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Using maximum entropy to predict the potential distribution of an invasive freshwater snail

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SUMMARY

1. Ecological niche modelling is a technique used to estimate potential distributions of invasive species based on available occurrence data and associated environmental conditions. Maximum entropy (Maxent) is a powerful method for ecological niche modelling and yet has only rarely been applied to aquatic species.
2. Here we applied Maxent to estimate the potential distribution of the invasive Chinese mystery snail (*Cipangopaludina chinesis*) in Wisconsin and analysed several methodological issues associated with using Maxent for lentic species.
3. To generate Maxent estimates of the potential distribution of *C. chinesis*, we used presence records from 292 lakes, five spatially explicit climatic variables, and two lake-specific environmental data sets (area, conductivity) from 7995 lakes. Our investigations included three aspects that could affect model prediction accuracy and transferability: (i) combining climate and lake variables into a single data set in two different ways, using each lake as a single observation and as a grid of 1 ha cells; (ii) varying the size of the background data set (locations without presences); and (iii) contrasting environmental conditions between locations with and without *C. chinesis*.
4. The lake-based model had higher accuracy than the grid-based model, although both models had accuracy values indicative of good performance. Conductivity and lake area were important predictor variables for both models, but had higher contribution to the lake-based model accuracy. Decreasing the background sample size minimally affected model accuracy and thus Maxent can be used even when background sampling does not meet the algorithm's default settings. Lastly, lakes that were environmentally dissimilar from lakes with known *C. chinesis* records were more likely to be predicted unsuitable by both grid-based and lake-based models.
5. Overall, the models predicted high potential suitability across Wisconsin lakes for *C. chinesis*, especially in lakes ≥60 ha. Our study provides evidence that small or environmentally biased presence data sets may underestimate the number of environmentally suitable locations of invasive species.

Keywords: *Bellamya chinensis*, chinese mystery snail, *Cipangopaludina chinensis*, ecological niche modelling, Maxent

Introduction

With growing recognition of the adverse impacts of invasive species, researchers have increasingly focused on modelling their potential spread and distribution (Kareiva, 1996; Sakai *et al.*, 2001; Leung *et al.*, 2005; Asner *et al.*, 2008; Vander Zanden & Olden, 2008; Papeş *et al.*, 2011). One commonly used approach for assessing potential distributions of invasive species is ecological niche modelling (Peterson, Papeş & Kluza, 2003; Arriaga *et al.*, 2004; Steiner *et al.*, 2008; Kulhanek, Leung & Ricciardi, 2011; Hill *et al.*, 2012). The general concept

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involves identifying statistically significant associations between known species occurrences and environmental variables (usually climate-based) and using these associations to locate suitable environmental conditions in a region of interest (Peterson & Vieglais, 2001).

Ecological niche modelling has benefitted from a recent proliferation of new methods and approaches (reviewed in Elith & Leathwick, 2009; Peterson *et al*., 2011). Methods vary in the type of species information needed (presence only or presence and absence), performance with low samples or spatially biased samples, and model transferability to new regions or environmental conditions (reviewed in Elith & Leathwick, 2009). Maxent, a maximum entropy algorithm (Phillips, Anderson & Schapire, 2006), has been widely used for ecological niche modelling in terrestrial systems and has been shown to produce high accuracy models (Hernandez *et al*., 2006). With Maxent, environmental conditions associated with species presence data are compared to those of a large random sample of background sites (sites without presence information; Phillips & Dudík, 2008). For predictors, Maxent studies generally use gridded (rasterised) climatic data sets such as WorldClim (Hijmans *et al*., 2005) or remotely sensed environmental data sets (Papeş, Peterson & Powell, 2012). These data are available as digital maps (GIS layers) and are highly amenable for niche modelling because they provide a sufficient number of background sites for the approach. Generally, Maxent is used to estimate the relative environmental suitability for a species (Phillips & Dudík, 2008; Guillera-Arroita, Lahoz-Monfort & Elith, 2014), but recent modifications to Maxent have been proposed to estimate intensity of occurrence through a Poisson Point Process modelling approach (Renner & Warton, 2013; Renner *et al*., 2015).

The extent to which aquatic species distributions are limited by climate may be debatable. While at broad geographic scales climate is likely to determine species distributions (Gaston, 2003), waterbody-specific factors are known to constrain species distributions at finer spatial scales (Brown, 2001), leading to patchy spatial distributions (Jackson, Peres-Neto & Olden, 2001; Papeş *et al*., 2011). Maxent has been widely used for terrestrial systems; in contrast, this method has rarely been applied to freshwater systems (close to 900 versus 23 publications respectively; Web of Science query, 2 July 2015). Maxent estimates of terrestrial species distributions generally rely on climatic predictor variables, whereas aquatic ecologists often focus on regional or finer spatial scales, with waterbody-specific variables such as lake size, pH, chlorophyll, and conductivity as potentially limiting freshwater species distributions (Mercado-Silva *et al*., 2006; Cordell, Tear & Bollens, 2010; Kornis & Vander Zanden, 2010; Kulhanek *et al*., 2011; Olden, Vander Zanden & Johnson, 2011; Stewart-Koster *et al*., 2013; Tamayo & Olden, 2014). Given the difficulties of collecting waterbody-specific data at broad scales and for thousands of rivers or lakes (e.g. Jähnig *et al*., 2012), most Maxent studies of freshwater species have used climate data as predictor variables and grid cells rather than individual waterbodies as the units of analysis (Table 1). As a result, in general, the potential distributions do not distinguish between terrestrial and

Table 1 Summary of published studies estimating aquatic invasive species potential distributions, using Maxent and grid-based environmental variables.

