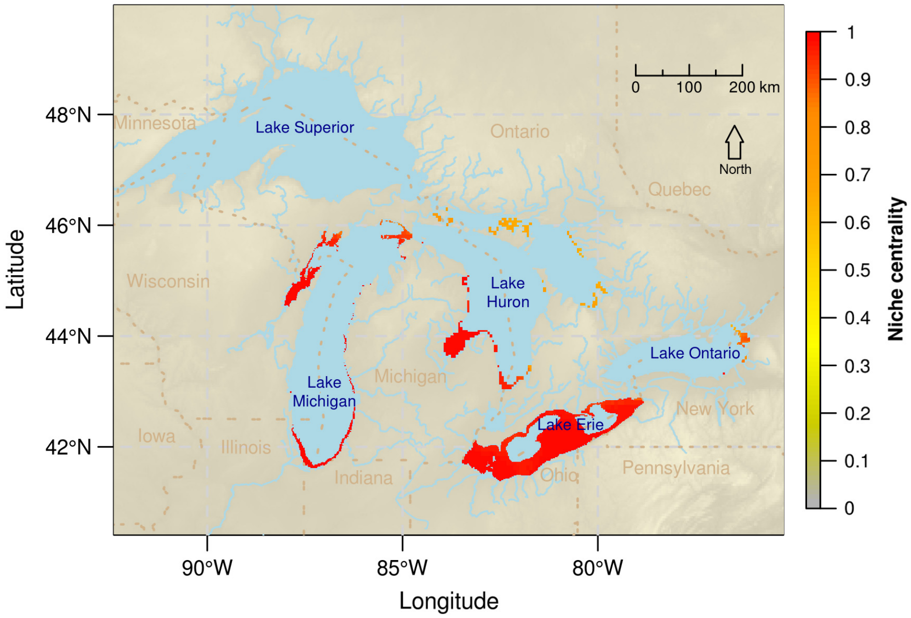

Fig. 8. Northern snakehead habitat suitability restricted by spawning habitat. Visualization of the climate-based niche in areas of the Great Lakes warm enough for snakehead spawning. Spawning can occur at benthic temperatures >18°C.

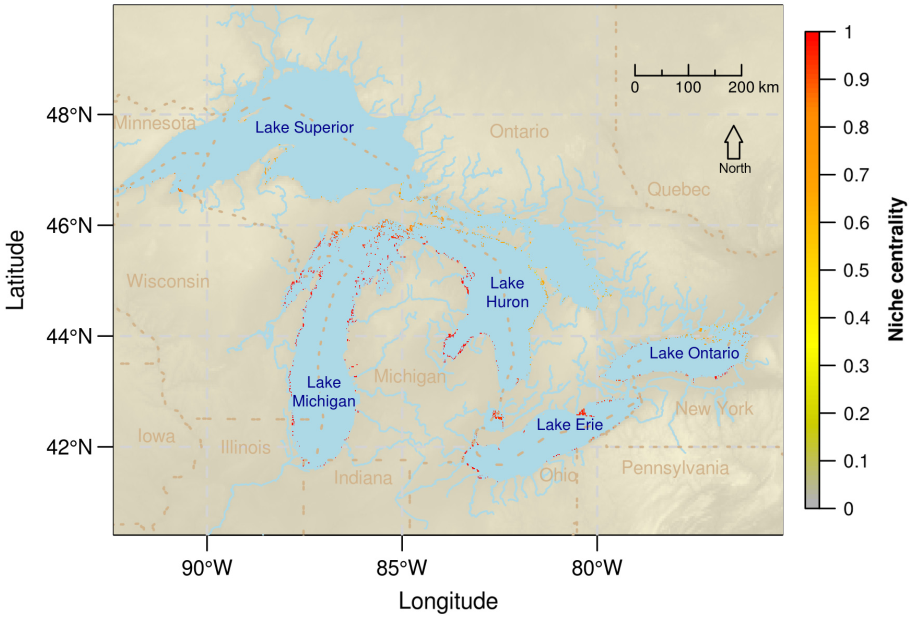

Fig. 9. Northern snakehead habitat suitability restricted by aquatic vegetation. Visualization of the climate-based niche in wetlands and areas of submerged aquatic vegetation (SAV). These are preferred habitat for northern snakehead. Note that SAV data are missing for Lake St. Clair.

enable population growth and spread. To generalize across species, Lake Erie and southern Lake Michigan contained the areas most similar to the current climate niche of these species, while Lake Superior was more peripheral. Further, shallow coastal habitats appear to be most at risk if these species become established in the Great Lakes, whereas deeper, colder benthic habitat of all lakes appears to be unsuitable.

