Comparing models using air and water temperature to forecast an aquatic invasive species response to climate change

Jake R. Walsh [1,2,†] Gretchen J. A. Hansen,[2] Jordan S. Read,[3] and M. Jake Vander Zanden[1]

[1]Center for Limnology, University of Wisconsin – Madison, 680 N. Park Street, Madison, Wisconsin 53706 USA
[2]Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota – Twin Cities, 2003 Upper Buford Cir, St Paul, Minnesota 55108 USA
[3]U.S. Geological Survey, 8505 Research Way, Middleton, Wisconsin 53562 USA

Abstract. Understanding invasive species spread and projecting how distributions will respond to climate change is a central task for ecologists. Typically, current and projected air temperatures are used to forecast future distributions of invasive species based on climate matching in an ecological niche modeling approach. While this approach was originally developed for terrestrial species, it has also been widely applied to aquatic species even though aquatic species do not experience air temperatures directly. In the case of lakes, species respond to lake thermal regimes, which reflect the interaction of climate and lake attributes such as depth, size, and clarity. The result is that adjacent waterbodies can differ notably in thermal regime. Given these obvious limitations of modeling aquatic species distributions using climate data, we take advantage of recent advances in simulating lake thermal regimes to model the distributions of invasive spiny water flea (*Bythotrephes cederströmii*) for current and projected future climates in the upper Midwest of the USA. We compared predictions and future projections from models based on modeled air temperatures with models based on modeled water temperature. All models predicted that the number of suitable lakes in the region will decrease with climate change. Models based on air and water temperature differed dramatically in the extent of this decrease. The air temperature model predicted 89% of study lakes to be suitable, with suitability declining dramatically in the late century with climate warming to just a single suitable lake. Lake suitability predictions from the water temperature model declined to a much lesser degree with warming (42% of lakes were predicted to be suitable, declining to 19% in the late century) and were more spatially independent. Our results expose the limitations of using air temperatures to model habitat suitability for aquatic species, and our study further highlights the importance of understanding lake-specific responses to climate when assessing aquatic species responses to climate change. While we project a contraction in the potential range of *Bythotrephes* with warming in the study region, we anticipate that *Bythotrephes* will likely continue to expand into new lakes that will remain suitable in the following decades.

Key words: aquatic invasive species; *Bythotrephes cederströmii*; climate change; ecological niche modeling; lakes.

† E-mail: jransom.walsh@gmail.com

INTRODUCTION

Predicting the spread of invasive species as the climate changes is a fundamental challenge for ecology (Peterson and Vieglais 2001, Guisan and Thuiller 2005, Wiens et al. 2009, Elith et al. 2010). Such studies are often carried out at broad (regional to continental) spatial scales and use current and future climate to estimate suitable habitat for species (e.g., Hijmans et al. 2005, Hijmans and Graham 2006). Given that freshwater systems are particularly vulnerable to the impacts of invasive species (Moorhouse and Macdonald 2015), this ecological niche modeling approach has also been widely applied to assessing habitat suitability for and forecasting spread of aquatic invasive species (e.g., Sharma et al. 2007, Montecino et al. 2014, Culumber and Tobler 2018).

One obvious limitation of models based on air temperatures is that aquatic species do not experience air temperatures directly—they experience water temperatures. Water temperatures are influenced by climate, but the effect of climate is mediated by lake attributes such as lake surface area, depth, morphometry, and water clarity (Rose et al. 2016). Moreover, many lakes exhibit thermal stratification, meaning that near-surface temperature dynamics become decoupled from those of deeper waters. Lake thermal regime refers to how temperature varies in lakes with depth over time. While thermal regimes tend to vary along climate gradients (e.g., high-latitude lakes are on average colder than low-latitude lakes), adjacent lakes experiencing the same climate can differ notably in thermal regimes due to these lake-specific characteristics (Fee et al. 1996, Benson et al. 2000, Read and Rose 2013, O'Reilly et al. 2015, Rose et al. 2016). Lake warming in response to climate change also differs among lakes. As an example, large and deep ice-covered lakes are warming faster than air temperatures, contrasting with smaller and shallower lakes that track more closely with air temperatures (O'Reilly et al. 2015). As a result, the most rapidly warming lakes are distributed globally rather than co-located geographically in the locations with the most rapidly warming air temperatures (O'Reilly et al. 2015). This lake-to-lake variation in how lakes respond to a changing climate may have important implications for how aquatic species respond to climate change.

In light of the above, we would expect that the traditional climate-based approach to ecological niche modeling should be limited in utility for modeling aquatic invasive species distribution at fine spatial resolutions such as that of individual lakes. A recent study simulated lake thermal regimes for current conditions and under future climate change scenarios for thousands of lakes across the upper Midwest region of the USA (Winslow et al. 2017). Lake-specific thermal regimes estimated for many thousands of lakes provide an opportunity to develop ecological niche models based on the thermal environment experienced by organisms, in turn providing a more direct physiological connection to organisms of interest.

In this study, we develop ecological niche models in order to predict suitable habitat for spiny water flea (*Bythotrephes cederströmii*; Korovchinsky and Arnott 2019) under current and future climate scenarios. *Bythotrephes* is an invasive predatory zooplankter that has spread and had adverse ecological and economic impacts across lakes of central North America (Yan et al. 2011, Walsh et al. 2016a). The importance of thermal conditions has been well-documented for this species, which does not tolerate summer temperatures above 25°C (Garton et al. 1990, Yurista 1999, Kim and Yan 2010, Kerfoot et al. 2011). In this way, climate change may lead to a reduction in the number of *Bythotrephes* suitable sites in the region. In addition to traditional ecological niche models based on air temperatures, we also develop models based on modeled lake thermal regimes. Lake thermal regimes respond to climate warming in complex ways that do not necessarily follow clear latitudinal gradients (Winslow et al. 2017), and this heterogeneity may lead to similarly heterogeneous patterns in *Bythotrephes* suitability (Fig. 1).

METHODS

Approach and study region

We used an ecological niche modeling approach to compare lake suitability for *Bythotrephes* under historical and projected future conditions modeled using either air temperatures from downscaled climate models or water temperatures simulated in over 10,000 lakes in Minnesota, Wisconsin, and Michigan. This region

1 | Using climate as a proxy for habitat temperatures

Climate informs regional understanding of aquatic species suitability

Climate

Lake thermal regime informs local-scale understanding of aquatic species suitability