Reference	Environmental data used	Spatial resolution	Extent
Barnes *et al*. (2014)	Temperature	0.5 degrees (50 km)	North America
Byers *et al*. (2013)	Climate	N/A	SE United States
Gallardo & Aldridge (2015)	Climate, elevation, geology, anthropogenic, land use	5 arc-minutes (9 km)	SE Europe, Great Britain
Gallardo and Aldridge ((2013)	Climate, geology, socio-economic	30 arc-seconds (1 km)	Great Britain, Ireland
Gallardo, Ermgassen and Aldridge (2013)	Climate, elevation, geology	5 arc-minutes (9 km)	Europe, North America
Kumar *et al*. (2009)	Climate, topography, land cover, vegetation index, geology, hydrology	30 arc-seconds (1 km)	United States
Larson, Olden and Usio (2010)	Climate	5 arc-minutes (9 km)	Japan, NW North America
Masin *et al*. (2014)	Climate, solar radiation, vegetation index	10 arc-minutes (18 km)	Global
McDowell, Benson and Byers (2014)	Climate	N/A	United States
Montecino *et al*. (2014)	Climate, topography, hydrology,geology, vegetation	30 arc-seconds (1 km)	Chile, United States
Morehouse and Tobler (2013)	Climate	30 arc-seconds (1 km)	United States
Poulos *et al*. (2012)	Climate, topography, hydrology	30 arc-seconds (1 km)	United States
Quinn, Gallardo and Aldridge (2014)	Climate, elevation, geology	2 arc-minutes (4 km)	Europe, United States
Reshetnikov and Ficetola (2011)	Climate	10 arc-minutes (18 km)	Eurasia

freshwater cells and thus are not waterbody-specific. However, state-level efforts to develop GIS databases of waterbody-specific environmental variables (e.g. Wisconsin Department of Natural Resources Surface Water Integrated Monitoring System, Minnesota Geospatial Information Office Surface Water Resource Data), as well as national (e.g. USGS National Water Information System) and multi-national initiatives (e.g. GLEON, CUAHSI; Ames *et al*., 2009; Weathers *et al*., 2013), indicate potential for future studies that are waterbody-specific, at regional and broader scales. Lastly, Maxent requires a large background data set, further limiting its application for freshwater systems, where data sets tend to be one or two orders of magnitude smaller than for terrestrial systems (Olden & Jackson, 2002). In essence, the contrast between freshwater and terrestrial species' estimations of potential distributions lies in the limitation to presence of water for the former and the associated challenges of variable and modelling algorithm selection (see Domisch *et al*., 2015 for a review of issues in riverine systems).

Although niche modelling tools such as Maxent may be powerful for identifying suitable freshwater environments, there are several issues pertaining to lakes that require in-depth investigations. In this study, we use Maxent to estimate the potential distribution of invasive Chinese mystery snail (*Cipangopaludina chinensis malleata* Gray 1863: Viviparidae) in Wisconsin, U.S.A. The Chinese mystery snail (hereafter CMS) has also been recognised as *Bellamya chinensis* (Smith, 2000), but the nomenclature is still uncertain, so we follow the name in most common usage (Turgeon *et al*., 1998). CMS is a large snail that was introduced from Asia into United States in the late 1800s and currently has established populations in 21 states (of a total of 34 states with confirmed records; Jokinen, 1982; U.S. Geological Survey, 2014). High resistance to air exposure suggests high potential for overland dispersal by boats (Havel, 2011). In the United States, large variation in population density and growth rates have been reported (Solomon *et al*., 2010; McCann, 2014). Nevertheless, CMS does not appear to have a strong effect on assemblages of native gastropods in north-temperate lakes (Solomon *et al*., 2010).

We use the case of CMS to investigate three methodological issues. First, the effect of combining gridded climate and lake attribute data to model accuracy has not been formally evaluated in ecological niche models, nor has the effect of treating lakes as individual observations versus grid cells. We compare models based on environmental data formatted as grids, where lakes are represented by cells, limited to the extent of lakes (thus eliminating the surrounding terrestrial cells), to models based on environmental data where each lake is represented by a single point (see Domisch *et al*., 2013 for a similar approach in riverine systems). Second, we investigate the large background sample size requirement of Maxent by evaluating model performance across a range of background sampling intensities. Third, studies of terrestrial and stream species have shown limitations of model transferability to environments that differ from the ones associated with species presences, used to calibrate the model (Peterson, Papeş & Eaton, 2007; Zhu *et al*., 2014; Gies *et al*., 2015). We investigate this issue in lakes by quantifying environmental similarities between presences and background samples through a multivariate environmental similarity surface analysis (MESS) and evaluating the effect of environmental dissimilarity on model accuracy. This case study thus allows us to address critical methodological issues and to provide guidance for future research on estimating potential distributions of aquatic species.

Methods

We compiled a data set of lake CMS records archived in the Wisconsin Department of Natural Resources Surface Water Integrated Monitoring System (SWIMS; http://dnr.wi.gov/topic/surfacewater/swims/). Records with locality descriptions that could not be matched with lakes in Wisconsin were eliminated. We retained a total of 292 presences with latitude and longitude coordinates for ecological niche modelling experiments. Each CMS record was represented by a single lake grid cell. Presence records were randomly separated into model training (calibrating) and testing (validating) data sets using a 70–30% split, respectively (Fig. 1).

