

ARTICLE

Freshwater Ecology

BioLake: A first assessment of lake temperature-derived bioclimatic predictors for aquatic invasive species

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Abstract

Aquatic invasive species (AIS) present major ecological and economic challenges globally, endangering ecosystems and human livelihoods. Managers and policy makers thus need tools to predict invasion risk and prioritize species and areas of concern, and they often use native range climate matching to determine whether a species could persist in a new location. However, climate matching for AIS often relies on air temperature rather than water temperature due to a lack of global water temperature data layers, and predictive power of models is seldom evaluated. We developed 12 global lake (water) temperature-derived “BioLake” bioclimatic layers for distribution modeling of aquatic species and compared “climatch” climate matching predictions (from climatchR package) from BioLake with those based on BioClim temperature layers and with a null model. We did this for 73 established AIS in the United States, training the models on their ranges outside of the United States and Canada. Models using either set of climate layers outperformed the null expectation by a similar (but modest) amount on average, but some species were occasionally found in locations with low climatch scores. Mean US climatch scores were higher for most species when using air temperature. Including additional climate layers in models reduced mean climatch scores, indicating that commonly used climatch score thresholds are not absolute but can be context specific and may require calibration based upon climate data used. Although finer resolution global lake temperature data would likely improve predictions, our BioLake layers provide a starting point for aquatic species distribution modeling. Climate matching was most effective for some species that originated at low latitudes or had small ranges. Climatch scores remain useful but limited for predicting AIS risk, perhaps because current ranges seldom fully reflect climatic tolerances (fundamental niches). Managers could consider climate matching as one of a suite of tools that can be used in AIS prioritization.

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KEYWORDS

aquatic invasive species (AIS), BioLake, CHELSA BioClim, climatch, climate matching, ERA5-Land climate reanalysis, fundamental niche, horizon scanning, invasion risk assessment, lake temperature, species distribution models (SDM)

INTRODUCTION

Invasive species present major ecological and economic challenges globally. Their negative effects include alteration or loss of ecosystem services (Charles & Dukes, 2008), disrupted food webs (David et al., 2017), and lost productivity for agriculture (Paini et al., 2016), fisheries (Lovell et al., 2006), wildlife (Usher, 1986), and forestry (Holmes et al., 2009). Aquatic invasive species (AIS) alone are responsible for at least US \$23 billion in global damages annually (Cuthbert et al., 2021), and invasive species threaten many native species with extinction (McGeoch et al., 2010; Tilman et al., 2017).

The prevalence and importance of invasive species make it critical that managers and policy makers can evaluate risks and target efforts toward species that present the highest risks (Marcot et al., 2019). Furthermore, the difficulty and expense of eradicating invasive species once they have become established make prevention of initial invasions the most efficient means of control (Ahmed et al., 2022; Cuthbert et al., 2022; Pyšek et al., 2020). Yet prevention also requires the ability to prioritize species based on their relative risks because overly inclusive lists of high-risk species can dilute prevention and detection efforts that could be directed toward species of highest risk of establishment and impact (Courtois et al., 2018). This is especially true when prioritizing among the many potential invaders globally that have not yet arrived or become established in an area.

Managers and policy makers use a variety of risk assessment methods to classify and prioritize invasive species including Ecological Risk Screening Summaries (ERSS) (Marcot et al., 2019), the Generic Nonindigenous Aquatic Organisms Risk Analysis Review Process of the U.S. Federal Aquatic Nuisance Species Task Force (Orr, 2003), Weed Risk Assessment (WRA) and related methods for other taxa (Pheloung et al., 1999; Vilizzi et al., 2019, 2021), and horizon scanning (Roy et al., 2014). The risk presented by a species is a function of its probabilities of arrival and establishment, as well as of the predicted biological and economic consequences that could result (Lodge et al., 2016; Magarey et al., 2018). These are in turn affected by the potential habitats (Marcot et al., 2019) and climates (Elith, 2017) that the species could occupy, the species' native range, and its life history traits (Howeth et al., 2016; Van Kleunen et al., 2016).

Each of these factors has value in predicting invasion risk, but the degree of climatic similarity is often used as the primary predictor of invasion risk due to its simplicity, or when additional information on species' traits, invasion history, and speed and methods of spread is unavailable (Hao et al., 2019; Hayes & Barry, 2008). This builds on a foundational principle in ecology, the fundamental niche (Hutchinson, 1957), which states that the maximum range of environmental conditions that a species can tolerate is dictated by its physiology and behavior. Fundamental niches thus set an outer limit on species' invasion potential, and modeling these niches can therefore provide an important starting point for invasion risk assessments (Elith, 2017). Furthermore, the potential for invasive species to cause ecological and economic damage (rather than merely to become established) is often higher in areas that better match species' climatic optimum (Iacarella et al., 2015), further underlining the importance of understanding climatic similarity. However, some species do adapt to inhabit novel environments (Bujan et al., 2021; Gallagher et al., 2010), and fundamental niches may prove broader than current realized niches (Soberón & Arroyo-Peña, 2017).

Climatic niche-based models of invasion risk thus have strong ecological foundations and have the potential to inform us about the effects of future climate change (Foden et al., 2019; Hulme, 2017). Yet such climatic niche-based models have had mixed success in predicting species invasion risk. Bioclimatic variables helped predict fish invasion success in the Great Lakes, and some species traits (e.g., fecundity) predicted invasive ability (Howeth et al., 2016). Distributions of several invasive weeds were predicted equally well by climate variables and expert opinion, with neither method producing highly supported predictions (Magarey et al., 2018). However, established invaders in Australia were shown to have a better climate match to local conditions than unsuccessful species of non-native reptiles, amphibians, lake fish, and mammals (Bomford et al., 2010; Bomford, Darbyshire, et al., 2009; Bomford, Kraus, et al., 2009), although in many cases other factors (like the number of introduction events, or species' invasion success elsewhere) were better predictors of risk of establishment.

One potential reason that climatic niche-based models may not perform well for some aquatic species may be that such models typically rely on air temperature-derived

bioclimatic layers like BioClim (Booth, 2018; Karger et al., 2017) rather than on water temperature. This is important because water temperature is imperfectly linked to air temperature—lakes have high thermal mass, buffering them from short-term extremes of heat and cold (Desai et al., 2009), and rivers can carry water that originates elsewhere and is also buffered against extremes (Caissie et al., 2005). Furthermore, the vertical stratification of lake layers that often occurs results in lake bottom and surface temperatures that are out of sync with rapidly fluctuating air temperatures (Desai et al., 2009). There is thus good reason to expect that water temperature-based predictions would outperform air temperature-based models for AIS.