2 | Accounting for habitat-specific temperature variation
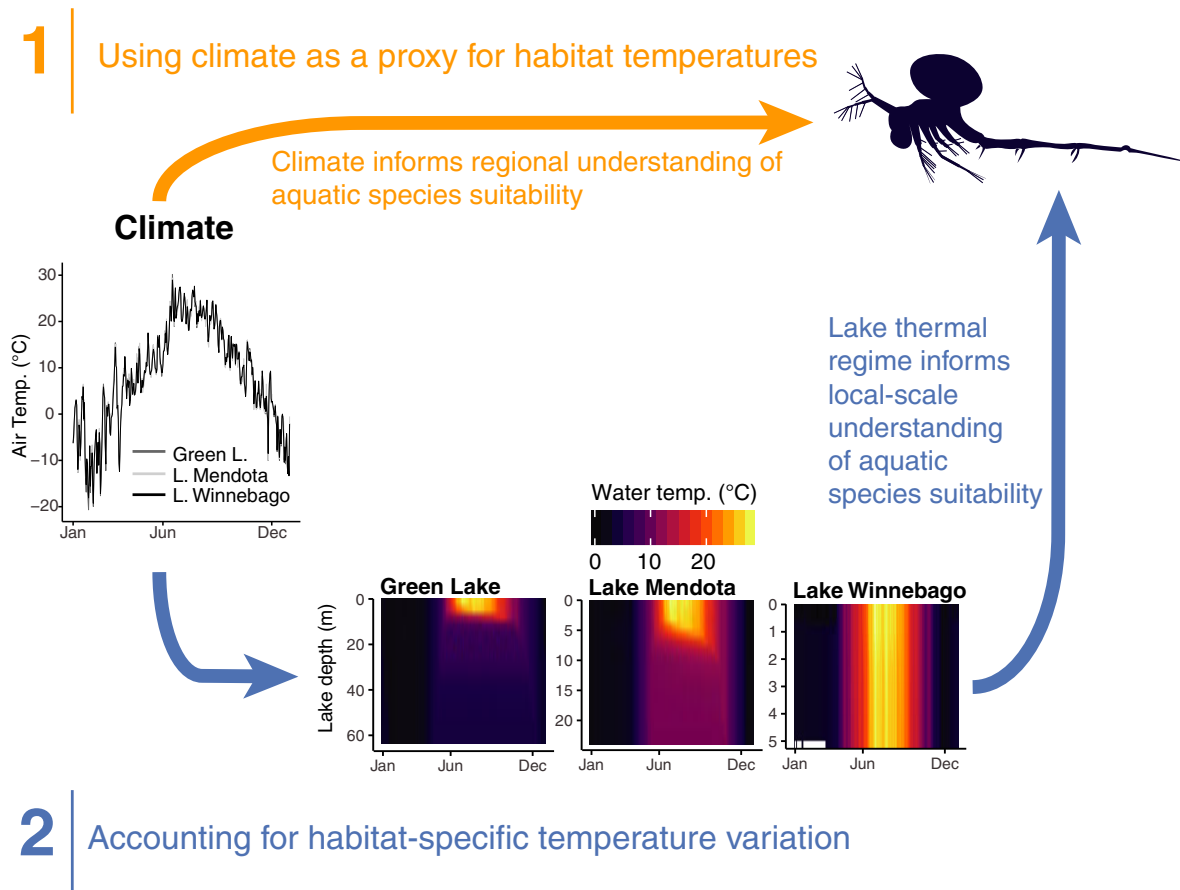
Fig. 1. Aquatic species ecological niche modeling is traditionally conducted using air temperatures and global climate models as proxies for lake temperature (1). However, lakes vary widely in their response to climate. As an example, we plot the thermal profiles (how temperature varies by depth over time) of three lakes in central and south-central Wisconsin with nearly identical air temperatures (Climate) that differ in their thermal regime (thermal profile heat maps with an inverted *y*-axis to represent water depth in the lake, warmer colors indicate warmer temperatures). Example data are from modeled lake temperatures and downscaled air temperatures in the year 2000. The differences between climate and thermal regime have important implications for understanding the ecological niche of aquatic organisms (2).

spans the western edge of *Bythotrephes* invaded range, including lakes that are likely suitable for *Bythotrephes* establishment (i.e., deep, clear, and cool lakes located near the Great Lakes; MacIsaac et al. 2000, Branstrator et al. 2006) both within and outside its current geographical range.

Study species and occurrence data

Bythotrephes is a cool-water species and is sensitive to changes in lake temperature and the effects of climate change (Kerfoot et al. 2011, Walsh et al. 2016*b*). *Bythotrephes* habitat suitability at the western edge of its range is thought to

be constrained primarily by water temperature (Kerfoot et al. 2011), as exposure to the warm temperatures reached in many of these lakes (Winslow et al. 2017) can lead to reproductive failure (>25°C; Garton et al. 1990, Yurista 1999) and growth rate declines (>20°C; Yurista 1992, Kim and Yan 2010).

We compiled *Bythotrephes* occurrence data from the USGS Nonindigenous Aquatic Species database, the Minnesota and Wisconsin Departments of Natural Resources (Minnesota Department of Natural Resources 2018, U.S. Geological Survey 2018, Wisconsin Department of Natural

Resources 2018), and existing literature (Branstrator et al. 2006, Kerfoot et al. 2011). *Bythotrephes* detection programs (e.g., conducted by MN and WI DNR either during routine monitoring or in response to reports of potential new detections) are conducted using horizontal zooplankton tows (~100 m in duration using a relatively large, ~50 cm in diameter, and coarse, >100-μm net) that sample large amounts of water to increase detection rates (Walsh et al. 2018). We included multiple recent discoveries of *Bythotrephes* in the USA over the past decade for a total of 40 inland lake occurrences in the study region that also have modeled lake temperatures.

Water and air temperature data

We used air and water temperatures modeled from downscaled climate models (Winslow et al. 2017). Winslow et al. (2017) used global climate models (GCM) downscaled to a 25-km horizontal grid and a daily output to drive mechanistic lake models to predict present and future water temperatures (Notaro et al. 2015). We used the water temperature predictions from these lake models for our water temperature niche models and the downscaled GCM air temperatures for our air temperature niche models. Future conditions were projected under the RCP8.5 emissions scenario using six global climate models (see Appendix S1: Table S1 for descriptions of the GCM codes used here; Winslow et al. 2017). Water temperatures for 10,774 lakes in the study region were modeled as daily depth profiles (this subset includes only lakes from the USGS National Hydrography Dataset with observed depth measurements or hypsometry) using a one-dimensional lake hydrodynamic model that uses lake-specific attributes (e.g., clarity, morphology, and surrounding land cover) and meteorological conditions (e.g., air temperatures, precipitation, and wind; General Lake Model; Hipsey et al. 2019). While data are generated as raw daily thermal profiles (with an RMSE for individual epilimnetic temperature observations of 1.9°C), they can be summarized by different depths and time periods (e.g., period, season, or year) as well as common limnological variables that describe thermal properties (e.g., stratification strength or duration). For each summary variable (e.g., annual mean surface temperatures in July), we calculated the long-term means from the backcasted modeled data (1982–2000) for model training and contemporary model projection, and from forecasted modeled data for model projection in the mid-century ("2050"; 2041–2059) and late-century ("2090"; 2081–2099) time periods.

In both the water and air model approaches, we selected a priori thermal variables that are likely to be tied to *Bythotrephes* biology while also weakly correlated with one another (Pearson's $r^2 < 0.5$; Papeş et al. 2016). We used air or water temperature degree days over 20°C as a measure of summer heat stress (Yurista 1992, Kim and Yan 2010) and fall temperatures (mean surface water temperatures and air temperatures in October; r^2[summer, fall] = 0.26), as fall is important for *Bythotrephes* resting egg production and overwintering success (Herzig 1985, Walsh et al. 2016b). Finally, we included a lake-specific variable, maximum lake depth (m, $\log_{10}$ transformed), to reflect vertical habitat available to *Bythotrephes* in lakes as the species is primarily pelagic (found in the open water of lakes) and can migrate vertically in the water column to avoid stressful surface water conditions (e.g., heat stress; Young and Yan 2008). Notably, lake depth (and other lake-specific variables such as water clarity or lake area) also plays an important role in driving lake-to-lake variation in surface water temperatures (Toffolon et al. 2014). Log-transformed lake depth is weakly correlated with mean October surface water temperatures (r^2[fall, depth] = 0.40, r^2[summer, depth] = 0.02), possibly reflecting milder temperature conditions in larger, deeper lakes that are cooler in summer but also cool more slowly in fall relative to smaller, shallower lakes (Toffolon et al. 2014).

Ecological niche modeling

We used the machine learning maximum entropy algorithm, Maxent, to construct the niche models (Phillips et al. 2006) and developed the models using the package maxnet in R (note the alternate spelling of the package name; Phillips 2017). The maxnet package fits environmental data to occurrence data using lasso regularization of generalized linear models to generate the Maxent probability distribution that can be used to describe site suitability for a species. Maxent is particularly useful for niche modeling with presence-only data and allows for

estimating non-linear effects of predictor variables (Phillips et al. 2006). To avoid model overfitting for projection under future scenarios, we increased Maxent's regularization multiplier from a default value of 1–2, reducing (but not eliminating) the non-linearity allowed in the effects of predictor variables (Peterson et al. 2008).