Climate data

We downloaded 19 climate variables in GIS grid format (1 km resolution) from the WorldClim global climate database (www.worldclim.org) and reduced them spatially to the extent of Wisconsin. To minimise collinearity among variables, we calculated Spearman rank correlation between all pairs of variables (standardised) and retained only one variable from pairs with $r^2 > 0.5$ (Dormann *et al*., 2013). Variables represented in the most pairs with $r^2 > 0.5$ were eliminated first. Doing so reduced the climate predictor data set to just five variables: mean diurnal temperature range, mean temperature of the warmest 3 months, annual precipitation,

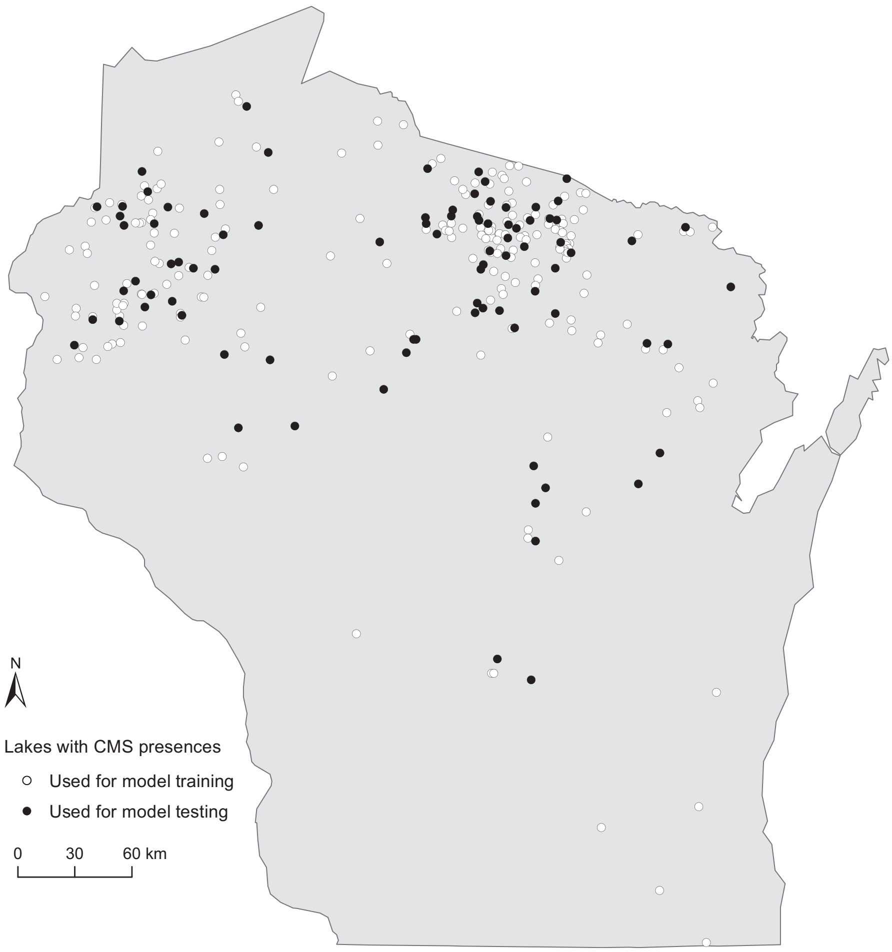


Fig. 1 Lakes with confirmed Chinese mystery snail records in Wisconsin, separated into data sets used for model training (white circles) and model testing (black circles).

precipitation seasonality, and precipitation of the wettest 3 months.