The high AUC values for the test data and the random cross-validation showed that the range bagging models were effective at determining the relative suitability of these species for their native and introduced range. These high AUC values were supported by positive Boyce indices, indicating the models did better than random at predicting suitability for presences in the test and random cross-validation datasets. These findings were also validated for killer shrimp and snakehead using the more challenging approach of spatially subdividing the datasets suggested by Wenger and Olden (2012). Models for golden mussel performed more poorly when fit to spatially defined subsets of the data than to all the data. In fact, the Boyce index suggested performance no better than random under this cross-validation. This highlights one of the difficulties of fitting SDMs to species in the process of invading multiple regions. This is unsurprising for golden mussel, given the distance and differences between the native range in East Asia and invaded areas in South America. One implication is that a model fit only to the native range would misrepresent and underestimate the suitability of various habitats, indicating that using all available occurrences from the native and introduced ranges is likely to produce the most reliable predictions. At the same time, this case reminds us that SDMs can perform poorly with non-analog climates. Accordingly, the analyses presented herein models represent an attempt to estimate risk as effectively as possible, but they may underestimate risk for particular locations.

To our knowledge, this is the first global niche model of golden mussel, an invader having strong impacts in its introduced ranges (Ricciardi 1998). While the Great Lakes climate is relatively distinct in seasonality and temperature from the observed niche, several other areas appear to be highly suitable for establishment of this species, including uninvaded parts of South America, the Gulf of Mexico, southeastern United States, the east coast of Australia, and parts of southeast Africa. Our analysis suggests that increasing surveillance in these areas may be warranted. If this species could establish in the relatively novel environment of the Great Lakes, its ability to reproduce would probably be limited to Lake Erie and the warmer and shallower parts of Lakes Michigan, Huron, and Ontario. However, this does allow that the lakes could still act as a beachhead for invasion (Rothlisberger and Lodge 2013) of the more suitable Lower Mississippi River via the Chicago Area Waterway System, potentially mirroring the historic spread of dreissenid mussels across North America. There is also potential for suitable spawning area to grow given expected increases in surface water temperatures in the Great Lakes (Trumpickas et al. 2009, Kao et al. 2015). The ability to incorporate these underwater-specific habitat data layers representing the golden mussel's temperature limitation improves the understanding of where surveillance efforts can be focused. Relevant environmental layers on water chemistry or substrate type are not yet available for the entirety of the lakes, but the tolerances of golden mussel are broad enough that few parts of the lake would fall outside their tolerance (Ricciardi 1998, Boltovskoy et al. 2006).

Our analysis provides a less clear prediction for killer shrimp in the Great Lakes. The niche centrality for the lakes is ambiguous, generally between 0.2 and 0.5, with Lake Superior again being the most peripheral. This could mean that the Great Lakes may be marginal but possibly suitable habitat for killer shrimp. However, the current distribution of killer shrimp is environmentally restricted by a contiguous geographic and climatic area, and our knowledge of this species is primarily derived from canal and riverine habitats (Pöckl 2009), which limits the ability to develop alternative environmental limits that can be applied within the lakes. Thus, it could be either that these are the only suitable environments or that the species simply has not yet been transported to other novel habitats, making nonstationarity a contributor to the uncertainty of predicting killer shrimp habitat. Moreover, given the existing distribution, the Great Lakes had the highest niche centrality of potential introduction regions globally, consistent with a previous analysis of European ports (Keller et al. 2011). Since killer shrimp can persist across the range of water temperatures observed in the Great Lakes and seem to have a broad diet, we were unable to further pinpoint high-risk areas based on local environmental conditions. For example, killer shrimp have been shown to successfully colonize hard substrates (i.e., stones) and low-density zebra mussel habitats (Kobak et al. 2015). While consistent spatial data on the distribution of these habitats are not yet available for the whole of the lakes, information on these habitats at the local scale could further inform assessments of risk for killer shrimp establishment.