Model evaluation

Invading species represent a particularly challenging case for niche modeling as species actively expand their geographical distribution into regions with many suitable, but unreached sites (Jiménez-Valverde et al. 2011). Selecting variables that are a direct representation of environmental characteristics that influence species physiology (e.g., heat stress) prior to modeling, as we do here, can help address this challenge (Jiménez-Valverde et al. 2011). Also, many studies characterize the ecological niche of invading species in a presence-only framework where suitability score thresholds for predicted presence are selected to ensure a high degree of model sensitivity (correctly predicting species presence), possibly at the cost of allowing more false presences (Peterson et al. 2008, Papeş et al. 2016). In this framework, false presences do not represent prediction errors but rather those lakes that may be habitable ecologically but have yet to be reached by the species (Peterson et al. 2008, Papeş et al. 2016). Model outputs in a presence-only framework can be evaluated using a modified receiver operating characteristic (ROC) analysis that focuses on evaluating model performance at high sensitivity (the ROC range of interest for invading species; see more details for generating the modified ROC ratio in Supplementary Information; Peterson et al. 2008). Briefly, models are evaluated using the ratio of the area under the test curve with a predefined maximum omission rate (E; here E = 5% or 2 of 40 occurrences) to the area under a 1:1 line representing the null expectation. Since the x-axis in this framework is modified to the proportion of lakes predicted present (rather than the false-positive rate, as in traditional ROC analysis), optimal models are defined as those that best balance model sensitivity and overprediction at a low omission rate. A modified ROC ratio near one indicates more potential for overprediction (e.g.,

a model predicting every lake as suitable would have a sensitivity of 1 but a modified ROC ratio of 1).

We compared spatial autocorrelation of predicted *Bythotrephes* occurrence from models developed using air and water temperatures. Higher spatial autocorrelation likely indicates a strong effect of broadscale climate patterns on niche predictions, and lower autocorrelation would highlight the importance of lake-specific variables in niche predictions. We used Moran's I to compare spatial autocorrelation of predictions from both models (both in terms of the raw Maxent suitability score and in terms of binary predicted presence using a suitability score threshold that accurately predicts 95% of known presences).

While we present model results and projections using models fitted with all lakes, we also evaluated each model's predictive ability by withholding 10% of lakes from model fitting for testing, then training models with the remaining lakes over 1000 random iterations for each of the four model formulations (air vs. water temperatures with and without lake depth). We evaluated predictor variable importance by removing each variable from the model and measuring model performance using the modified ROC ratio (i.e., jackknifing).

RESULTS

Model fitting

Generally, *Bythotrephes* is found in lakes that are relatively deep, warm in fall, and cool in summer (Fig. 2a). Both niche models—models fit using downscaled air temperatures (air models) and those fit using modeled surface water temperatures (water models)—reveal a negative effect of summer heat stress (degree days >20°C) and positive effect of lake depth ($\log_{10}$ maximum depth in m) on *Bythotrephes* suitability (Fig. 2b–g). However, the models differed in the effect of fall temperatures (mean surface water or air temperatures in °C in October) on suitability. Fall surface water temperatures had a weak positive effect on *Bythotrephes* suitability in the water models, but fall air temperatures did not affect suitability in the air models. Variable effects remained consistent when modeling with and without lake depth, except for the effect of fall
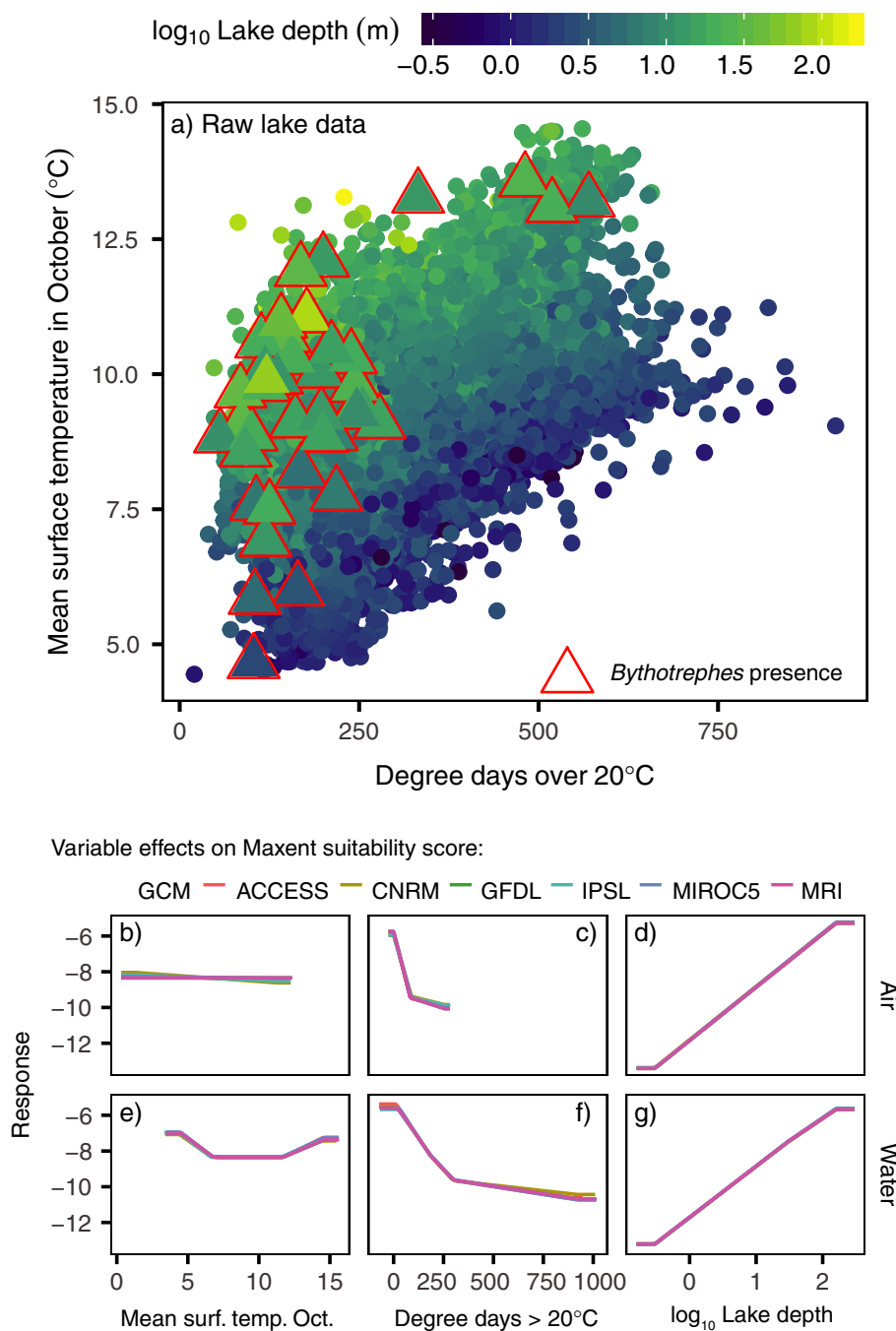
Fig. 2. Raw modeled lake temperature data are plotted in a: Lakes are plotted as filled circles colored by lake depth according to the key. *Bythotrephes* known presences are highlighted as larger triangles outlined in red. Variable effects (*x*-axes) on suitability (*y*-axes) are plotted for the air (b–d) and water (e–g). Colored lines represent suitability models fit using one of the six different climate models (colored according to key; see Appendix S1: Table. S1 for GCM identification details) used to generate modeled air and water temperatures.

surface water temperatures. Fall surface water temperatures positively affected suitability when modeling without lake depth (Appendix S1: Fig. S2), but this effect was u-shaped when modeling with lake depth (minimum suitability between 6° and 12°C; Fig. 2e). Fall air temperatures negatively affected suitability when modeling without lake depth (Appendix S1: Fig. S2) and did not affect suitability when modeling with lake depth (Fig. 2b). Since there was little variation in models fitted from different GCM projections (Fig. 2b–g), we averaged maxent suitability scores across the models fit using the six different GCM air and water temperature projections to evaluate air and water model predictions and fit.

Cross-validation results

Because we were more interested in correctly predicting presences (i.e., high model sensitivity) for the case of an invading species, we used a modified AUC ratio to evaluate model predictive ability with cross-validation (Appendix S1: Fig. S3; Table 1). By the modified AUC ratio, all models performed well (ratio $\gg 1$, where 1 indicates a model that overpredicts all lakes as suitable while correctly predicting 95% of known presences). The air model resulted in the lowest modified AUC ratio, but the improvement in the

Table 1. Comparison of the air and water model formulations.