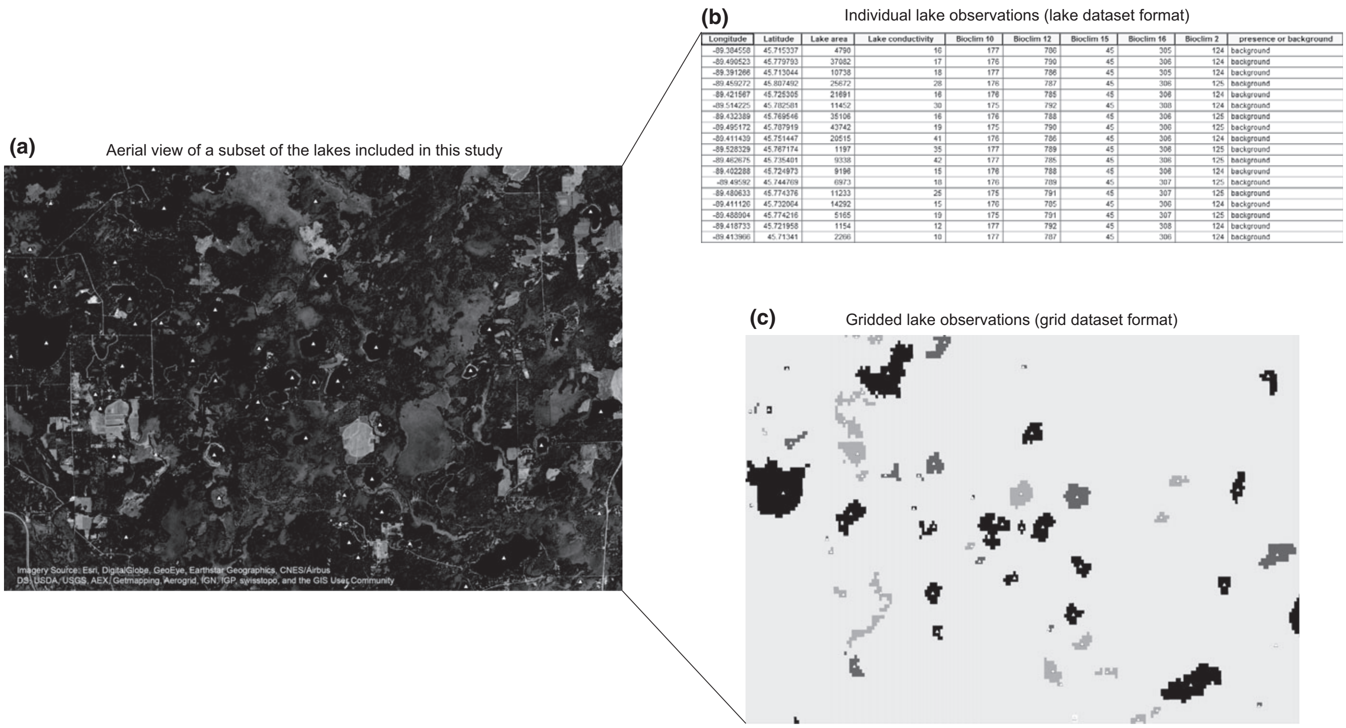
Lake data compilation and formatting

Lake-specific data for lakes ≥1 ha in size were assembled from various state and federal sources (Papeş *et al.*, 2011). We included only lake area and conductivity as predictors, as these variables were frequently represented in our database of lakes (thus maximising the number of lakes considered in the analysis) and have been shown to be most influential for the distribution of snails (Brown, 2001; Hrabik *et al.*, 2005; Latzka *et al.*, 2015). The final lake data set used for the modelling experiments included 7995 lakes, which represent 53% of lakes in Wisconsin.

We combined climate and lake variables into a single data set in two distinct ways, in order to compare how different data set formats affect model predictions (Fig. 2). The first approach treats each individual lake as a single observation (hereafter termed 'lake'). The second approach treats individual lakes as comprised of multiple 1-ha grid cells (hereafter termed 'grid'). In the grid approach, a given lake is represented by multiple grid cells, such that the number of grid cells for a lake is proportional to lake area. All grid cells representing a single lake had the same area and conductivity values, corresponding to that particular lake. Note that we did not estimate CMS distributions for all grid cells in the state of Wisconsin (waterbodies and surrounding terrestrial matrix), but rather only for grid cells that represent lakes. Our lake data set included 7995 records (the number of lakes), while the grid data set included 82 000 observations (the number of 1-ha cells that represent lakes).

Ecological niche modelling experiments

We used the environmental data and CMS presence records in Maxent 3.3.3k (https://www.cs.princeton.edu/~schapire/maxent/) to generate models of environmental suitability and to map CMS potential distribution in Wisconsin. Maxent is based on the maximum entropy theory that, in ecological modelling,



Longitude	Latitude	Lake area	Lake conductivity	Bioclim 10	Bioclim 12	Bioclim 15	Bioclim 16	Bioclim 2	presence or background
-89.384558	45.715337	4790	16	177	786	45	305	124	background
-89.490523	45.779793	37082	17	176	790	45	306	124	background
-89.391266	45.713044	10738	18	177	786	45	305	124	background
-89.459272	45.807492	25672	28	176	787	45	306	125	background
-89.421567	45.725305	21691	16	176	785	45	306	124	background
-89.514225	45.782581	11452	30	175	792	45	308	124	background
-89.432389	45.769546	35106	16	176	788	45	306	125	background
-89.495172	45.787919	43742	19	175	790	45	306	125	background
-89.411439	45.751447	20515	41	176	786	45	306	124	background
-89.528329	45.767174	1197	35	177	789	45	308	125	background
-89.462675	45.735401	9338	42	177	785	45	306	125	background
-89.402288	45.724973	9196	15	176	788	45	306	124	background
-89.49592	45.744769	6973	18	176	789	45	307	125	background
-89.480633	45.774376	11233	25	175	791	45	307	125	background
-89.411126	45.732064	14292	15	176	785	45	306	124	background
-89.488904	45.774216	5165	19	175	791	45	307	125	background
-89.418733	45.721958	1154	12	177	792	45	308	124	background
-89.413966	45.71341	2266	10	177	787	45	306	124	background

Fig. 2 A subset of the lakes in Wisconsin included in this study (a; white triangles) and the two representations of lakes in the environmental data sets used in the models: individual observations for each lake (b; lake data set format) and gridded variables in 1-ha cells (c; grid data set format, showing conductivity values in grey scale).

estimates the probability distribution that is maximised when considering a set of constraints (Phillips *et al.*, 2006). The constraints are defined in relation to the environmental values associated with species known presences. Models that assign higher probability values to presence sites compared to a random set of background samples (sites without presences) are characterised by higher log likelihood values. We used the default parameter settings in Maxent 3.3.3k (for features used as constraints, maximum number of background points, maximum model iterations of 500, and model convergence threshold) to run models using both grid and lake data sets.