Climate conditions throughout much of the Great Lakes significantly overlap with the estimated niche of northern snakehead. This is consistent with predictions of Herborg et al. (2007) as well as observations of occurrences of this species elsewhere in North America, including watersheds adjacent to the Great Lakes. However, our inclusion of within-lake environmental conditions produced a refinement on previous models based on surface temperature, and helped identify specific habitats vulnerable to this species. Required spawning temperatures indicate that specific and, outside of Lake Erie, relatively limited areas would be available for reproduction. Submerged aquatic vegetation/wetland regions in the Great Lakes overlapped with the suitable spawning temperatures, suggesting that these habitats may be vulnerable to snakehead establishment.

Modeling these three species reinforces the benefits and challenges of relying on climate variables to apply SDMs in aquatic systems, particularly large lakes and rivers that are poorly coupled to proximal air temperature and precipitation (Boyce et al. 1989, Gronewold and Stow 2013). This is especially relevant for the Great Lakes where the bottom temperature changes little throughout the year in areas deeper than about 30 m. Range bagging SDMs effectively estimated the intensity of occurrence in the current range, providing important information on relative suitability of locations at the regional and global scales. The analysis suggests the relative importance of precipitation at a global scale as surrogates for riverine hydrologic regime (Leathwick et al. 2011), although these variables are likely to have limited relevance within the waters of the Great Lakes themselves and are correlated with each other. Further, the microhabitat variations that are known to be important for many aquatic species are often unrelated to surface climatic measurements. Here, we build on previous Great Lakes case studies (US Environmental Protection Agency 2008) that have combined satellite-derived data layers with climatic data, and show how well-characterized subsurface aquatic habitat variables can also be used to improve spatial risk assessment.

The visualizations of habitat suitability produced here could be an important tool for natural resource managers, and advance the understanding of the risk of invasion by these three species. This process of combining information from species locations and studies of environmental tolerances will have value for many other aquatic species. This process also highlights the need for the development of a standardized set of global or regional aquatic habitats data layers and measurements. By associating additional data on variables such as pH, nitrogen, phosphorus, calcium, substrate, and water temperature with species presences, more direct, high-resolution models could be produced. The substantial ecological and economic costs posed by AIS should motivate the collection of such datasets and continued advances in integrating different types of information.

ACKNOWLEDGMENTS

This research was funded by Environmental Protection Agency Great Lakes Restoration Initiative and NOAA Center for Sponsored Coastal Ocean Research: NA09NOS4780192, NA10NOS4780218. Color producing agent (CPA) retrieval images produced by the Michigan Tech Research Institute (MTRI) were funded by the Great Lakes Observing System (GLOS) and NASA. This is NOAA GLERL Contribution No. 1852. This is CIGLR contribution number 1115.

LITERATURE CITED

Amanov, A. A. 1974. Morphology and mode of life in the Amur snakehead (*Ophiocphalu argus warpachowskii*) in Chimkurgan reservoir. Journal of Ichthyology 14:713–717.

Araújo, M. B., and A. T. Peterson. 2012. Uses and misuses of bioclimatic envelope modeling. Ecology 93:1527–1539.

Austin, M. P., and K. P. Van Niel. 2011. Improving species distribution models for climate change studies:

variable selection and scale. Journal of Biogeography 38:1–8.

Barve, N., V. Barve, A. Jiménez-Valverde, A. Lira-Noriega, S. P. Maher, A. T. Peterson, J. Soberón, and F. Villalobos. 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecological Modelling 222:1810–1819.

Beletsky, D., N. Hawley, and Y. R. Rao. 2013. Modeling summer circulation and thermal structure of Lake Erie. Journal of Geophysical Research: Oceans 118: 6238–6252.

Bisrat, S. A., M. A. White, K. H. Beard, and D. Richard Cutler. 2012. Predicting the distribution potential of an invasive frog using remotely sensed data in Hawaii. Diversity and Distributions 18:648–660.

Boets, P., K. Lock, M. Messiaen, and P. L. M. Goethals. 2010. Combining data-driven methods and lab studies to analyse the ecology of *Dikerogammarus villosus*. Ecological Informatics 5:133–139.