Evaluation metric	Model formulation	Air	Water
Modified AUC ratio	Summer + Fall + Depth	1.97 (0.05)	1.97 (0.06)
	Fall + Depth	1.96 (0.06)	1.96 (0.06)
	Summer + Depth	1.96 (0.06)	1.96 (0.06)
	Summer + Fall	1.80 (0.21)	1.95 (0.08)
True-positive rate	Summer + Fall	0.99 (0.04)	0.99 (0.04)
	Summer + Fall + Depth	0.98 (0.06)	0.96 (0.10)
	Fall + Depth	0.98 (0.07)	0.98 (0.08)
	Summer + Depth	0.98 (0.07)	0.98 (0.07)

Note: Air and water model formulations compared (summer = degree days >20°C, fall = mean surface water temperatures or mean air temperatures in October in °C, depth = $\log_{10}$ lake depth in m) by calculating a modified AUC ratio (where a ratio near 1 indicates a model that predicts all lakes as present; Peterson et al. 2008) and the true-positive rate (proportion of out-of-sample occurrences accurately predicted by the model) over 1000 cross-validation simulations (mean with standard deviation in parentheses) where we withheld 10% of the data for evaluating model predictions.

ratio from the air to the water temperature model was variable over all cross-validations (mean(ratio$_{water}$ − ratio$_{air}$) = +0.14, SD = 0.22, p (0) = 0.22; Table 1). Also, all models predicted out-of-sample presences at an extremely high rate (>0.95; Table 1), likely reflecting thresholds selected to produce modes with high sensitivity (E = 5%).

Lake depth was the most important variable for improving model performance, and models that included either summer or fall temperatures and lake depth outperformed models that included both summer and fall temperatures without lake depth (Table 1). To contrast air and water models, we compared the air and water models (with both summer and fall temperatures) with and without lake depth.

Model projections

We projected and compared model outputs using final models fit from all known occurrences. When modeling with downscaled air temperatures alone under contemporary climate conditions, geographical patterns in *Bythotrephes* suitability followed closely with patterns in climate (Fig. 3a) with high spatial autocorrelation (Moran's I of the raw suitability score = 0.40; Table 2). The air model contrasted with suitability patterns from the water model which were more spatially independent (Fig. 3c; Moran's I of the raw suitability score = 0.20; Table 2). The air model predicted 89% of lakes to be suitable under contemporary conditions (Maxent suitability score at least as high as the 5th percentile of known presences), again differing from the water model which predicted 42% contemporary suitability. Adding lake depth to the niche models decreased spatial autocorrelation in both models (Table 2), leading to more spatially independent predictions of suitability (Fig. 3b, d), and more comparable predictions of suitability (39% of lakes suitable with the air model compared to 30% suitable with the water model).

Bythotrephes suitability declined under the mid- and late-century climate scenarios leading to fewer suitable lakes in the study region with both air and water models. However, the magnitude of the decline varied considerably between modeling approaches (Fig. 4). The air models, which predicted nearly all lakes to be suitable under contemporary conditions,
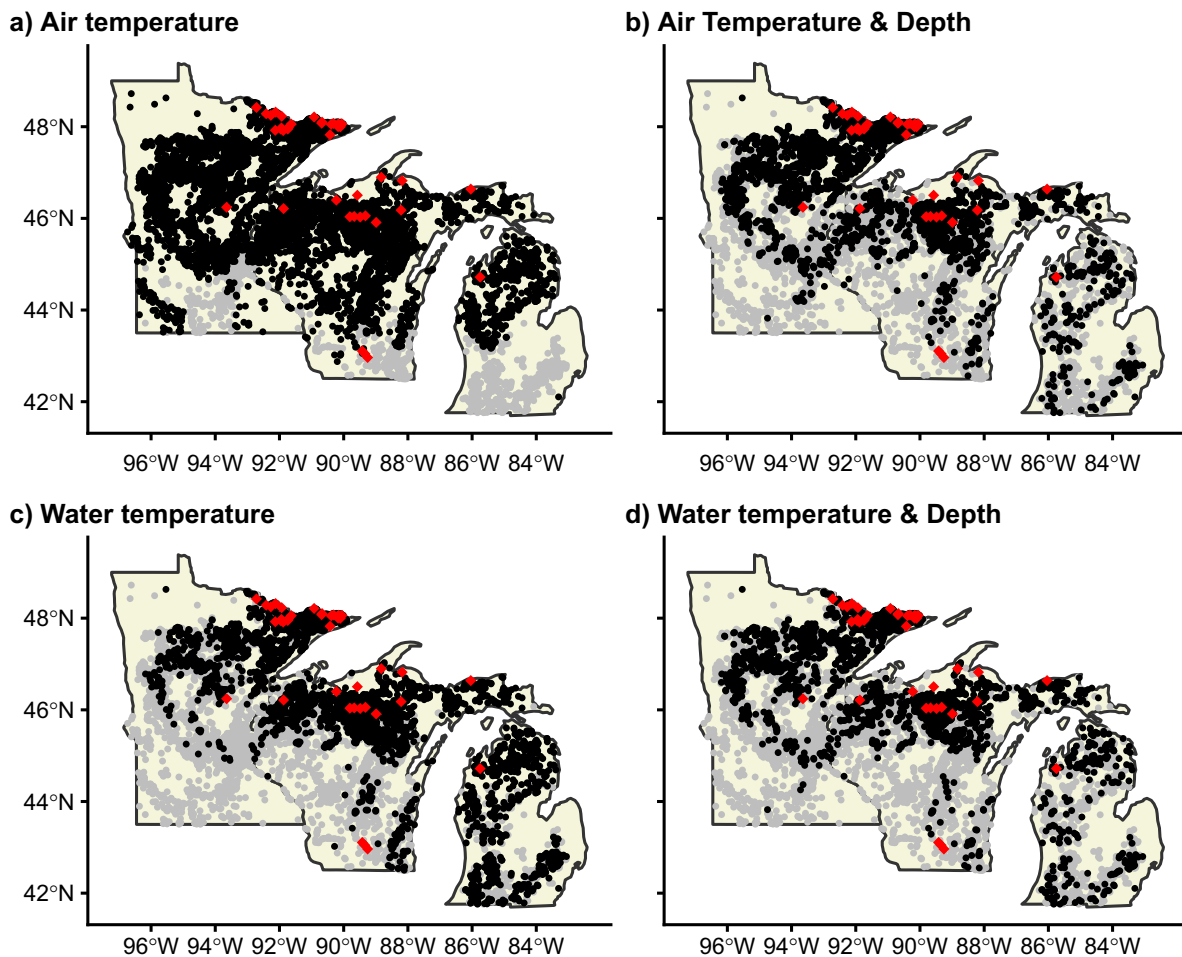
Fig. 3. Prediction map under contemporary conditions for each of the four niche models. Predicted presences are in black, predicted absences are in grey, and observed presences are in red diamonds in each panel.

Table 2. Moran's *I* values of spatial autocorrelation in the air and water model predictions of lake suitability for *Bythotrephes*.

Model output	Model formulation	Air	Water
Raw suitability score	Without lake depth	0.40	0.20
	With lake depth	0.19	0.15
Binary prediction	Without lake depth	0.26	0.15
	With lake depth	0.13	0.10

Notes: Higher values of Moran's *I* indicate higher spatial autocorrelation. Models are compared with and without lake maximum depth, and suitability is represented as the raw suitability score output from the Maxent algorithm and binary prediction as present or absent based on a threshold score. All *I* values are highly significant ($P \ll 0.001$, calculated by comparing *I* to 1000 random permutations of each score or prediction using the same spatial weighting scheme; Cliff and Ord 1981), suggesting some degree of spatial autocorrelation in each case.

predicted just a single suitable lake in the late century scenario, compared to 19% future suitability with the water model. Suitability differences declined with lake depth added to the models, but suitability was still almost twice as high in the water model (16% compared to 8.8% in the air model).