During model iteration Maxent performs several evaluation tests. First, to rank importance of environmental variables, the contribution of each variable to overall model accuracy gain is expressed as a proportion of contributions of all variables. Second, the area under the curve of the receiver operating characteristic (ROC AUC) is used to assess model performance by plotting model sensitivity (fraction of occurrences predicted suitable) on the y axis and 1 - specificity (fraction of background samples predicted suitable) on the x axis. A ROC AUC score closer to 1 indicates high model accuracy, while a value $\leq$0.5 indicates models that are no better than random (Hanley & McNeil, 1982). The applicability of ROC to evaluating performance of models obtained with presence-background modelling algorithms has been questioned in recent literature and modifications of ROC have been proposed (Lobo, Jiménez-Valverde & Real, 2008; Peterson, Papeş & Soberón, 2008; Jiménez-Valverde, 2012). As an additional measure of model accuracy, Maxent also calculates omission error, which is the proportion of presence records in the testing data set incorrectly predicted as unsuitable. To calculate omission error, a threshold is needed to transform the model output that contains continuous suitability values between 0 and 1 to a categorical form, unsuitable-suitable. We used the 'lowest presence threshold' (Anderson, Lew & Peterson, 2003), representing the Maxent model output value at which all CMS presences in the training data set were predicted suitable. The omission error calculations were done separately for the two models obtained with lake and grid data set formats. We also calculated true skills statistic for the two models, using the same threshold, unsuitable-suitable model outputs. The true skills statistic (TSS) is calculated as sensitivity plus specificity minus 1 and thus it accounts for correct predictions of both presences and absences to evaluate model performance (Allouche, Tsoar & Kadmon, 2006). TSS ranges from −1 to 1, with values <0 attributable to a random model and has been shown to be unaffected by the size of the validation data set or species' prevalence (Allouche *et al*., 2006). As we studied the invasive potential of CMS, we did not have absence data, thus the TSS was calculated using the background samples.

Finally, we summarised the mismatch between the binary suitable-unsuitable predictions of the grid and lake-based models by calculating the percent of lakes predicted suitable and unsuitable by one or both models. We visualised these results on a consensus map showing lakes for which predictions of the two models agreed or disagreed.

Multivariate analysis of lake environmental similarity

Model transferability to environmental conditions that are markedly different can be unreliable, resulting in unrealistic or incomplete predictions of potential distributions (Peterson *et al*., 2007). To assess if our results would be affected by model transferability, we used a second set of modelling experiments to estimate the differences between the environmental conditions of the lakes with CMS and those in the entire study region. We used the multivariate environmental similarity surface analysis (MESS) implemented in Maxent 3.3.3k to calculate the percentage of lakes associated with CMS presences (292 lakes) that differ in their environmental values compared to the rest of Wisconsin lakes (7703 lakes). MESS determines f_i, the percentage of reference sites that have lower environmental variable values than the site of interest, and calculates the similarity value for the site of interest as $2 * f_i$ if $0 < f_i \leq 50$ and $2(100 - f_i)$ if $50 < f_i \leq 100$, for each environmental dimension; the minimum similarity value across all environmental variables represents the multivariate similarity of the site of interest (Elith, Kearney & Phillips, 2010). We then revised the CMS consensus prediction map obtained with the first set of Maxent experiments to identify the lakes (sites of interest) estimated with MESS as having environmental conditions that are distinct from those of the presence records (reference sites). Such environmental differences could indicate higher uncertainty of the prediction.

Background sampling experiment

The default setting in Maxent of 10 000 background samples may not be feasible for freshwater species studies due to the limited availability of lake-specific (or river-specific) environmental data. To investigate the effect of background sample size on model accuracy, we withheld randomly selected subsets of lakes from the available 7703 lakes. Specifically, we decreased the background sample size by increasing the presence/background ratio from the observed value of 0.03 (292 presence lakes/7703 background lakes), to 0.1, 0.25, 0.3, 0.5, 0.75, 1, 1.25, 1.5, 1.75 and 2. Thus, the background data sets in our 10 simulations ranged from approaching the default 10 000 background samples option in Maxent, to nearly two orders of magnitude lower (background sample of 146 lakes; presence/background = 2). We then compared the ROC AUC, TSS, test omission error, and proportion of lakes predicted suitable across the 10 simulations to evaluate the sensitivity of Maxent performance to background sample sizes.

Results

Ecological niche modelling experiments

We obtained two different rankings of environmental variables that contributed most to the ecological niche models using grid and lake data set formats. However, the highest contributing variable for both models was lake area. Most of the lakes (95%) predicted suitable for CMS by the lake-based model had area ≥65 ha and most (95%) of the unsuitable predictions were for lakes with area ≤60 ha. In the case of grid-based model prediction, we obtained some overlap in lake area values of most lakes (95%) predicted suitable (≥35 ha) and unsuitable (≤65 ha). The tendency for larger lakes to be predicted present may be explained by the high proportion (70%) of large lakes (≥65 ha) in the presence data set used to train the models, probably because larger lakes are more likely to be accessible and sampled for invasive species. A cumulative variable contribution >90% to model accuracy gain was achieved with four variables for the grid-based model and just two variables for the lake-based model (Table 2). Conductivity contributed towards the cumulative 90% accuracy gain of both models, but in contrast with lake area, we did not observe a distinct separation of conductivity values between suitable and unsuitable lakes.

The performance of the grid-based model was lower than that of the lake-based model, as measured by ROC AUC (Table 2). Nevertheless, both models had ROC AUC scores that are considered indicative of good performance (>0.7; Swets, 1988). The second measure of model performance, omission error (lakes with known CMS records predicted unsuitable) calculated using the minimum training presence threshold, produced more comparable values between the two models (Table 2): of the known CMS presences (in the testing data set), 3% were incorrectly predicted unsuitable by the grid-based model and 0% by the lake-based model. The third evaluation method, TSS, indicated good performance of both models (Table 2, TSS > 0; Allouche *et al.*, 2006).