Among a suite of existing climatic niche-based modeling methods, the “climatch” algorithm has been widely used, especially in Australia and the United States (Bomford et al., 2010; Bomford, Kraus, et al., 2009; Crombie et al., 2008; Howeth et al., 2016). This method recently became more easily accessible via its implementation in the climatchR R package (Erickson et al., 2021, 2022). Climatch considers multiple temperature- and precipitation-based axes of climatic niches and calculates climate match scores for new locations for a given species, based on these locations’ Euclidean distances (in multidimensional climate space) from the climate at locations where that species currently occurs (Crombie et al., 2008). This R package uses the Climatologies at high resolution for the earth’s land surface areas (CHELSA) BioClim “bio” layers (Karger et al., 2017), which summarize daily and yearly air temperature and precipitation patterns in biologically relevant ways. However, a lack of comparable water temperature-derived bioclimatic layers potentially reduces the utility of this method for AIS. Recently, however, global lake temperature estimates became available from the ERA5-Land climate reanalysis (Muñoz-Sabater et al., 2021), a physics-based climate model that estimates hourly values from 1950 to the present. This data source provides hourly estimates of lake temperature for several strata, including the lake mixed (surface) layer, the lake bottom, and the total lake water column. The mixed layer is defined as the uppermost layer of a lake that is well mixed (Muñoz-Sabater et al., 2021).

Here, we used these lake temperature estimates to develop a set of 12 global lake temperature-derived bioclimatic layers (“BioLake”) that correspond to BioClim temperature layers (Table 1). BioClim precipitation layers can be used with both sets of temperature layers. To compare the predictive value of BioClim and BioLake layers for AIS that have not yet invaded the United States, we tested the climatch algorithm predictions for 73 current US aquatic plant and animal invaders. We fit the models to records from the Global Biodiversity Information Facility (GBIF) from outside of the United States and Canada and used

these models to calculate climate matching scores for the contiguous United States. We then compared these scores from both BioLake and BioClim to the distributions of GBIF records of each species from within the contiguous United States, evaluating the models relative to each other and to a null model. We asked:

1. How well do climatch scores for the contiguous United States, based on AIS species’ occurrences outside of the United States and Canada, perform relative to a null model?
2. Do lake temperature-based (BioLake) methods outperform those based on air temperature (BioClim) for AIS?

METHODS

Bioclimatic layers

In order to compare air temperature- and water temperature-based climate match predictions for AIS, we created global lake temperature-derived bioclimatic layers (BioLake, 2022a; Table 1 and Figure 1; Appendix S1: Figures S1 and S2) that correspond to the CHELSA BioClim (Karger et al., 2017) bio1–bio11 layers (<https://chelsa-climate.org/bioclim/>). These BioClim layers summarize air temperature over a 30-year period in ways that are relevant for biological organisms, and our BioLake layers do the same (Burner & Erickson, 2022a). We did this using lake temperature estimates from the ERA5-Land climate reanalysis (Muñoz-Sabater et al., 2021), a physics-based climate model that provides estimates of hourly values from 1950 to the present at $\sim 9 \times 9$ -km resolution globally. Lake temperature estimates are available for three lake strata, including the mixed (surface) layer, bottom layer, and mean total lake water column (“lake_mix_layer_temperature,” “lake_bottom_temperature,” and “lake_total_layer_temperature,” respectively) and we created a full set of BioLake layers for each of these three lake strata.

We summarized hourly, daily, and monthly mean lake temperature for each of these three strata for a 30-year period (1991–2020) using the Python toolbox on the Climate Data Store (<https://cds.climate.copernicus.eu/>). This online method allowed us to process large amounts of data in the cloud rather than downloading the data and processing on local resources. We then downloaded these daily and monthly summaries as global raster files and calculated the BioLake layers using the raster (Hijmans, 2019) package in R 4.0.5 (R Core Team, 2022), following the formulas in Table 1. CHELSA bio8–bio9 layers summarize temperature values for the wettest and driest quarters of the year, respectively. To calculate the

TABLE 1 BioLake lake temperature-derived layer definitions and correspondence to climatologies at high resolution for the earth's land surface areas (CHELSA) BioClim layers (Karger et al., 2017).

BioLake layer ^a	Corresponds to BioClim layer ^a	Description	Definition ^b
BioLake01	bio1	Annual mean temperature	Mean of each month's 30-year mean temperature
BioLake02 ^b	bio2	Mean diurnal range	Mean of difference between warmest and coolest hourly temp for all days across 30 years
BioLake03 ^b	bio3	Isothermality	BioLake02/BioLake07 × 100
BioLake04 ^b	bio4	Temperature seasonality	SD of all months' 30-year mean temperatures
BioLake05	bio5	Max temperature of warmest month	Mean of the yearly maximum hourly temperature across 30 years
BioLake06	bio6	Min temperature of coldest month	Mean of the yearly minimum hourly temperature across 30 years
BioLake07	bio7	Temperature annual range	BioLake05–BioLake06
BioLake08	bio8	Mean temperature of wettest quarter	Mean temperature of the three consecutive months with highest combined precipitation across 30 years
BioLake09	bio9	Mean temperature of driest quarter	Mean temperature of the three consecutive months with lowest combined precipitation across 30 years
BioLake10	bio10	Mean temperature of warmest quarter	Mean temperature of the three warmest months across 30 years
BioLake11	bio11	Mean temperature of coldest quarter	Mean temperature of the three coldest months across 30 years
[bio12] ^c	bio12	Annual precipitation	Mean total annual precipitation across 30 years
[bio13] ^c	bio13	Precipitation of wettest month	Mean total precipitation of the wettest month across 30 years
[bio14] ^c	bio14	Precipitation of driest month	Mean total precipitation of the driest month across 30 years
[bio15] ^c	bio15	Precipitation seasonality	SD of all months' 30-year mean total precipitation
[bio16] ^c	bio16	Precipitation of wettest quarter	Mean total precipitation of the three wettest months across 30 years
[bio17] ^c	bio17	Precipitation of driest quarter	Mean total precipitation of the three driest months across 30 years
[bio18] ^c	bio18	Precipitation of warmest quarter	Mean total precipitation of the three warmest months across 30 years
[bio19] ^c	bio19	Precipitation of coldest quarter	Mean total precipitation of the three coldest months across 30 years
BioLake20 ^b	NA	Mean no. months with non-zero ice cover	Mean number of months with non-zero ice cover across 30 years

^aAll BioLake layers were calculated across 30 years (1991–2020). Lake temperature values are based on the ERA5-Land climate reanalysis (Muñoz-Sabater et al., 2021) and were calculated separately for lake mixed (surface) layer, lake bottom, and total lake water column. Precipitation-based BioClim layers, also shown, were included in both lake and air temperature models. BioLake layers available from Burner and Erickson (2022a).

^bBioLake layers 2, 3, 4, and 20 were excluded from the main BioLake lake temperature model for comparability to the CHELSA BioClim layers included in the climatchR R package (Erickson et al., 2021); for a BioLake model including all layers refer to Supplemental results in Appendix S1.

^cCHELSA precipitation-based layers were used in climatchR along with BioLake temperature layers to capture precipitation-based niche dimensions.

corresponding BioLake layers, we also obtained monthly precipitation estimates from ERA5-Land to determine which months to include. We calculated one BioLake layer (BioLake20) that does not have a

CHELSA equivalent but that is relevant for aquatic organisms—the number of months with ice cover. This was calculated from the ERA5-Land “lake_ice_depth” data field and does not vary among the lake strata.