Model predictions and projections were sensitive to the suitability score threshold selected for predicted presences (here, a maximum omission rate of 5%). However, the general patterns in contrasting the air and water models are consistent across a range of model thresholds (see Appendix S1: Fig. S4 for tests ranging the maximum omission rate from 0% to 10%, or 0 to 4 false negatives, respectively).
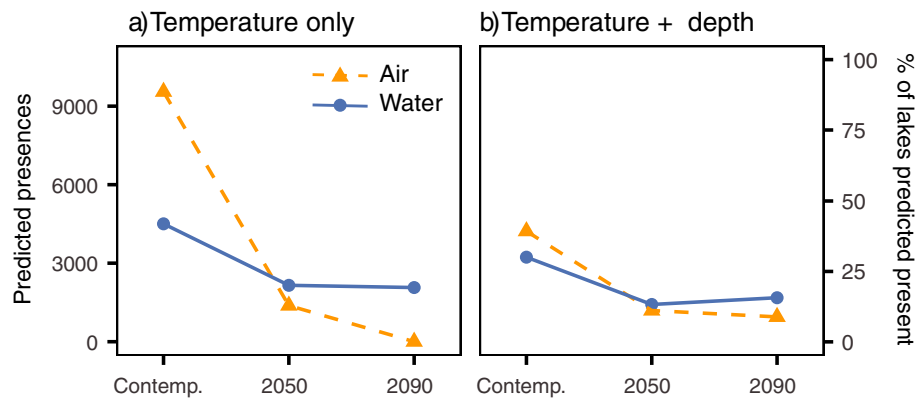
Fig. 4. Model predictions (number and percent of 10,774 study lakes predicted as suitable for *Bythotrephes*) are plotted under contemporary and future (mid-century, 2050, and late-century, 2090) climate conditions. Air temperature model predictions are plotted in dashed orange lines and triangles, while water model predictions are plotted in blue circles and solid lines. The models were fitted with temperature variables alone (a) and with temperature variables and lake depth (b).

Discussion

We contrasted two niche modeling approaches for an aquatic invasive species: (1) modeling using air temperatures projected from downscaled climate models and (2) modeling using an estimate of water temperatures from mechanistic models driven by the downscaled air temperatures and other meteorological variables (i.e., long and shortwave radiation, air temperature, wind speed, relative humidity, rainfall, and snowfall; Hipsey et al. 2019). Because we forced models to have high sensitivity (sensu Peterson et al. 2008, Papeş et al. 2016), by definition all models accurately predict known presences out-of-sample. However, each approach produced very different pictures of *Bythotrephes* suitability in our study region (i.e., differing potential for overprediction; Peterson et al. 2008). All models predict the number of suitable sites in the study region, the western edge of *Bythotrephes* invaded range, to decline with climate change. Declining suitability contrasts with more common reports of aquatic invasive species range expansion with warming (Rahel and Olden 2008). The air model predicted the vast majority of lakes as suitable under contemporary conditions and just a single lake as suitable under late century conditions, and suitability was spatially autocorrelated, reflecting broad patterns in climate. The water model predicted 42% contemporary suitability

which declined to 19% under late century conditions, and suitable lakes were more independently distributed in the study region, reflecting lake-specific thermal regimes. The water temperature and lake depth model predicted that 30% of our study lakes are suitable under present-day conditions, declining to 16% of lakes under future conditions (26 of 40 known presences and 1654 of 10,734 background lakes). As in the predictions under contemporary conditions, these suitable lakes are distributed across the study region (Fig. 5).

Both air and water temperature models accurately predict current distribution of *Bythotrephes* but predict dramatically different future conditions. The different projections resulting from using air or water temperatures highlight important nuances in thermal habitats that are only captured in the water models. For example, if temperatures exceeding 20°C are a physiological limitation for *Bythotrephes* growth and reproduction (Yurista 1992, Kim and Yan 2010) that has limited its current distribution within its invaded range (Kerfoot et al. 2011), we can illustrate the distinction between using air temperatures and water temperature using a simpler model: the number of lakes that are at least as cool as the warmest lake with a population of *Bythotrephes*. For example, 2012 lakes are predicted to have fewer degree days >20°C than the warmest known *Bythotrephes* occurrence (coincidentally,

a) Always suitable

b) Unsuitable to suitable

c) Always unsuitable

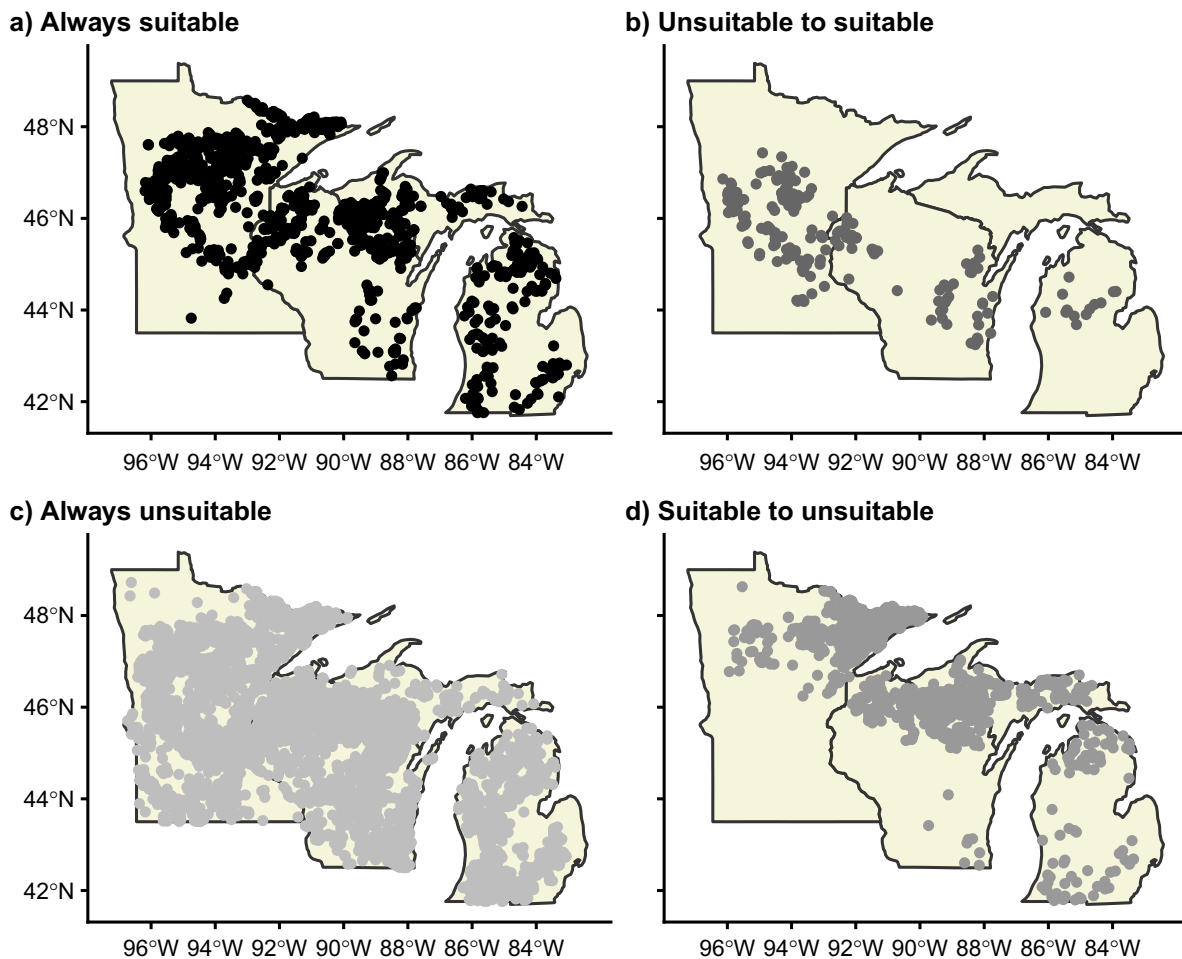**d) Suitable to unsuitable**

Fig. 5. Late-century model (water temperature and lake depth as predictors of suitability) predictions of suitability broken into four categories: lakes predicted as suitable under both contemporary and late-century climate conditions (a), lakes predicted as unsuitable under contemporary conditions but suitable under late-century conditions (b), lakes predicted as unsuitable under both contemporary and late-century conditions (c), and lakes predicted as suitable under contemporary conditions but unsuitable under late-century conditions (d).