Both models predicted that a high proportion of lakes should be suitable for CMS: 47% of lakes by the lake-based model and 55% by the grid-based model. In addition to overall number of lakes predicted suitable, we compared model predictions from lake-based and grid-based approaches for each lake (Fig. 3a and b). There was disagreement between the two approaches for 11% of the lakes (Table 3). Overall, there was no obvious spatial pattern to the lake suitability predictions (Fig. 3a). We used consensus maps of CMS potential distribution to further evaluate the geographic distribution of the agreement (89% of the lakes; Fig. 4a) and disagreement (11% of the lakes; Fig. 4b) between the two models. The model agreement and disagreement did not show particular geographic patterns, indicating lack of model bias towards a geographic region.

Multivariate analysis of lake environmental similarity

Given that transferability of models to new regions and new environmental conditions could generate unreliable predictions (Zhu *et al.*, 2014), we refined the consensus map based on environmental similarity of lakes. The MESS analysis identified 51% of the lakes as environmentally dissimilar from lakes with CMS presences and 49% as similar (Fig. 5a and b, respectively). Of the 51% lakes that were environmentally dissimilar from lakes with CMS records, 75% were predicted unsuitable by both models, 17% were predicted suitable by one model, and 8% were predicted suitable by both models (Fig. 5a). Thus, the model unreliability due to environmental dissimilarity was largely associated with predictions of unsuitability. In contrast, of the lakes that were environmentally similar to CMS presence lakes (49%), most (86%) were predicted suitable by both models (Fig. 5b). Of the remainder, 4% by one model and 10% were predicted unsuitable by both models (Fig. 5b). For environmentally dissimilar lakes, the MESS analysis identified lake area as the variable most frequently (82%) different between background lakes and those with CMS. Small lakes (<8 ha) represented the majority (94%) of the dissimilar lakes, whereas lakes similar to the ones used to train the models were concentrated in the medium size range (8–80 ha).

Background sampling experiment

Our background sampling experiment using the lake data set format indicated that Maxent generates models that perform well (ROC AUC >0.7; omission error <0.01) with background sample sizes down to one order of magnitude lower than the default 10 000 (Fig. 6). The omission error remained low (<0.1) for all models, regardless of background sample size, indicating good model performance (Fielding & Bell, 1997). ROC AUC scores of models decreased steadily with decreasing sample sizes (Fig. 6), but remained above 0.7, also indicating good model performance (Hanley & McNeil, 1982), until reaching the lowest two background sample sizes (167 and 146 samples), close to two orders of magnitude lower than the default 10 000 background samples. Similarly, the TSS values decreased with sample sizes, but remained above zero (indicative of models better than random). However, the proportion of lakes predicted suitable increased steadily, suggesting that discrimination between suitable and unsuitable lakes becomes more difficult with decreasing background sample sizes (Fig. 6). Decreasing the number of background samples had the strongest effect on the proportion of lakes predicted suitable for CMS: we obtained an average 3% increase with each reduction of background sample size, from 40% of lakes predicted suitable by the model that used all background samples, to 80% by the

Table 2 Summary of accuracy measures and environmental variable contribution to models obtained using environmental data sets representing lakes as individual observation (lake data set format) or gridded (grid data set format)

Type of lake representation	Omission error	TSS	ROC AUC	Highest contribution (variable; value)	Variables with summed contribution >90%
Individual observations (lake data set format)	0	0.54	0.92	Lake area; 85.5%	Lake area, conductivity
Gridded observations (grid data set format)	0.03	0.37	0.79	Lake area; 71.7%	Lake area, conductivity, precipitation of the wettest quarter, mean diurnal temperature range