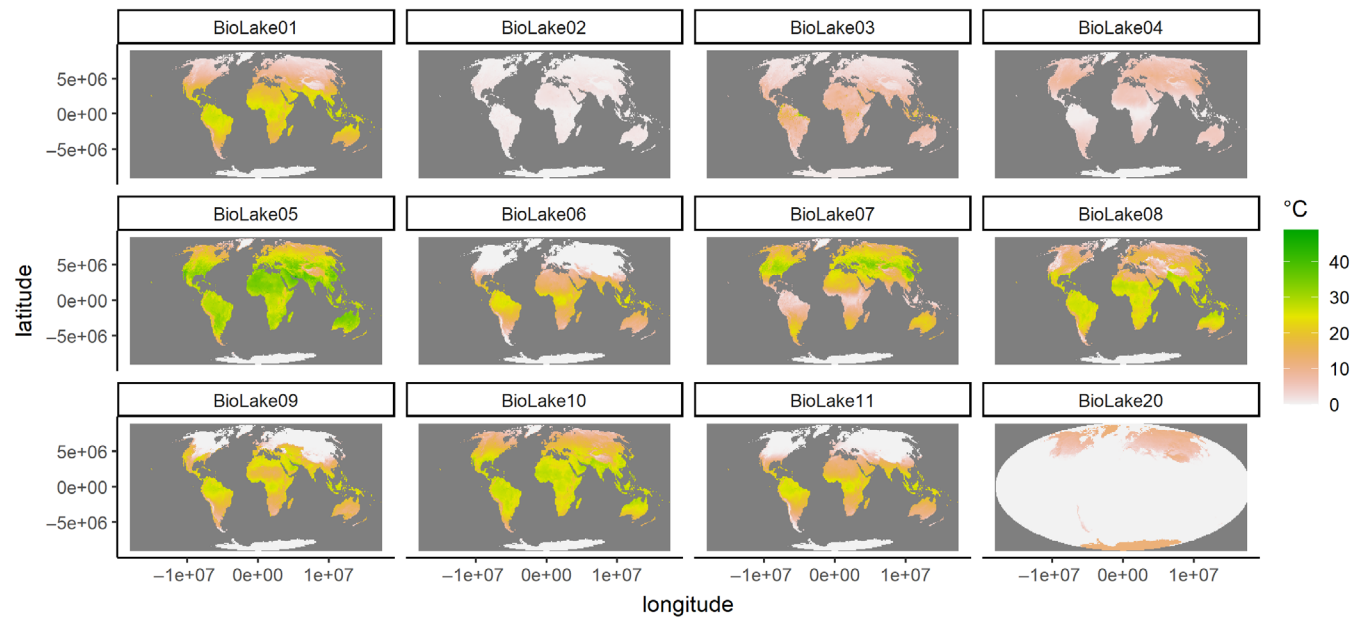


FIGURE 1 Lake temperature-derived “BioLake” bioclimatic layers (Burner & Erickson, 2022a) for lake mixed (surface) layer. For BioLake layer definitions, refer to Table 1. Note that units for BioLake20 are “months per year” (with surface ice) rather than degrees Celsius as in the legend and other layers. Raster layers shown here have been reprojected to an equal-area projection (Mollweide) with a resolution of $10,000 \times 12,400$ m. We generated BioLake layers for three lake strata: mixed (surface) layer, lake bottom, and total lake water column. For lake bottom and total water column refer to Appendix S1: Figures S1 and S2, respectively.

We reprojected all climate layers to the Mollweide projection, which maintains an equal area across the globe (Snyder, 1987), with a resolution of 10×12.4 km. For use in the climatchR package, we then centered and scaled all values in each layer to range from zero to one. Python and R code for these steps are available from Burner and Erickson (2022b). Precipitation-based layers (bio12–bio19) remain equally relevant for aquatic organisms whether air or water temperature is used, in part due to the relationship between precipitation and hydrology (Hellmann et al., 2008), so these CHELSA layers were included in all models (refer to details below).

Invasive species selection

Our goal was to test whether climatic similarity between a new region of concern and a species’ native range and other currently invaded regions is a good predictor of that species’ invasion success in the new region. We thus selected plant and animal AIS that (1) were well established in the United States, (2) lived primarily in lakes, and (3) had more than 50 GBIF (gbif.org) records that were not in rivers (details below) outside of the United States and Canada (for model fitting) and more than 50 records in the contiguous United States (for model testing). To do this, we first selected 283 species for screening (Appendix S1: Table S1) from the 1375 species

tracked by the U.S. Geological Survey (USGS) Nonindigenous Aquatic Species (NAS) Database (<https://nas.er.usgs.gov/>). This subset represented fully aquatic species (as opposed to semiaquatic), found primarily in fresh water, and considered invasive or of management concern (based on the authors’ knowledge). For each of these 283 AIS species of interest, we then extracted all records from GBIF (accessed 09 June 2022) using the climatchR R package (Erickson et al., 2021), removing all records with location uncertainty >1 km and several obviously erroneous records based on a visual inspection (e.g., those in open ocean).

Because our lake temperature estimates are not intended to apply to rivers, we then removed all records of each species that appeared to occur in or near rivers using the HydroRIVERS global database (Lehner & Grill, 2019). To do this, we rasterized the HydroRIVERS vector data at 500×500 -m resolution and removed all species records that fell within a cell containing a river. However, we did not want to inadvertently exclude any records that were from reservoirs located on rivers because our lake temperature data layers are relevant to reservoirs as well. Therefore, we retained any species records that fell within a lake or large reservoir, based on the HydroSHEDS Global Lakes and Wetlands Database raster (glwd_3; water bodies with surface area ≥ 0.1 km², i.e., level 1 and level 2 retained) (Lehner & Döll, 2004), even if they occurred in a grid cell with a river. Next, we

removed any species that had records from 50 or fewer unique climate grid cells either outside of the United States and Canada (model training data) or in the contiguous United States (model testing data) in order to have adequate representations of the species' ranges. This step resulted in 86 potential AIS for inclusion. We then used expert judgment to classify each of these species as occurring primarily in lakes or primarily in rivers. Experts on fishes ($n = 2$; refer to *Acknowledgments*), invertebrates ($n = 1$), and plants ($n = 1$) based these assessments on habitats in which species were known to occur (primarily from the USGS NAS database) and on personal experience with the species. We then eliminated all species occurring primarily in rivers because our BioLake bioclimatic layers are most relevant to lakes and thus results could be misleading for species most likely to invade rivers. This left 73 species remaining for analysis (54 plants and 19 animals; Table 2).

Analyses

After compiling species records, we estimated climatch scores for the contiguous United States for each species, based only on species records from outside of the United States and Canada, using the climatchR package. We did this twice for each species: once using BioLake layers from the mixed (surface) stratum, and once using the BioClim air temperature-derived layers. For our lake temperature model, we included BioLake01 and BioLake05–11, as well as the precipitation-based CHELSA bio12–bio19 layers (v2.1, resampled to match the BioLake resolution), for comparability to the BioClim layers included in the climatchR package (Erickson et al., 2021). BioClim layers bio1 and bio5–bio19 (CHELSA v1.2) from climatchR were used in the air temperature model. Additionally, we fit a lake temperature model that included all BioLake layers (BioLake01–11 and 20) and present these results in Supplemental results in Appendix S1. BioLake also includes a set of layers based on lake bottom temperature and total water column temperature, but we did not determine these to be most suitable for any of our AIS.