19%); however, just one lake is predicted to experience fewer degree days >20°C using air temperatures (also the same as the model prediction). These large differences further highlight the importance of understanding heterogeneous ecosystem responses to climate in order to understand species responses to climate change (Levin 1992, Kearney and Porter 2009, Dobrowski 2011, Nadeau et al. 2017), particularly for aquatic organisms that do not experience air temperatures directly.

Lakes that were deep, relatively cool in summer, and warm in fall were more suitable for

Bythotrephes (Fig. 2). Four extremely warm lakes (250 degree days >20°C and surface temperatures in October exceeding 12°C; Fig. 2a) shaped *Bythotrephes* fall temperature response curves, where the air and water models differed most significantly (Fig. 2b, e). These lakes are distributed across the study region, located in both Wisconsin (the Madison chain of lakes; Lake Mendota, Lake Monona, Lake Waubesa, and Lake Kegonsa; note that Monona and Waubesa are one water body in the medium resolution National Hydrography dataset) and Minnesota (Mille Lacs Lake). Both the air and the water

models predicted suitability in Lake Kegonsa to be below the threshold for suitability, while the air model also predicted suitability in Lakes Monona and Waubesa to be below the threshold.

Bythotrephes populations in these four lakes share similar seasonal and long-term population dynamics that, in the context of our results here, might inform our understanding of *Bythotrephes* response to climate change. In each of these lakes, population densities plummet in mid-summer as surface water temperatures warm to exceed *Bythotrephes* thermal optimum in late July and early August, and recover to high densities in fall as temperatures cool (Jodie Hirsch, MNDNR, *personal communication*; Walsh et al. 2016*b*, 2019). These lakes were previously believed to be thermally unsuitable for *Bytho-trephes* (Kerfoot et al. 2011), but may now represent an important thermal regime characterized by hot, unfavorable summers paired with warmer or longer favorable fall conditions that allow *Bythotrephes* to persist in otherwise unfavorable climates (e.g., southwestern lakes in Fig. 5a and most lakes in Fig. 5b). Similarly, in a previous study (Walsh et al. 2016*b*), we used temperature-dependent population models to demonstrate how unusually cool conditions in the summer of 2009 may have led to *Bythotrephes* outbreak in Lake Mendota. At the time, we hypothesized that a pattern of outbreak under favorable conditions may provide rationale for the timing of *Bythotrephes* detection in Mille Lacs Lake, also in 2009 (Appendix S1: Fig. S5). In short, we found that Lake Mendota demonstrates the potential for climate stochasticity to drive temporary changes in suitability that lead to abrupt and persistent changes in invasive populations. While climate change is underpinned by long-term gradual change, abrupt ecological changes are increasingly common and understanding them depends on detailed ecosystem-specific understanding (Ratajczak et al. 2018).

Our results suggest that lake depth will be a critical factor influencing *Bythotrephes* response to lake warming in the study region, which may reflect broader patterns in cool-water species responses to climate change. In addition to our modeling results here, *Bythotrephes* is typically found in deep lakes in its invaded (Branstrator et al. 2006) and native (MacIsaac et al. 2000) ranges. Lake depth plays an important role in providing moderate summer and fall conditions—relatively large, deep lakes tend to be cooler in summer and warmer in fall (Toffolon et al. 2014). The effect of lake depth on surface water temperatures is consistent with the effect of surface water temperatures on *Bythotrephes* suitability (cooler summers and warmer fall surface temperatures are associated with higher suitability). As a result, in addition to providing cooler deep-water habitat, more moderate surface water temperature conditions in deeper lakes may lessen the effect of climate change on cool-water aquatic species and serve as refuge habitats in otherwise unsuitable regions. The importance of lake depth as vertical habitat for *Bythotrephes* has been described in detail in the case of the deep, cool, alpine Lago Maggiore. Warming in Lago Maggiore likely resulted in increases in *Bythotrephes* abundance due to the emergence of a low-light, warm-water refuge from predation as the top of the hypolimnion deepened in the lake (Manca and DeMott 2009). So, while lake warming may have obvious negative effects on *Bythotrephes* suitability in shallow lakes in our study region, responses may be more nuanced in larger, deeper lakes as a result of changes in vertical temperature profiles (as in Lago Maggiore) or late season surface temperatures (here).

Despite our prediction of a reduction in the number of lakes that are suitable for *Bythotrephes*, we predict many lakes to remain suitable in the region with warming (Fig. 5a, b). If *Bythotrephes* range expansion has been limited by its opportunity to reach these sites (as it has been historically; Gertzen et al. 2011), we expect *Bythotrephes* to continue to expand its range as it invades the many suitable lakes in the region. While seemingly paradoxical, this conclusion may be important for managing cool-water invasive species: Aquatic invasive species prevention efforts should not be curtailed because of expected range contraction due to climate change. Our ability to identify the relatively small number of lakes that may or do provide refuge to aquatic invasive species (or, conversely, imperiled or declining native species; Hansen et al. 2017) allows us to prioritize management efforts, as in the case of conservation planning using terrestrial microrefugia (Keppel et al. 2015, Morelli et al. 2016). For example, using either of our models, the number of lakes predicted to be

suitable for *Bythotrephes* populations was greatly reduced under future climate conditions. We predicted roughly one fifth of lakes in our study region to be thermally suitable for *Bythotrephes* in the late century (or a single suitable lake in the air model). Targeting invasive species prevention and outreach efforts to suitable northern lakes that are relatively deep, cool in summer, and warm in fall would allow for more efficient allocation of management resources in the region (sensu Stewart-Koster et al. 2015).

Predicting the response of aquatic species to climate change

Air temperatures and basic lake characteristic data (e.g., lake depth) are often widely available relative to modeled or measured lake water temperatures. Since lake depth is a primary driver of the lake-to-lake variation in surface water temperatures (Toffolon et al. 2014), including lake depth in the air temperature model may provide as much predictive power as water temperatures alone. This specific case raises a question with both basic and applied relevance for predicting aquatic species responses to climate change: Does a combination of air temperatures and lake depth provide an adequate substitute for water temperatures? Adding lake depth to the air model reduced air and water model disagreement from 53% to 22%. However, the remaining disagreement in the models was still biased whereby the air temperature and lake depth model underpredicted suitability in cool, shallow lakes that were relatively warm in fall, and overpredicted suitability in warm, deep lakes that were relatively cool in fall relative to a water model. The differences highlighted by this comparison make clear the importance of additional lake characteristics other than lake depth (e.g., lake area) in determining lake thermal regimes and suitability.

There are several fundamental challenges inherent to modeling how species are projected to respond to climate change (Peterson et al. 2018); here, we present some specific caveats to our approach. Overprediction (e.g., a high false-positive rate) serves a purpose in niche modeling by identifying a species potential range which is fundamentally broader than its observed range (Peterson et al. 2008, Jiménez-Valverde et al. 2011). Yet, the best approach for evaluating niche models, particularly for invading species, is to balance high

model sensitivity and overprediction (after all, one path to achieving high model sensitivity is to predict all lakes as suitable; Peterson et al. 2008). By deemphasizing the modeling importance of absences (or just background lakes here), we needed to take additional steps to ensure that our occurrence data and modeling approach led to predictions that represented *Bythotrephes* potential range. To do so, we updated our understanding of *Bythotrephes* occurrence in our study region (though our models would be improved further by including occurrences from other invaded ranges, e.g., Canada, or *Bythotrephes* native range) and calibrated our models to avoid overfitting (Jiménez-Valverde et al. 2011).

While we use climate projections from six GCMs, we only project under the most extreme scenario (RCP8.5). However, present-day carbon emissions reflect the RCP8.5 scenario used here (Hayhoe et al. 2017, Le Quéré et al. 2018). While GCM uncertainty accounts for the majority of uncertainty in mid-century air temperature projections, RCP uncertainty becomes increasingly more important in late-century scenarios (possibly as high as 70% of total variance in 2090; Northrop et al. 2014). Therefore, we note that late-century projections of lake suitability for *Bythotrephes* may change with differing long-term trajectories in emissions.