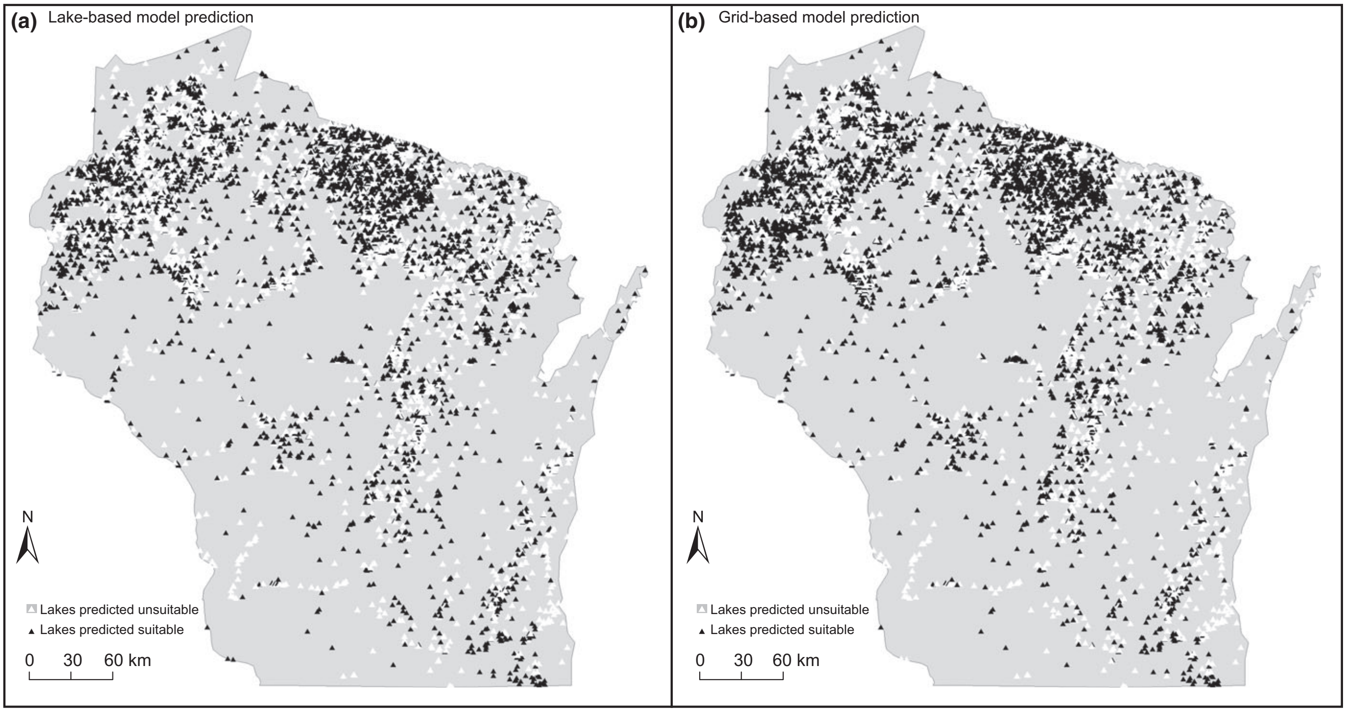


Fig. 3 The potential distribution of Chinese mystery snail in Wisconsin lakes obtained with models based on the two formats of environmental data: lake data set (individual lake observations; a) and grid data set (gridded lake observations; b). Lakes predicted unsuitable are identified by the white triangles and suitable lakes by the black triangles. The maps are comparable given the overall prediction agreement between the two models (89% of the lakes; see also Fig. 4).

Table 3 Comparison of predictions obtained with models using lake and grid data set formats. Numbers represent the percent of lakes for which the model predictions agreed or disagreed (in bold)

	Grid	
	Suitable	Unsuitable
Lake		
Suitable	46	**2**
Unsuitable	**9**	43

model that used the lowest number of background samples.

Discussion

Estimates of potential distributions of invasive species are increasingly a part of invasive species prevention and management efforts, thereby allowing for proactive management (Leung & Mandrak, 2007; Vander Zanden & Olden, 2008; Papeş *et al.*, 2011). Ecological niche modelling studies traditionally rely on climate predictor variables and estimate species potential distributions at broad spatial scales, at which climate is likely to constrain species distributions (Jiménez-Valverde *et al.*, 2011). The local environmental factors that presumably determine species distributions at finer scales are typically not incorporated (but see Hopkins & Burr, 2009; Oliveira *et al.*, 2010; Wilson, Roberts & Reid, 2011; Breece *et al.*, 2013; Stewart-Koster *et al.*, 2013; Kuemmerlen *et al.*, 2014 for examples of riverine studies). These constraints stem from unavailability of such information for large data sets of waterbodies and are well-illustrated when we consider predicting invasive species in lakes. A traditional ecological niche modelling framework of predicting species occurrence in grid cells from climate variables may not capture lake-specific patterns.

Our models predicted roughly half of lakes in Wisconsin to be suitable for CMS (Table 3). The grid-based model predicted higher suitability compared to the lake-based approach (55% versus 48% of the lakes, Table 3). This difference is likely due to the fact that the grid-based approach treats an individual lake as comprised of multiple cells, with the number of cells being proportional to lake area, and large lakes are more likely to be suitable. Since individual lakes or river segments (rather than grid cells) are the unit of analysis for limnologists, results of the lake-based modelling approach are more