Boltovskoy, D., N. Correa, D. Cataldo, and F. Sylvester. 2006. Dispersion and ecological impact of the invasive freshwater bivalve *Limnoperna fortunei* in the Río de la Plata watershed and beyond. Biological Invasions 8:947–963.

Boyce, F. M., M. A. Donelan, P. F. Hamblin, C. R. Murthy, and T. J. Simons. 1989. Thermal structure and circulation in the great lakes. Atmosphere-Ocean 27:607–642.

Brenden, T. O., L. Wang, and P. W. Seelbach. 2008. A river valley segment classification of Michigan streams based on fish and physical attributes. Transactions of the American Fisheries Society 137:1621–1636.

Bruijs, M. C. M., B. Kelleher, G. Van Der Velde, and A. B. De Vaate. 2001. Oxygen consumption, temperature and salinity tolerance of the invasive amphipod *Dikerogammarus villosus*: indicators of further dispersal via ballast water transport. Archiv für Hydrobiologie 152:633–646.

Casellato, S., G. La Piana, L. Latella, and S. Ruffo. 2006. *Dikerogammarus villosus* (Sowinsky, 1894) (Crustacea, Amphipoda, Gammaridae) for the first time in Italy. Italian Journal of Zoology 73:97–104.

Chu, P. Y., J. G. W. Kelley, G. V. Mott, A. Zhang, and G. A. Lang. 2011. Development, implementation, and skill assessment of the NOAA/NOS Great Lakes Operational Forecast System. Ocean Dynamics 61:1305–1316.

Cord, A., and D. Rödder. 2011. Inclusion of habitat availability in species distribution models through multi-temporal remote-sensing data? Ecological Applications 21:3285–3298.

Council of Great Lakes Governors. 2013. Communication from the Council of Great Lakes Governors (2013) Governors and Premiers unite to block "least wanted" aquatic invasive species. Chicago, Illinois, USA.

Courtenay, W. R., and J. D. Williams. 2004. Snakeheads (Pisces, Channidae): a biological synopsis and risk assessment. U.S. Department of the Interior, U.S. Geological Survey, Reston, Virginia, USA.

Cucherousset, J., and J. D. Olden. 2011. Ecological impacts of nonnative freshwater fishes. Fisheries 36:215–230.

Devin, S., C. Piscart, J. N. Beisel, and J. C. Moreteau. 2003. Ecological traits of the amphipod invader *Dikerogammarus villosus* on a mesohabitat scale. Archiv für Hydrobiologie 158:43–56.

Dick, J. T. A., and D. Platvoet. 2000. Invading predatory crustacean *Dikerogammarus villosus* eliminates both native and exotic species. Proceedings of the Royal Society of London B: Biological Sciences 267:977–983.

Dick, J. T. A., D. Platvoet, and D. W. Kelly. 2002. Predatory impact of the freshwater invader *Dikerogammarus villosus* (Crustacea: Amphipoda). Canadian Journal of Fisheries and Aquatic Sciences 59:1078–1084.

Drake, J. M. 2015. Range bagging: a new method for ecological niche modelling from presence-only data. Journal of the Royal Society Interface 12: 20150086.

Elith, J., and J. R. Leathwick. 2009. Species distribution models: ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics 40:677–697.

ESRI. 2014. ArcMap 10.2. Environmental Systems Research Institute, Redlands, California, USA.

Fahnenstiel, G., T. Nalepa, S. Pothoven, H. Carrick, and D. Scavia. 2010. Lake Michigan lower food web: long-term observations and *Dreissena* impact. Journal of Great Lakes Research 36(Supplement 3):1–4.

Frank, S. 1970. Acclimatization experiments with amur snake head, *Ophiocephalus argus warpachowskii* Berg, 1909 in Czechoslovakia. Acta Societatis Zoologicae Bohemoslovacae 34:277–283.

Froese, R. and D. Pauly. 2011. FishBase. http://www.fishbase.org

Gallardo, B., and D. C. Aldridge. 2012. Priority setting for invasive species management: risk assessment of Ponto-Caspian invasive species into Great Britain. Ecological Applications 23:352–364.