We also focused our measure of lake suitability on temperatures and physical habitat, and many biological and chemical factors not included here are likely to influence *Bythotrephes* persistence and population growth rates in lakes (e.g., water clarity, predator abundance; Young et al. 2011). Therefore, in an applied context, we advise using these projections as a first pass at lake suitability that provides a coarse estimate of contemporary and future thermal suitability for *Bythotrephes* in the absence of adaptation, preceding more detailed predictions from review of the literature conducted in other ecological modeling contexts (e.g., MacIsaac et al. 2000, Branstrator et al. 2006, Gertzen et al. 2011, Weisz and Yan 2011, Gertzen and Leung 2011, Young et al. 2011, Jokela et al. 2011, Kerfoot et al. 2011, Muirhead and MacIsaac 2011, Potapov et al. 2011, Wang and Jackson 2011).

The contrast between using air and water temperature predictors may be more obvious when modeling habitat suitability for other aquatic species. Since we were constrained by the

number of *Bythotrephes* occurrences for presence-only modeling (40 lakes), we used a small number of relatively simple water temperature variables for prediction here. However, many more are available with advances in lake temperature profile modeling (Winslow et al. 2017, Hipsey et al. 2019, Read et al. 2019). Further, multiple additional metrics can be computed from daily temperature profiles (e.g., stratification measures or the onset/duration of lake thermal properties) that may better link to the physiology of other aquatic species.

Aquatic species responses to climate change

Modeling habitat suitability depends on selecting predictor variables that link directly to species physiological limitations and requirements, particularly in the cases of modeling invasive species suitability and predicting species responses to climate change (Jiménez-Valverde et al. 2011, Blaise et al. 2017). The conditions that determine species thermal suitability are a result of the interaction between habitat features and climate (e.g., the effect of canopy cover in forested and urban ecosystems; Ziter et al. 2019), and therefore, climate data alone fail to account for the broader range of thermal characteristics that allow species to persist in habitats. For aquatic species, regional variation in lake thermal regime mirrors the variation in local terrain that can lead to spatial heterogeneity in habitat suitability (Benson et al. 2000). We used predictor variables that are closely linked to *Bythotrephes* physiological limitations (Yurista 1992, Kim and Yan 2010), and our results closely match previous ecological understanding of *Bythotrephes* optimal thermal range. We found that the water temperature model limited the potential for overprediction compared to the air temperature model. Additionally, selecting variables that link directly to *Bythotrephes* physiology may be the best ecological argument for selecting the water models over the air models in our study. As such, we must continue to refine and expand our understanding of habitat (e.g., lake) responses to climate change to better predict species responses to climate change.

Acknowledgments

Literature Cited

Benson, B. J., J. D. Lenters, J. J. Magnuson, M. Stubbs, T. K. Kratz, P. J. Dillon, R. E. Hecky, R. C. Lathrop, R. E. Hecky, and R. C. Lathrop. 2000. Regional coherence of climatic and lake thermal variables of four lake districts in the Upper Great Lakes Region of North America. Freshwater Biology 43:517–527.

Blaise, P., B. Olivier, K. Christoph, D. Curtis, G. Antoine, and J. Alberto. 2017. Selecting predictors to maximize the transferability of species distribution models: lessons from cross-continental plant invasions. Global Ecology and Biogeography 26:275–287.

Branstrator, D. K., M. E. Brown, L. J. Shannon, M. Thabes, and K. Heimgartner. 2006. Range expansion of *Bythotrephes longimanus* in North America: evaluating habitat characteristics in the spread of an exotic zooplankter. Biological Invasions 8:1367–1379.

Cliff, A. D., and J. K. Ord. 1981. Spatial processes. Pion, London, UK.

Culumber, Z. W., and M. Tobler. 2018. Correlated evolution of thermal niches and functional physiology in tropical freshwater fishes. Journal of Evolutionary Biology 31:722–734.

Dobrowski, S. Z. 2011. A climatic basis for microrefugia: the influence of terrain on climate. Global Change Biology 17:1022–1035.

Elith, J., M. Kearney, and S. Phillips. 2010. The art of modelling range-shifting species. Methods in Ecology and Evolution 1:330–342.

Fee, E. J., R. E. Hecky, S. E. M. Kasian, and D. R. Cruikshank. 1996. Effects of lake size, water clarity, and climatic variability on mixing depths in Canadian Shield lakes. Limnology and Oceanography 41:912–920.

Garton, D. W., D. J. Berg, and R. J. Fletcher. 1990. Thermal tolerance of the predatory cladocerans *Bythotrephes cederstroemi* and *Leptodora kindtii* relationship to seasonal abundance in Lake Erie.

Canadian Journal of Fisheries and Aquatic Sciences 47:731–738.

Gertzen, E. L., and B. Leung. 2011. Predicting the spread of invasive species in an uncertain world: accommodating multiple vectors and gaps in temporal and spatial data for *Bythotrephes longimanus*. Biological Invasions 13:2433–2444.

Gertzen, E. L., B. Leung, and N. D. Yan. 2011. Propagule pressure, allee effects and the probability of establishment of an invasive species (*Bythotrephes longimanus*). Ecosphere 2:1–17.

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

Hansen, G. J. A., J. S. Read, J. F. Hansen, and L. A. Winslow. 2017. Projected shifts in fish species dominance in Wisconsin lakes under climate change. Global Change Biology 23:1463–1476.

Hayhoe, K., J. Edmonds, R. E. Kopp, A. N. LeGrande, B. M. Sanderson, M. F. Wehner, and D. J. Wuebbles. 2017. Chapter 4 in Climate Models, Scenarios, and Projections. Climate Science Special Report: Fourth National Climate Assessment. Volume I. U.S. Global Change Research Program, Washington, D.C., USA.

Herzig, A. 1985. Resting eggs - a significant stage in the life cycle of crustaceans Leptodora kindti and Bythotrephes Longimanus. Verhandlungen Des Internationalen Verein Limnologie 22:3088–3098.

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.

Hijmans, R. J., and C. H. Graham. 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. Global Change Biology 12:2272–2281.

Hipsey, M. R., et al. 2019. A General Lake Model (GLM 3.0) for linking with high-frequency sensor data from the Global Lake Ecological Observatory Network (GLEON). Geoscientific Model Development 12:473–523.

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.

Jokela, A., S. E. Arnott, and B. E. Beisner. 2011. Patterns of *Bythotrephes longimanus* distribution relative to native macroinvertebrates and zooplankton prey. Biological Invasions 13:2573–2594.

Kearney, M., and W. Porter. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters 12:334–350.

Keppel, G., K. Mokany, G. W. Wardell-Johnson, B. L. Phillips, J. A. Welbergen, and A. E. Reside. 2015.

The capacity of refugia for conservation planning under climate change. Frontiers in Ecology and the Environment 13:106–112.

Kerfoot, W. C., F. Yousef, M. M. Hobmeier, R. P. Maki, S. T. Jarnagin, and J. H. Churchill. 2011. Temperature, recreational fishing and diapause egg connections: dispersal of spiny water fleas (*Bythotrephes longimanus*). Biological Invasions 13:2513–2531.

Kim, N., and N. D. Yan. 2010. Methods for rearing the invasive zooplankter *Bythotrephes* in the laboratory. Limnology and Oceanography Methods 8:552–561.

Korovchinsky, N. M., and S. E. Arnott. 2019. Taxonomic resolution of the North American invasive species of the genus Bythotrephes Leydig, 1860 (Crustacea: Cladocera: Cercopagididae). Zootaxa 4691:125–138.

Le Quéré, C., et al. 2018. Global carbon budget 2018. Earth System Science Data 10:2141–2194.

Levin, S. A. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur Award lecture. Ecology 73:1943–1967.

MacIsaac, H. J., H. A. M. Ketelaars, I. A. Grigorovich, C. W. Ramcharan, and N. D. Yan. 2000. Modeling *Bythotrephes longimanus* invasions in the Great Lakes basin based on its European distribution. Archiv Fur Hydrobiologie 149:1–21.

Manca, M., and W. R. DeMott. 2009. Response of the invertebrate predator *Bythotrephes* to a climate-linked increase in the duration of a refuge from fish predation. Limnology and Oceanography 54:2506–2512.