We then extracted predicted climatch scores for each of the GBIF validation locations in the contiguous United States for each species (maximum one location per unique climate grid cell) for both the BioLake- and CHELSA BioClim-based predictions. Climatch scores range from 0 to 10 (unsuitable to most suitable). Managers generally consider climatch scores of 6 or more to indicate a high potential for invasion (U.S. Fish and Wildlife Service, 2020). To determine the mean climatch score across all locations where a given species was

present, we calculated the mean of these values. These mean values are important because managers commonly consider the numeric value of climatch scores as an indicator of a species' risk of establishment.

However, comparing mean climatch values among models (air temperature vs. lake temperature) of sites at which a species occurs does not indicate definitively which method is better because a model that predicts overall higher scores across the entire continent would score higher where species are present due to chance alone. To compare among model types while controlling for the overall distribution of climatch scores across the contiguous United States, we used a null model approach for each species. Conceptually, a null model compares the observed values in a given analysis to the distribution of values that would be predicted as a result of random chance alone (Gotelli & Graves, 1996). In our case, we randomly permuted all contiguous United States climatch scores 500 times, extracting these random scores in each iteration from each grid cell that contained a species record. We then subtracted the true climatch score for that grid cell from all 500 of these random values to generate the distribution of these difference values. Positive values in this distribution thus indicate true climatch scores higher than those predicted by the null model (indicating true predictive power of the model). Negative or zero scores indicate that predictions do no better than expected by chance, allowing us to test the value of the climatch algorithm in predicting invasion risk. To compare the relative predictive power of BioLake versus CHELSA bio layers, we compared the distributions of these difference values among model types for each species (using a t test).

To determine whether species range size or median latitude were good predictors of how well climate matching performed, we plotted the difference between the null expectation and median scores where present for each species against median non-US/Canada latitude, and against the number of non-US/Canada countries occupied (a rough proxy for range size), and fit quadratic linear models.

RESULTS

We generated climatch scores for 54 plants and 19 animal AIS (73 total) across the contiguous United States using BioLake bioclimatic layers and compared them with those generated using CHELSA BioClim bioclimatic layers (Figure 2). Median climatch scores were typically high at known species locations (Figures 3 and 4; Appendix S1: Figure S3), averaging 7.88 (95% CI: 6.16–8.69) among species when using the BioClim bioclimatic layers, and 6.48 (95% CI: 3.34–8.22) when using BioLake. Mean BioClim

TABLE 2 Aquatic invasive species already established in the United States that were selected for this study.

Species ^a	English name
<i>Acorus calamus</i>	Single-vein sweetflag
<i>Agrostis gigantea</i>	Redtop
<i>Alopecurus geniculatus</i>	Water foxtail
<i>Alternanthera philoxeroides</i>	Alligatorweed
<i>Arundo donax</i>	Giantreed
<i>Butomus umbellatus</i>	Flowering rush
<i>Callitriche stagnalis</i>	Pond water-starwort
<i>Cirsium palustre</i>	Marsh thistle
<i>Colocasia esculenta</i>	Wild taro
<i>Cotula coronopifolia</i>	Common brassbuttons
<i>Cyperus blepharoleptos</i>	Cuban bulrush
<i>Cyperus difformis</i>	Smallflower umbrella sedge
<i>Cyperus papyrus</i>	Papyrus
<i>Hydrilla verticillata</i>	Hydrilla
<i>Hydrocharis morsus-ranae</i>	European frogbit
<i>Iris pseudacorus</i>	Yellow iris
<i>Juncus compressus</i>	Roundfruit rush
<i>Limnophila sessiliflora</i>	Asian marshweed
<i>Ludwigia grandiflora</i>	Large-flower primrose-willow
<i>Ludwigia peploides</i>	Floating primrose-willow
<i>Lysimachia punctata</i>	Large yellow loosestrife
<i>Lythrum hyssopifolia</i>	Hyssop loosestrife
<i>Lythrum salicaria</i>	Purple loosestrife
<i>Mentha piperita</i>	Peppermint
<i>Murdannia keisak</i>	Marsh dewflower
<i>Myosotis scorpioides</i>	Forget-me-not
<i>Myriophyllum aquaticum</i>	Parrot feather
<i>Myriophyllum spicatum</i>	Hybrid watermilfoil
<i>Najas minor</i>	Brittle waternymph
<i>Nelumbo nucifera</i>	Sacred lotus
<i>Nitellopsis obtusa</i>	Starry stonewort
<i>Nymphaeodes peltata</i>	Yellow floating-heart
<i>Oryza sativa</i>	Rice
<i>Panicum repens</i>	Torpedo grass
<i>Persicaria hydropiper</i>	Marshpepper knotweed
<i>Phalaris arundinacea</i>	Reed canarygrass
<i>Phragmites australis</i>	Common reed
<i>Pistia stratiotes</i>	Water lettuce
<i>Pontederia crassipes</i>	Common water-hyacinth
<i>Potamogeton crispus</i>	Curly-leaf pondweed
<i>Reynoutria japonica</i>	Japanese knotweed
<i>Rorippa sylvestris</i>	Keek

(Continues)

TABLE 2 (Continued)

Species ^a	English name
<i>Sagittaria montevidensis</i>	Giant arrowhead
<i>Salvinia minima</i>	Water spangles
<i>Salvinia molesta</i>	Giant salvinia
<i>Schoenoplectiella mucronata</i>	Bog bulrush
<i>Solanum dulcamara</i>	Bitter nightshade
<i>Spirodela punctata</i>	Dotted duckweed
<i>Symphotrichum subulatum</i>	Southeastern annual saltmarsh aster
<i>Trapa natans</i>	Water chestnut
<i>Typha angustifolia</i>	Narrow-leaved cattail
<i>Typha glauca</i>	White cattail
<i>Veronica anagallis-aquatica</i>	Water speedwell
<i>Zantedeschia aethiopica</i>	Calla lily
<i>Belonesox belizanus</i>	Pike killifish
<i>Bithynia tentaculata</i>	Mud bithynia/faucet snail
<i>Bythotrephes longimanus</i>	Spiny waterflea
<i>Carassius auratus</i>	Goldfish
<i>Channa argus</i>	Northern snakehead
<i>Cichlasoma bimaculatum</i>	Black acara
<i>Clarias batrachus</i>	Walking catfish
<i>Corbicula fluminea</i>	Asian clam
<i>Craspedacusta sowerbii</i>	Freshwater jellyfish
<i>Ctenopharyngodon idella</i>	Grass carp
<i>Cyprinus carpio</i>	Common carp
<i>Cyprinus rubrofuscus</i>	Koi
<i>Daphnia lumholtzi</i>	Waterflea sp.
<i>Dreissena polymorpha</i>	Zebra mussel
<i>Dreissena rostriformis</i>	Quagga mussel
<i>Hoplosternum littorale</i>	Brown hoplo
<i>Mayaheros urophthalmus</i>	Mayan cichlid
<i>Neogobius melanostomus</i>	Round goby
<i>Pomacea canaliculata</i>	Channeled applesnail

^aList includes plants (top; 54 species alphabetized by genus) and animals (bottom; 19 species alphabetized by genus) used in this study. Taxonomy follows the Global Biodiversity Information Facility taxonomic backbone (GBIF Secretariat, 2021).

climatch scores at species locations were significantly higher than BioLake scores for all species ($p < 0.01$). Climatch scores where present did not significantly differ between plants and animals using either BioClim ($p = 0.33$) or BioLake ($p = 0.24$). For a full lake model with all BioLake climate layers, mean climatch scores where present were lower than in the main BioLake model (5.74; refer to Supplemental results in Appendix S1).