Gallien, L., R. Douzet, S. Pratte, N. E. Zimmermann, and W. Thuiller. 2012. Invasive species distribution models: how violating the equilibrium assumption can create new insights. Global Ecology and Biogeography 21:1126–1136.

Gantz, C. A., D. R. Gordon, C. L. Jerde, R. P. Keller, W. L. Chadderton, P. D. Champion, and D. M. Lodge.

2015. Managing the introduction and spread of non-native aquatic plants in the Laurentian Great Lakes: a regional risk assessment approach. Management of Biological Invasions 6:45–55.

Gormley, A. M., D. M. Forsyth, P. Griffioen, M. Lindeman, D. S. L. Ramsey, M. P. Scroggie, and L. Woodford. 2011. Using presence-only and presence–absence data to estimate the current and potential distributions of established invasive species. Journal of Applied Ecology 48:25–34.

Graham, C. H., and R. J. Hijmans. 2006. A comparison of methods for mapping species ranges and species richness. Global Ecology and Biogeography 15: 578–587.

Great Lakes Coastal Wetland Consortium. 2004. Great Lakes Coastal Wetland Inventory. http://glc.org/projects/habitat/coastal-wetlands/cwc-inventory/

Gronewold, A. D., and C. A. Stow. 2013. Unprecedented seasonal water level dynamics on one of the Earth's largest lakes. Bulletin of the American Meteorological Society 95:15–17.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8:993–1009.

Herborg, L.-M., N. E. Mandrak, B. C. Cudmore, and H. J. MacIsaac. 2007. Comparative distribution and invasion risk of snakehead (Channidae) and Asian carp (Cyprinidae) species in North America. Canadian Journal of Fisheries and Aquatic Sciences 64:1723–1735.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965–1978.

Hirzel, A. H., G. Le Lay, V. Helfer, C. Randin, and A. Guisan. 2006. Evaluating the ability of habitat suitability models to predict species presences. Ecological Modelling 199:142–152.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposium 22:415–427.

Jiménez-Valverde, A., A. T. Peterson, J. Soberón, J. M. Overton, P. Aragón, and J. M. Lobo. 2011. Use of niche models in invasive species risk assessments. Biological Invasions 13:2785–2797.

Josens, G., A. B. de Vaate, P. Usseglio-Polatera, R. Cammaerts, F. Chérot, F. Grisez, P. Verboonen, and J.-P. V. Bossche. 2005. Native and exotic Amphipoda and other Peracarida in the River Meuse: New assemblages emerge from a fast changing fauna. Hydrobiologia 542:203–220.

Kao, Y., C. P. Madenjian, D. B. Bunnell, B. M. Lofgren, and M. Perroud. 2015. Temperature effects induced by climate change on the growth and consumption by Salmonines in Lakes Michigan and Huron. Environmental Biology of Fishes 98:1089–1104.

Karatayev, A. Y., D. Boltovskoy, D. K. Padilla, and L. E. Burlakova. 2007. The invasive bivalves *Dreissena polymorpha* and *Limnoperna fortunei*: parallels, contrasts, potential spread and invasion impacts. Journal of Shellfish Research 26:205–213.

Keller, R. P., J. M. Drake, M. B. Drew, and D. M. Lodge. 2011. Linking environmental conditions and ship movements to estimate invasive species transport across the global shipping network. Diversity and Distributions 17:93–102.

Keller, R. P., D. M. Lodge, M. A. Lewis, and J. F. Shogren. 2009. Bioeconomics of invasive species: integrating ecology, economics, policy, and management. Oxford University Press, Oxford, UK.

Kerfoot, W. C., F. Yousef, S. A. Green, J. W. Budd, D. J. Schwab, and H. A. Vanderploeg. 2010. Approaching storm: disappearing winter bloom in Lake Michigan. Journal of Great Lakes Research 36 (Supplement 3):30–41.

Kilroy, C., T. H. Snelder, O. Floerl, C. C. Vieglais, and K. L. Dey. 2008. A rapid technique for assessing the suitability of areas for invasive species applied to New Zealand's rivers. Diversity and Distributions 14:262–272.

Kobak, J., Ł. Jermacz, and A. Dzierżyńska-Białończyk. 2015. Substratum preferences of the invasive killer shrimp *Dikerogammarus villosus*. Journal of Zoology 297:66–76.