Minnesota Department of Natural Resources. 2018. Infested waters list. St. Paul, Minnesota, USA. http://www.dnr.state.mn.us/invasives/ais/infested.html

Montecino, V., X. Molina, S. Kumar, M. Castillo, and R. Bustamante. 2014. Niche dynamics and potential geographic distribution of *Didymosphenia geminata* (Lyngbye) M. Schmidt, an invasive freshwater diatom in Southern Chile. Aquatic Invasions 9:507–519.

Moorhouse, T. P., and D. W. Macdonald. 2015. Are invasives worse in freshwater than terrestrial ecosystems? Wiley Interdisciplinary Reviews: Water 2:1–8.

Morelli, T. L., et al. 2016. Managing climate change Refugia for climate adaptation. PLOS ONE 11: e0159909.

Muirhead, J. R., and H. J. MacIsaac. 2011. Evaluation of stochastic gravity model selection for use in estimating non-indigenous species dispersal and establishment. Biological Invasions 13:2445–2458.

Nadeau, C. P., M. C. Urban, and J. R. Bridle. 2017. Coarse climate change projections for species living in a fine-scaled world. Global Change Biology 23:12–24.

Northrop, P. J., R. E. Chandler, P. J. Northrop, and R. E. Chandler. 2014. Quantifying sources of uncertainty in projections of future climate. Journal of Climate 27:8793–8808.

Notaro, M., V. Bennington, S. Vavrus, M. Notaro, V. Bennington, and S. Vavrus. 2015. Dynamically downscaled projections of lake-effect snow in the Great Lakes Basin. Journal of Climate 28:1661–1684.

O'Reilly, C. M., et al. 2015. Rapid and highly variable warming of lake surface waters around the globe. Geophysical Research Letters 42:10773–10781.

Papeş, M., J. E. Havel, and M. J. Vander Zanden. 2016. Using maximum entropy to predict the potential distribution of an invasive freshwater snail. Freshwater Biology 61:457–471.

Peterson, A. T., M. E. Cobos, and D. Jiménez-García. 2018. Major challenges for correlational ecological niche model projections to future climate conditions. Annals of the New York Academy of Sciences 1429:66–77.

Peterson, A. T., M. Papeş, and J. Soberón. 2008. Rethinking receiver operating characteristic analysis applications in ecological niche modeling. Ecological Modelling 213:63–72.

Peterson, A. T., and D. A. Vieglais. 2001. Predicting species invasions using ecological niche modeling: New approaches from bioinformatics attack a pressing problem. BioScience 51:363–371.

Phillips, S. J. 2017. maxnet: fitting "Maxent" Species Distribution Models with "glmnet". R package version 0.1.2. https://cran.r-project.org/web/packages/maxnet/index.html

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190:231–259.

Potapov, A., J. Muirhead, N. Yan, S. Lele, and M. Lewis. 2011. Models of lake invasibility by *Bythotrephes longimanus*, a non-indigenous zooplankton. Biological Invasions 13:2459–2476.

Rahel, F. J., and J. D. Olden. 2008. Assessing the effects of climate change on aquatic invasive species. Conservation Biology 22:521–533. https://doi.org/10.1111/j.1523-1739.2008.00950.x.

Ratajczak, Z., S. R. Carpenter, A. R. Ives, C. J. Kucharik, T. Ramiadantsoa, M. A. Stegner, J. W. Williams, J. Zhang, and M. G. Turner. 2018. Abrupt change in ecological systems: inference and diagnosis. Trends in Ecology & Evolution 33:513–526.

Read, J. S., et al. 2019. Process-guided deep learning predictions of lake water temperature. Water Resources Research 55:9173–9190.

Read, J. S., and K. C. Rose. 2013. Physical responses of small temperate lakes to variation in dissolved organic carbon concentrations. Limnology and Oceanography 58:921–931.

Rose, K. C., L. A. Winslow, J. S. Read, and G. J. A. Hansen. 2016. Climate-induced warming of lakes can be either amplified or suppressed by trends in water clarity. Limnology and Oceanography Letters 1:44–53.

Sharma, S., D. A. Jackson, C. K. Minns, and B. J. Shuter. 2007. Will northern fish populations be in hot water because of climate change? Global Change Biology 13:2052–2064.

Stewart-Koster, B., J. D. Olden, and P. T. J. Johnson. 2015. Integrating landscape connectivity and habitat suitability to guide offensive and defensive invasive species management. Journal of Applied Ecology 52:366–378.

Toffolon, M., S. Piccolroaz, B. Majone, A.-M. Soja, F. Peeters, M. Schmid, and A. Wüest. 2014. Prediction of surface temperature in lakes with different morphology using air temperature. Limnology and Oceanography 59:2185–2202.

U.S. Geological Survey. 2018. Nonindigenous Aquatic Species Database. Gainesville, Florida. http://nas.er.usgs.gov

Walsh, J. R., S. R. Carpenter, and M. J. Vander Zanden. 2016*a*. Invasive species triggers a massive loss of ecosystem services through a trophic cascade. Proceedings of the National Academy of Sciences of the United States of America 113:4081–4085.

Walsh, J. R., S. E. Munoz, and M. J. Vander Zanden. 2016*b*. Outbreak of an undetected invasive species triggered by a climate anomaly. Ecosphere 7. https://doi.org/10.1002/ecs2.1628

Walsh, J. R., E. J. Pedersen, and M. J. Vander Zanden. 2018. Detecting species at low densities: a new theoretical framework and an empirical test on an invasive zooplankton. Ecosphere 9:e02475.

Walsh, J. R., M. J. Spear, T. P. Shannon, P. J. Krysan, and M. J. Vander Zanden. 2019. Using eDNA, sediment subfossils, and zooplankton nets to detect invasive spiny water flea *(Bythotrephes longimanus)*. Biological Invasions 21:377–389.

Wang, L., and D. A. Jackson. 2011. Modeling the establishment of invasive species: habitat and biotic interactions influencing the establishment of *Bythotrephes longimanus*. Biological Invasions 13:2499–2512.

Weisz, E. J., and N. D. Yan. 2011. Shifting invertebrate zooplanktivores: watershed-level replacement of the native *Leptodora* by the non-indigenous *Bythotrephes* in Canadian Shield lakes. Biological Invasions 13:115–123.

Wiens, J. A., D. Stralberg, D. Jongsomjit, C. A. Howell, and M. A. Snyder. 2009. Niches, models, and climate change: assessing the assumptions and uncertainties. Proceedings of the National Academy of Sciences of the United States of America 106:19729–19736.

Winslow, L. A., G. J. A. Hansen, J. S. Read, and M. Notaro. 2017. Large-scale modeled contemporary and future water temperature estimates for 10774 Midwestern U.S. Lakes. Scientific Data 4:170053.

Wisconsin Department of Natural Resources. 2018. AIS list: spiny water flea. Madison, Wisconsin, USA. http://dnr.wi.gov/lakes/invasives/AISLists.aspx?species=SPINY_WATERFLEA

Yan, N. D., B. Leung, M. A. Lewis, and S. D. Peacor. 2011. The spread, establishment and impacts of the spiny water flea, *Bythotrephes longimanus*, in temperate North America: a synopsis of the special issue. Biological Invasions 13:2423–2432.

Young, J. D., A. L. Strecker, and N. D. Yan. 2011. Increased abundance of the non-indigenous zooplanktivore, *Bythotrephes longimanus*, is strongly correlated with greater spring prey availability in Canadian Shield lakes. Biological Invasions 13:2605–2619.

Young, J. D., and N. D. Yan. 2008. Modification of the diel vertical migration of *Bythotrephes longimanus* by the cold-water planktivore, *Coregonus artedi*. Freshwater Biology 53:981–995.

Yurista, P. M. 1992. Embryonic and postembryonic development in *Bythotrephes cederstroemii*. Canadian Journal of Fisheries and Aquatic Sciences 49:1118–1125.

Yurista, P. M. 1999. A model for temperature correction of size specific respiration in *Bythotrephes cederstroemi* and *Daphnia middendorffiana*. Journal of Plankton Research 21:721–734.

Ziter, C. D., E. J. Pedersen, C. J. Kucharik, and M. G. Turner. 2019. Scale-dependent interactions between tree canopy cover and impervious surfaces reduce daytime urban heat during summer. Proceedings of the National Academy of Sciences of the United States of America 116: 7575–7580.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3137/full