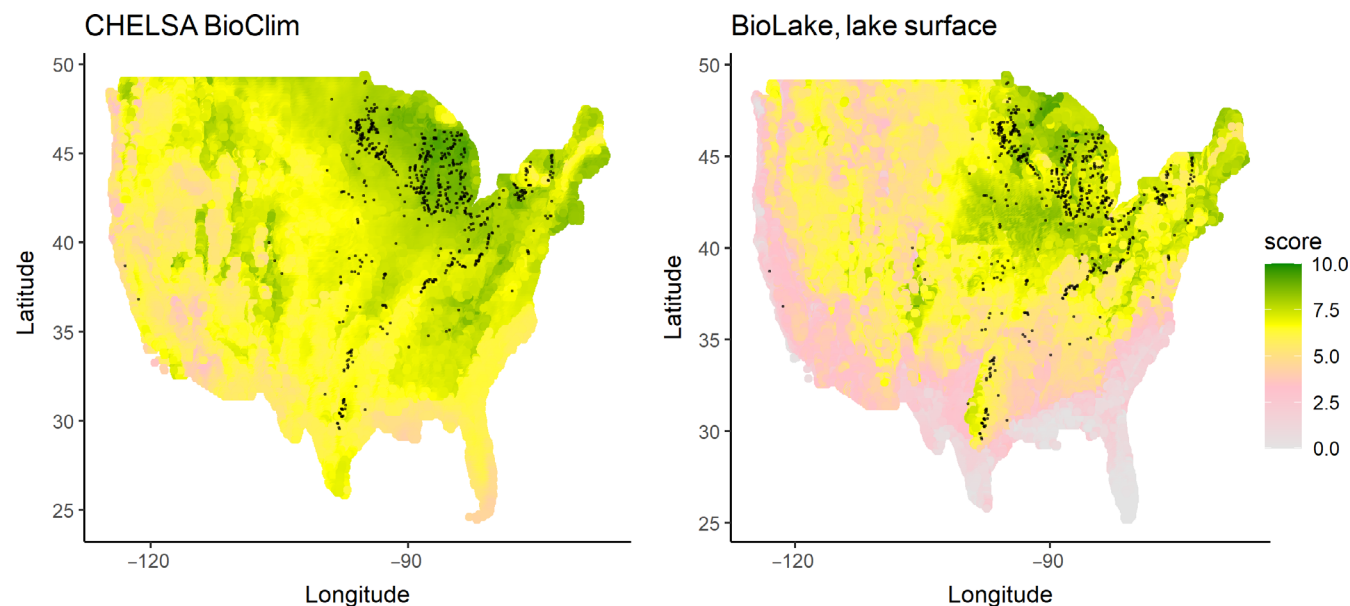


FIGURE 2 Known locations of *Dreissena polymorpha* (zebra mussel) and climatch scores in the United States, estimated based on records from this species' native range and other currently invaded regions. Higher scores indicate higher climate similarity. Climatch scores were estimated using the climatchR R package (Erickson et al., 2021) using air temperature-derived layers (left; BioClim; Karger et al., 2017) as well as lake water temperature-based layers (right; BioLake lake mixed [surface] layer; Burner & Erickson, 2022a). Analyses use an equal-area projection (Mollweide), but maps are plotted using latitude and longitude (WGS84). Species locations are from Global Biodiversity Information Facility (<https://www.gbif.org/>). CHELSA, Climatologies at high resolution for the earth's land surface areas.

The mean climatch score at known species locations was higher than in the null model for all but one species (98.6%) using BioClim and all but six species (91.8%) using BioLake (Figures 3 and 4; Appendix S1: Figure S3), indicating that each method has predictive value. Mean climatch scores exceeded the null expectation by 0.20–5.86 (95% CIs; mean = 1.429) for BioClim and –0.41 to 5.25 (95% CIs; mean = 1.431) for BioLake across species. This difference between climatch scores and the respective null expectations did not significantly differ between BioClim and BioLake ($p = 0.99$). Pearson correlation coefficients between BioClim and BioLake scores at species locations had a mean of 0.44 (95% CI: 0.13–0.76; Appendix S1: Figure S4). Models for both BioLake and BioClim performed best, as indicated by mean climatch units above null expectation where present, for a subset of those species that occurred outside the United States at low absolute latitudes and in fewer countries (Figure 5).

DISCUSSION

Climatch scores were relatively high at most locations occupied by many of our AIS, indicating that species spread primarily to areas with climate relatively similar to their native ranges and other invaded locations outside of

the United States and Canada. Yet the predictive power of climatch for assessing relative risk of sites within the United States was relatively low for many species, as indicated by our null model approach. BioClim-based models resulted in higher climatch scores where present for most species than did BioLake, but predictive power did not differ between the two sets of bioclimatic data layers.

Raw climate matching scores are often used to predict species invasions, with mixed success (Bomford et al., 2010; Bomford, Darbyshire, et al., 2009; Bomford, Kraus, et al., 2009; Elith, 2017; Howeth et al., 2016). However, another important consideration is how climatch scores at US sites occupied by a given species compared to US sites chosen at random. High climatch scores where a species is present may reflect strong predictive ability of the model, but alternatively may simply result from high estimates across the entire country, with the potential danger that models with inflated climatch scores are rewarded.