Kolar, C. S., and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. Trends in Ecology & Evolution 16:199–204.

Kulhanek, S. A., B. Leung, and A. Ricciardi. 2011. Using ecological niche models to predict the abundance and impact of invasive species: application to the common carp. Ecological Applications 21: 203–213.

Lacey Act. 1900. An act to enlarge the powers of the Department of Agriculture, prohibit the transportation by interstate commerce of game killed in violation of local laws, and for other purposes. Chapter 553. Pages 187–189. US Government, Washington, D.C., USA.

Leathwick, J. R., D. Rowe, J. Richardson, J. Elith, and T. Hastie. 2005. Using multivariate adaptive regression splines to predict the distributions of New Zealand's freshwater diadromous fish. Freshwater Biology 50:2034–2052.

Leathwick, J. R., T. Snelder, W. L. Chadderton, J. Elith, K. Julian, and S. Ferrier. 2011. Use of generalised dissimilarity modelling to improve the biological discrimination of river and stream classifications. Freshwater Biology 56:21–38.

Leung, B., D. M. Lodge, D. Finnoff, J. F. Shogren, M. A. Lewis, and G. Lamberti. 2002. An ounce of prevention or a pound of cure: Bioeconomic risk analysis of invasive species. Proceedings of the Royal Society of London Series B: Biological Sciences 269: 2407–2413.

Leung, B., et al. 2012. TEASIng apart alien species risk assessments: a framework for best practices. Ecology Letters 15:1475–1493.

Lockwood, J. L., P. Cassey, and T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology & Evolution 20: 223–228.

Lods-Crozet, B., and O. Reymond. 2006. Bathymetric expansion of an invasive gammarid (*Dikerogammarus villosus*, Crustacea, Amphipoda) in Lake Léman. Journal of Limnology 65:141.

MacNeil, C., et al. 2010. The Ponto-Caspian ‘killer shrimp’, *Dikerogammarus villosus* (Sowinsky, 1894), invades the British Isles. Aquatic Invasions 5: 441–445.

McKenna Jr., J. E., and C. Castiglione. 2010. Hierarchical multi-scale classification of nearshore aquatic habitats of the Great Lakes: Western Lake Erie. Journal of Great Lakes Research 36:757–771.

Michigan Tech Research Institute. 2012. Satellite-derived lake submerged aquatic vegetation (SAV). http://www.mtri.org/cladophora.html.

Mohseni, O., and H. G. Stefan. 1999. Stream temperature/air temperature relationship: a physical interpretation. Journal of Hydrology 218:128–141.

Okada, Y. 1960. Studies of the freshwater fishes of Japan, II, Special part. Journal of the Faculty of Fisheries Prefectural University of Mie 4:31–860.

Pagel, J., and F. M. Schurr. 2012. Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. Global Ecology and Biogeography 21:293–304.

Pagnucco, K. S., G. A. Maynard, S. A. Fera, N. D. Yan, T. F. Nalepa, and A. Ricciardi. 2015. The future of species invasions in the Great Lakes-St. Lawrence River basin. Journal of Great Lakes Research 41: 96–107.

Petitpierre, B., C. Kueffer, O. Broennimann, C. Randin, C. Daehler, and A. Guisan. 2012. Climatic niche shifts are rare among terrestrial plant invaders. Science 335:1344–1348.

Phillips, S. J., and J. Elith. 2013. On estimating probability of presence from use–availability or presence–background data. Ecology 94:1409–1419.

Pöckl, M. 2009. Success of the invasive Ponto-Caspian amphipod *Dikerogammarus villosus* by life history traits and reproductive capacity. Biological Invasions 11:2021–2041.

Ricciardi, A. 1998. Global range expansion of the Asian mussel *Limnoperna fortunei* (Mytilidae): another fouling threat to freshwater systems. Biofouling 13:97–106.

Ricciardi, A., and H. J. MacIsaac. 2000. Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. Trends in Ecology & Evolution 15:62–65.

Ricciardi, A., and J. B. Rasmussen. 1998. Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. Canadian Journal of Fisheries and Aquatic Sciences 55:1759–1765.

Rothlisberger, J. D., and D. M. Lodge. 2013. The Laurentian Great Lakes as a beachhead and a gathering place for biological invasions. Aquatic Invasions 8:361–374.