Our null model approach allowed us not only to quantify the mean score where present (as others have done) but also to test whether the algorithm was able to identify the sites at highest risk within the United States, a high priority for managers (Courtois et al., 2018; Hussner et al., 2017; Lodge et al., 2016). We found that BioClim- and BioLake-based climatch models each resulted in scores somewhat higher than the null

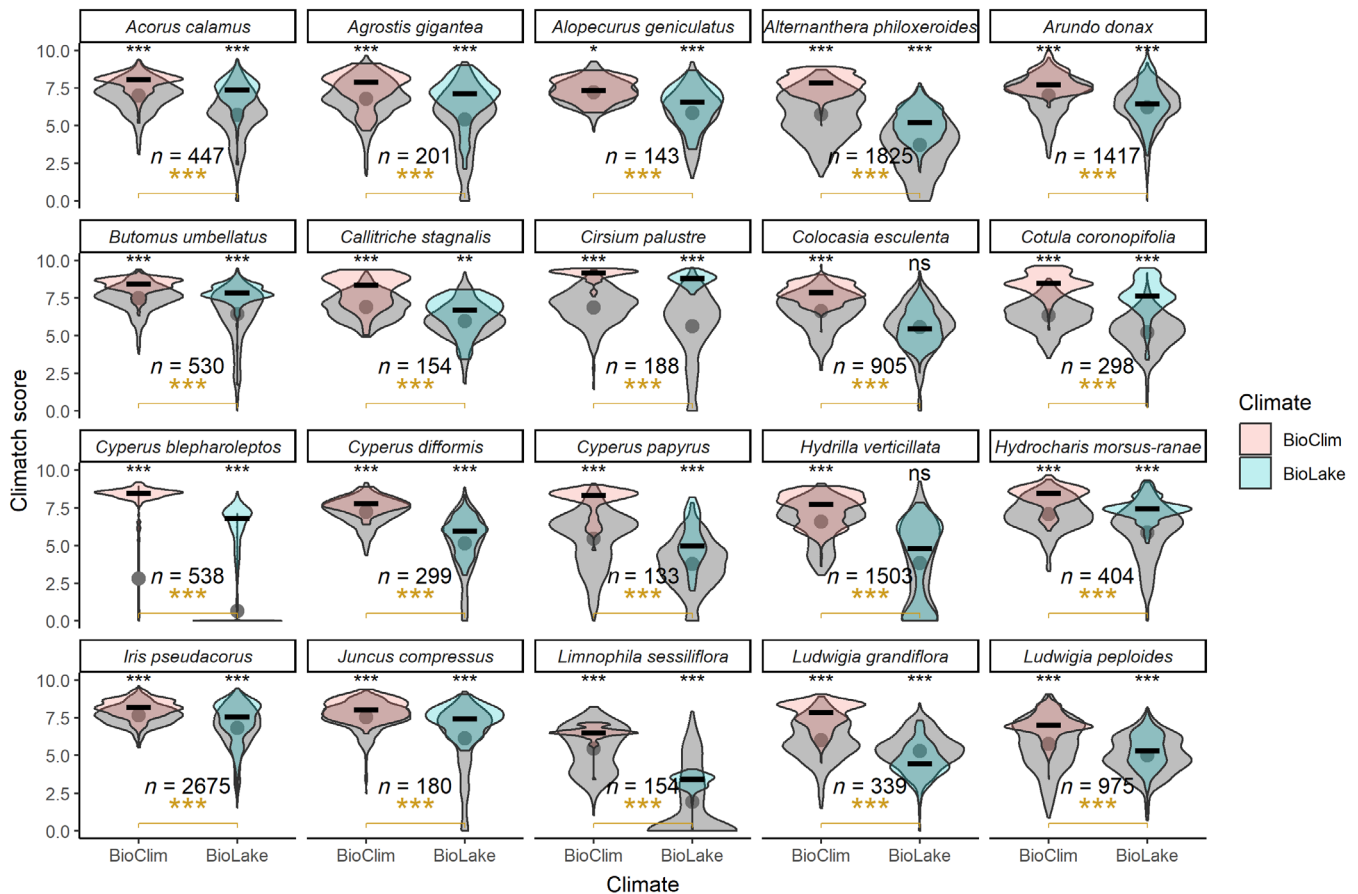


FIGURE 3 Climatch scores for known aquatic invasive plant species locations in the contiguous United States. Colored violins show the distribution of climatch scores where species are present based on air temperature (BioClim; Karger et al., 2017) and water temperature (BioLake; Burner & Erickson, 2022a); both scores also include precipitation layers from BioClim. Horizontal black bars show the median, and gray violins show the null distribution (with gray dots indicating mean) based on 500 randomly sampled points. Species names are shown in facet titles. For simplicity, plots show the first 20 plant species, alphabetized by genus. For the 34 remaining plant species, refer to Appendix S1: Figure S3. Species locations are from Global Biodiversity Information Facility (<https://www.gbif.org/>). Symbols above violins indicate significant differences between means of the true and null distributions (* $p \leq 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns, $p > 0.05$). Golden stars in the bottom center indicate differences in mean true climatch scores among the two climate data types. For animal species, refer to Figure 4.

expectation at known species locations (Figures 3 and 4; Appendix S1: Figure S3). Although climatch thus offered some predictive value, and in some species performed very strongly, species' prioritization would likely benefit from inclusion of other biotic and human factors as well, given the relatively weak predictive power of climatch for many species. This is in keeping with past findings that climatic similarity is often less important than human vectors, habitat suitability, species traits, and biotic interactions (Elith, 2017; Howeth et al., 2016; Hulme, 2017; Magarey et al., 2018; Marcot et al., 2019; Tuckett et al., 2021).

In addition to testing the predictive power of the climatch algorithm for AIS, we also asked how our BioLake lake temperature-derived bioclimatic layers performed relative to air temperature-derived BioClim

for AIS. At occupied sites, climatch scores for the two sets of layers were correlated for most species but were highly correlated (>0.75) for only three species, indicating differences in ranking of site risk among the two methods. These two sets of bioclimatic layers did not differ on average across species in how values at occupied sites differed from the null expectation (i.e., in their predictive value). However, for most species predicted scores were slightly lower for BioLake compared with BioClim, although mean score when present across species for BioLake (6.48) was still above the typically used threshold (6) for invasion risk (U.S. Fish and Wildlife Service, 2020). An alternative lake model, based on all BioLake layers (refer to Supplemental results in Appendix S1), had lower mean scores when present (mean = 5.74 across all species), which is below this threshold. This is not unexpected

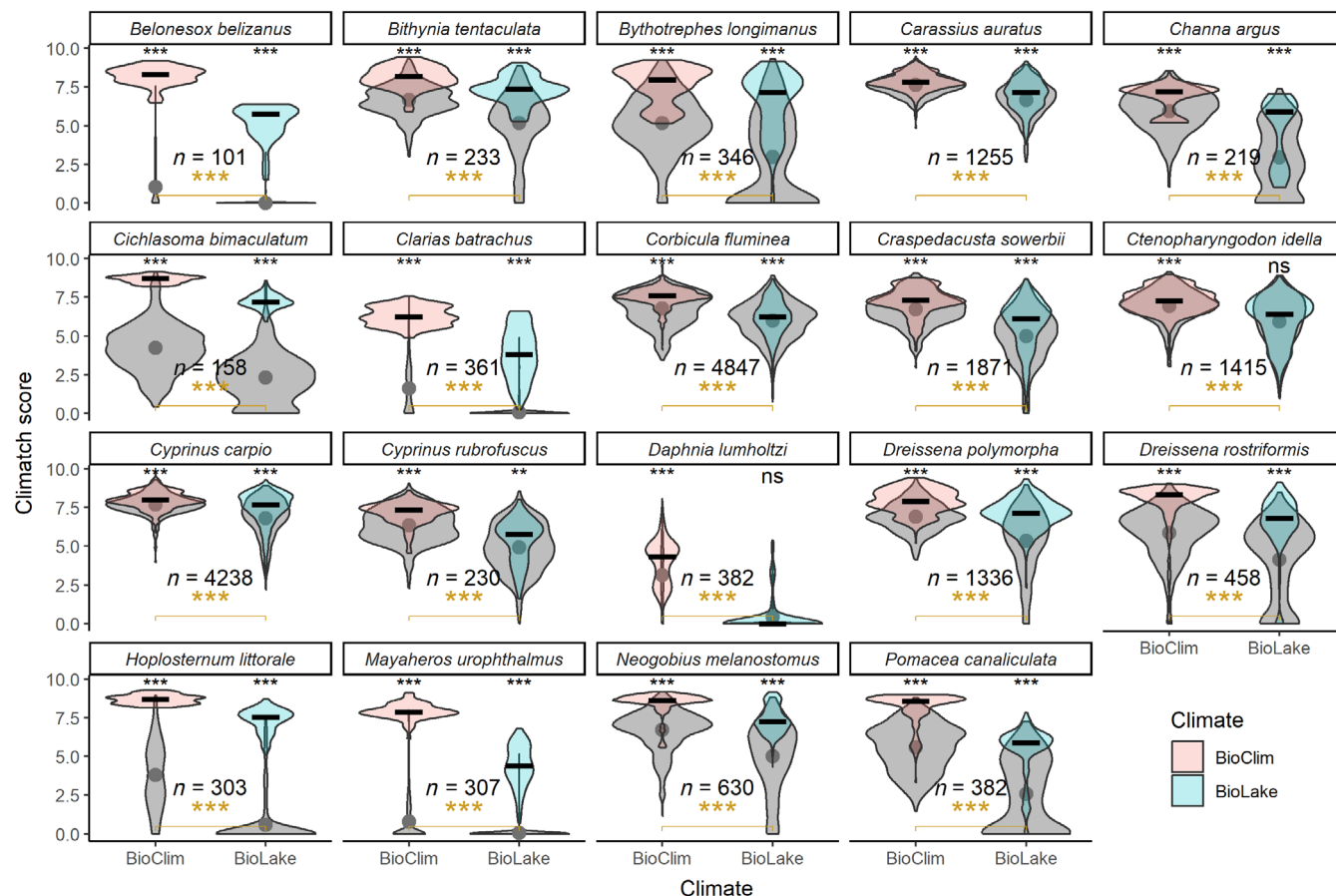


FIGURE 4 Climatch scores for known aquatic invasive animal species locations in the contiguous United States. Colored violins show the distribution of climatch scores where species are present based on air temperature (BioClim; Karger et al., 2017) and water temperature (BioLake; Burner & Erickson, 2022a); both scores also include precipitation layers from BioClim. Horizontal black bars show the median, and gray violins show the null distribution (with gray dots indicating mean) based on 500 randomly sampled points. Species names are shown in facet titles. Plots show all 19 animal species, alphabetized by genus. Species locations are from Global Biodiversity Information Facility (<https://www.gbif.org/>). Symbols above violins indicate significant differences between means of the true and null distributions ($*p \leq 0.05$; $**p < 0.01$; $***p < 0.001$; ns, $p > 0.05$). Golden stars in the bottom center indicate differences in mean true climatch scores among the two climate data types. For plant species, refer to Figure 3 and Appendix S1: Figure S3.

because additional climate layers capture more sources of variation and so present stricter criteria for climate matching. This is an important consideration for managers because standard climatch score thresholds for action may not be optimum for assessments that use varying numbers of input layers.

Intuitively, aquatic species are more directly exposed to water temperature than to air temperature, so we expected predictions based on lake temperature to perform better than air temperature, especially because air and water temperatures are not always strongly linked, such as near the surface of large lakes (Desai et al., 2009). The relatively coarse scale of ERA5-Land lake temperature estimates may obscure important differences due to, for example, lake size and topography (Deblauwe et al., 2016). If finer scale global water temperature estimates similar to those recently developed for parts of the

United States (Willard et al., 2022) become available, these may substantially improve predictions. Additionally, ERA5 lake temperature estimates may be biased for regions of the globe with few long-term water temperature datasets, given the global scale of the estimates and the model focus on atmospheric climate rather than water temperature. However, air temperature may be just as important in limiting distributions as water temperature for, for example, emergent plant species, as appears to be the case for mangroves (Cavanaugh et al., 2019; Stevens et al., 2006).

One challenge is that an ideal climate matching method would require that sampling covers the full extent of a species' range, a criterion rarely met outside of well-studied regions in North America and Europe, and that appropriate abiotic measures are considered (Jiménez-Valverde et al., 2011). Also, our null model method is best suited for species that have already

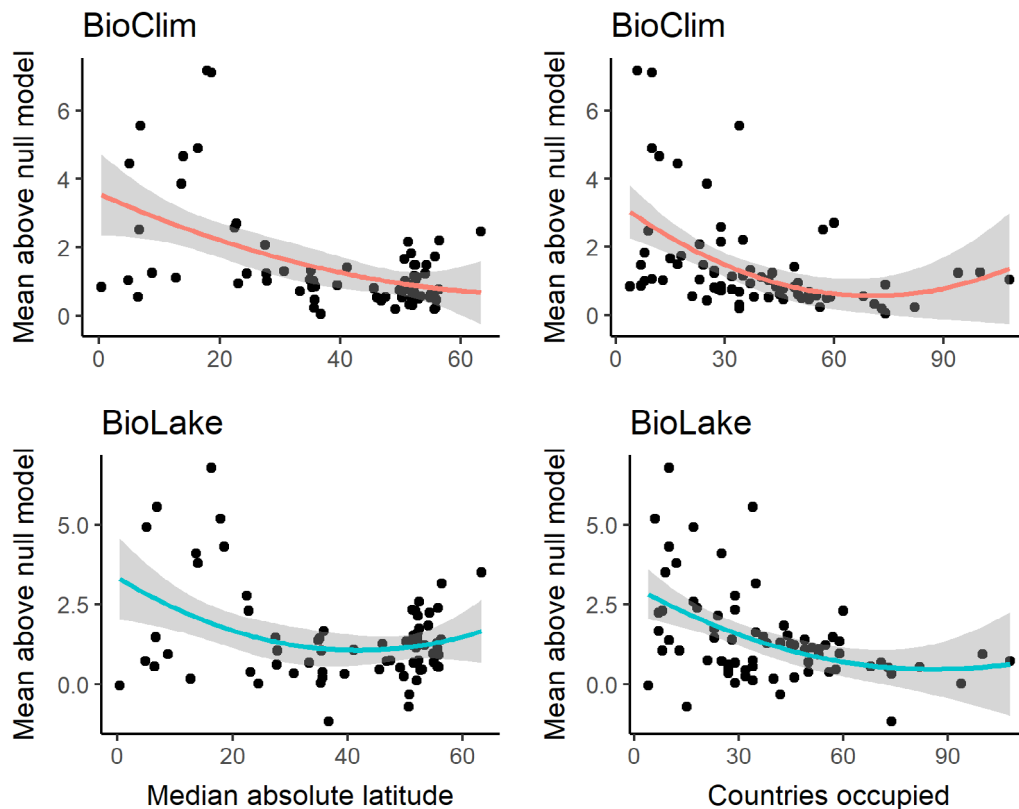


FIGURE 5 Difference between mean climatch score where species are present in the contiguous United States and the null climatch score expectation for each of 73 aquatic invasive species. Mean scores minus the null expectation are plotted against median absolute non-US latitude and total number of countries occupied for BioClim and BioLake climate layers. Mean latitude and total number of countries are based on Global Biodiversity Information Facility locations from outside the United States and Canada that were used to train climatch models. Each point represents one species, and lines show quadratic linear models with 95% CIs.