Schwab, D. J., and K. W. Bedford. 1994. Initial implementation of the great lakes forecasting system: a real-time system for predicting lake circulation and thermal structure. Water Quality Research Journal of Canada 292–3:203–220.

Shuchman, R. A., M. J. Sayers, and C. N. Brooks. 2013. Mapping and monitoring the extent of submerged aquatic vegetation in the Laurentian Great Lakes with multi-scale satellite remote sensing. Journal of Great Lakes Research 39(Supplement 1):78–89.

Snelder, T. H., et al. 2006. Development of an ecologic marine classification in the New Zealand region. Environmental Management 39:12–29.

Trumpickas, J., B. J. Shuter, and C. K. Minns. 2009. Forecasting impacts of climate change on Great Lakes surface water temperatures. Journal of Great Lakes Research 35:454–463.

Tyberghein, L., H. Verbruggen, K. Pauly, C. Troupin, F. Mineur, and O. De Clerck. 2012. Bio-ORACLE: a global environmental dataset for marine species distribution modelling. Global Ecology and Biogeography 21:272–281.

US Environmental Protection Agency. 2008. Predicting future introductions of nonindigenous species to the Great Lakes, EPA/600/R-08/066F. National Center for Environmental Assessment, Washington, D.C., USA.

USACE. 2011. Great Lakes and Mississippi Interbasin Study: non-native species of concern and dispersal risk for the Great Lakes and Mississippi River Interbasin Study. U.S. Army Corps of Engineers, Chicago, Illinois, USA.

Václavík, T., J. A. Kupfer, and R. K. Meentemeyer. 2012. Accounting for multi-scale spatial autocorrelation improves performance of invasive species distribution modelling (iSDM). Journal of Biogeography 39:42–55.

Václavík, T., and R. K. Meentemeyer. 2012. Equilibrium or not? Modelling potential distribution of invasive species in different stages of invasion. Diversity and Distributions 18:73–83.

Vanderploeg, H. A., J. R. Liebig, T. F. Nalepa, G. L. Fahnenstiel, and S. A. Pothoven. 2010. Dreissena and the disappearance of the spring phytoplankton bloom in Lake Michigan. Journal of Great Lakes Research 36(Supplement 3):50–59.

VanDerWal, J., H. T. Murphy, A. S. Kutt, G. C. Perkins, B. L. Bateman, J. J. Perry, and A. E. Reside. 2013. Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. Nature Climate Change 3:239–243.

van der Velde, G., R. S. E. W. Leuven, D. Platvoet, K. Bacela, M. A. J. Huijbregts, H. W. M. Hendriks, and D. Kruijt. 2009. Environmental and morphological factors influencing predatory behaviour by invasive non-indigenous gammaridean species. Biological Invasions 11:2043–2054.

Veloz, S. D., J. W. Williams, J. L. Blois, F. He, B. Otto-Bliesner, and Z. Liu. 2012. No-analog climates and shifting realized niches during the late quaternary: implications for 21st-century predictions by species distribution models. Global Change Biology 18: 1698–1713.

Wenger, S. J., and J. D. Olden. 2012. Assessing transferability of ecological models: an underappreciated aspect of statistical validation. Methods in Ecology and Evolution 3:260–267.

Wijnhoven, S., M. C. van Riel, and G. van der Velde. 2003. Exotic and indigenous freshwater gammarid species: physiological tolerance to water temperature in relation to ionic content of the water. Aquatic Ecology 37:151–158.

Wittmann, M. E., G. Annis, A. M. Kramer, L. Mason, C. Riseng, E. S. Rutherford, W. L. Chadderton, D. Beletsky, J. M. Drake, and D. M. Lodge. 2017. Refining species distribution model outputs using landscape-scale habitat data: forecasting grass carp and *Hydrilla* establishment in the Great Lakes region. Journal of Great Lakes Research 43:298–307.

Xu, M., Z. Wang, C. C. Lin, B. Pan, and N. Zhao. 2013. Experimental study of invasion and biofouling of freshwater mussel *Limnoperna fortunei*. International Journal of Geosciences 04:1–7.

DATA AVAILABILITY

Data and code are archived at Dryad (https://doi.org/10.5061/dryad.d4144).

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1883/full