expanded across most of their suitable range in the United States. In some cases, species may be present only in certain sites or even regions not because they cannot inhabit others but merely because they have not had time to expand. We mitigated this to some extent by only choosing well-established invaders that occurred in more than 50 unique climate grid cells in the contiguous United States, but this effect may lower the apparent predictive value for some species.

Another challenge in relying on climate matching alone for predicting invasion risk is that it implicitly assumes that a species' current realized niche accurately reflects its fundamental niche (i.e., its abiotic tolerances) (Elith, 2017; Jackson & Overpeck, 2000). However, species' fundamental niches are often larger than realized niches (Soberón & Arroyo-Peña, 2017), meaning that species are often able to inhabit a wider range of abiotic conditions than indicated by their present ranges. This is likely due in part to release from biotic limitations such as competition, disease, or predation in new regions, and to plasticity that allows some species to take advantage of new areas when available (Soberón & Arroyo-Peña, 2017). Because we train our climatch models on all species locations outside the

United States and Canada, and thus include locations not only from species' native ranges but also from other currently invaded regions (Jiménez-Valverde et al., 2011), our results likely provide an overestimate of the ability of climate matching to predict invasion success for new invaders. If many species can invade sites with somewhat novel climates relative to their native ranges, as is implied by past work (Bujan et al., 2021; Elith, 2017; Soberón & Arroyo-Peña, 2017), then including invaded sites in climate matching algorithms will result in broader inferred climatic niches compared with native range sites alone, leading to higher climate match scores for a wider range of sites. Managers using climate matching can thus keep in mind that some species may prove much more adaptable than their native ranges would predict.

Alternatively, however, invasive species may have wider tolerances or higher plasticity than do species that do not readily become invasive (Gallagher et al., 2010; Higgins & Richardson, 2014). If this is the case, then asking how well climate matching performs for known invaders would underestimate how well it would work for potential future invaders because current AIS may represent a particularly adaptable or plastic subset of

species, or a subset of species with broad fundamental niches that are not revealed by their more restricted native ranges. Future work could test this hypothesis by comparing climatch scores of current AIS with scores for species that are known to have been introduced to the contiguous United States, but which did not become invasive (Ellender & Weyl, 2014; Komdeur & Hammers, 2014; Marchetti et al., 2004).

We found that climate matching performed best for a subset of those species that occurred primarily at low absolute latitudes outside of the United States (Figure 5) and that occurred in relatively few countries (a proxy for range size). This is likely because climatic differences within the United States are more extreme for tropical and subtropical (i.e., low latitude) species, and because some species with smaller non-US ranges are less tolerant of climatic variation. Howeth et al. (2016), for example, found that climate matching worked well to predict invasion success in the relatively harsh climate of the Great Lakes region. However, caution is warranted, even for low-latitude species, given the variability in predictive power for these species (Figure 5).

One limitation of our study is that we lack global river temperature estimates and so our focus was only on lakes and their associated AIS. Temperature dynamics of rivers differ from those of lakes, and some species excluded from lakes in a region may be able to inhabit rivers there (and vice versa). Our results are thus most useful for AIS that primarily occur in lakes, although expert knowledge-based determinations of primary habitat are also by nature somewhat subjective. We also restrict our study to a limited subset of AIS due to data availability, and some of our animal species are congeners (several fish, mussels), which may affect the generalizability of our results.

Understanding the extent to which climatic conditions can be used to predict species invasions in turn provides clues to the factors limiting these species. This is especially important for predicting invasion risk under future climate change (Foden et al., 2019; Hulme, 2017). If species are currently limited by climate, then climate change would likely result in important changes to species' invasion risk. For species that are less climate limited, climate change would likely have weaker direct effects, although indirect effects, via, for example, biotic interactions or habitat shifts, may likewise be important (Elith, 2017; Hulme, 2017). Hulme (2017) also notes, however, that many future range expansions of AIS may occur simply because those species have not yet spread into their entire habitable ranges, rather than because of climate change.

Precipitation, as well as temperature, may change under climate change, and this is also likely to be important for aquatic species (Hellmann et al., 2008).

For example, many fish species have spawning cues based upon hydrographic peaks due to flooding or other high water flow events (e.g., bigheaded carp [*Hypophthalmichthys nobilis*]; Lenaerts et al., 2021). Our results support the idea that climate plays a role in determining invasions, but also show that some species can persist outside of the climatic window indicated by their inhabited ranges in other regions, given the low climatch scores at some occupied US locations for some species (Figures 3 and 4). Predicting future invasions would be helped by more than an understanding of projected future climate, but these projections are nonetheless important, in part because the ecological effects of invasive species can be worse in areas where the climate matches their optimum (Iacarella et al., 2015), even if they can persist outside of that range.

Conclusions

Climate matching remains an important tool in the AIS risk assessment toolbox, but predictive power could likely be increased by combining climate with other predictors. Matching was most effective for some (but not all) species that originated at low latitudes or had small ranges. Differences between fundamental and realized niches and imprecision of lake temperature layers at small spatial scales likely limited predictive ability. Future research that clarifies links between species traits and fundamental niches could further improve model predictions (Pacifi et al., 2015; Van Kleunen et al., 2016). Our BioLake climate layers provide a global dataset for species distribution modeling of aquatic species that could be used in comparison to air temperature in future studies. Future modeling efforts could examine the use of finer scale lake and river temperature data in areas where they are available (e.g., contiguous United States; Willard et al., 2022) as a robust comparison of air versus lake temperature for AIS risk assessments.

AUTHOR CONTRIBUTIONS

Ryan C. Burner, Wesley M. Daniel, and Richard A. Erickson conceived the study. Wesley M. Daniel compiled the species list. Ryan C. Burner developed the methodology and analyzed the data. Ryan C. Burner and Peder S. Engelstad validated the code and data. Ryan C. Burner wrote the first manuscript draft. Ryan C. Burner, Wesley M. Daniel, Peder S. Engelstad, Christopher J. Churchill, and Richard A. Erickson edited the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Burner & Erickson, 2022a) are available from USGS ScienceBase-Catalog: <https://doi.org/10.5066/P96QLN5Y>. Code (Burner & Erickson, 2022b) is available from the USGS Code Archive: <https://doi.org/10.5066/P9X2XEZL>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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