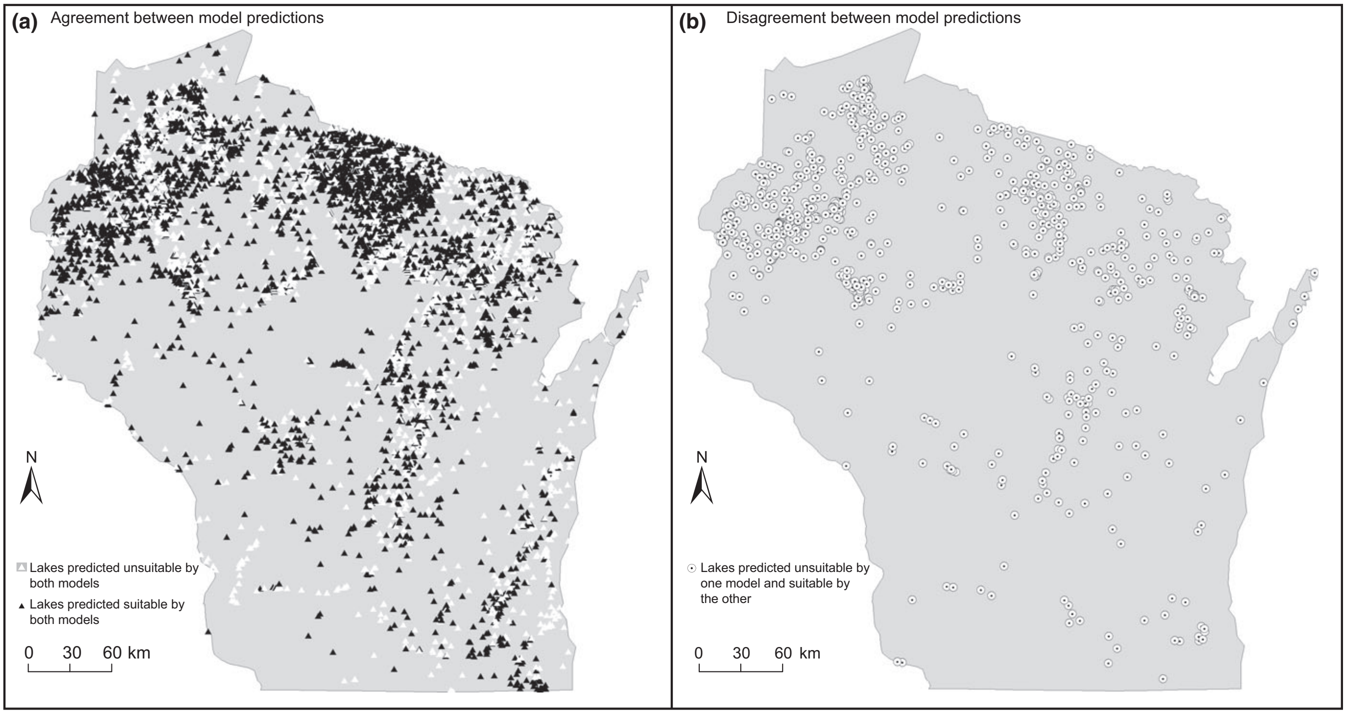


Fig. 4 A consensus map of potential distributions of Chinese mystery snail obtained with the two models based on lake and grid data sets. Lakes predicted unsuitable (white triangles) or suitable (black triangles) by both models are shown in panel a; prediction mismatch, suitable lakes according to one model and unsuitable according to the other (dotted circles), is shown in panel b.

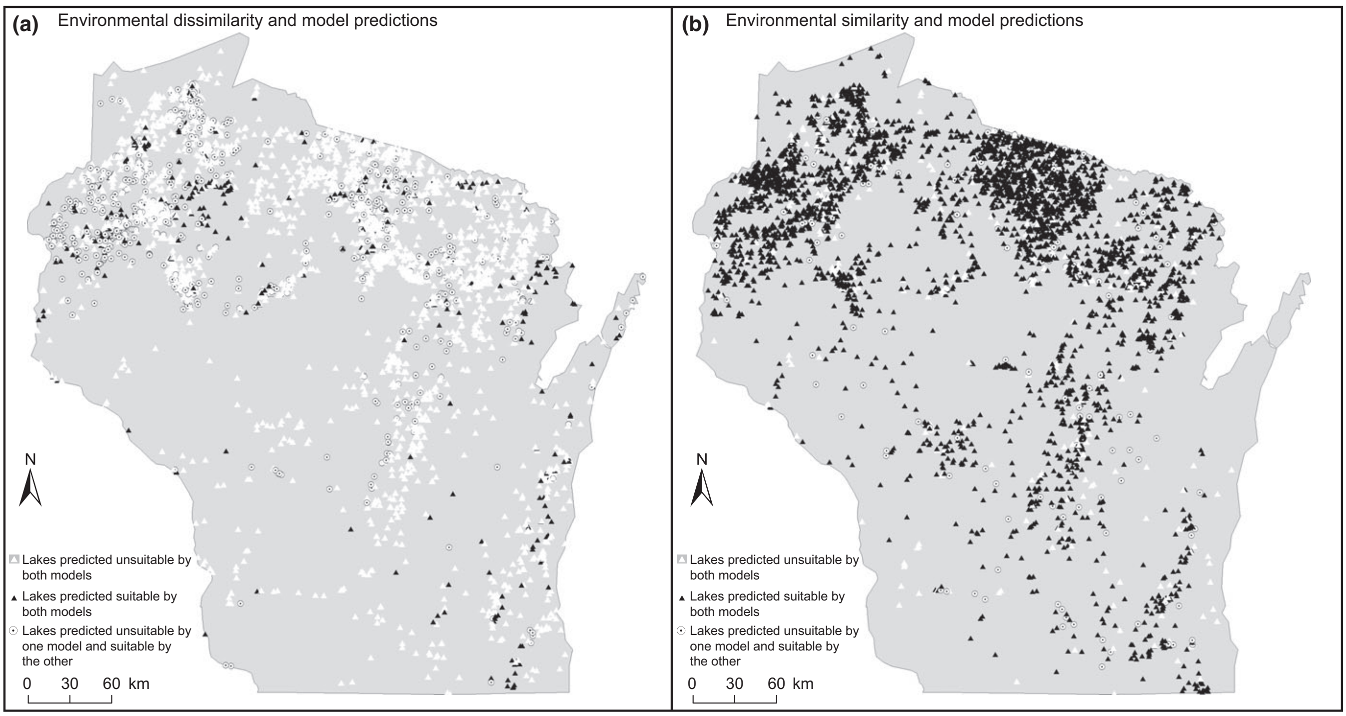


Fig. 5 Potential distribution variability in relation to environmental dissimilarity and similarity between lakes without and lakes with Chinese mystery snail records in Wisconsin. Note that for environmentally dissimilar lakes (panel a), both models predict most of the lakes unsuitable for Chinese mystery snail (74.7% of the dissimilar lakes), whereas for similar lakes (panel b), both models predict most of the lakes suitable for Chinese mystery snail (86% of the similar lakes).

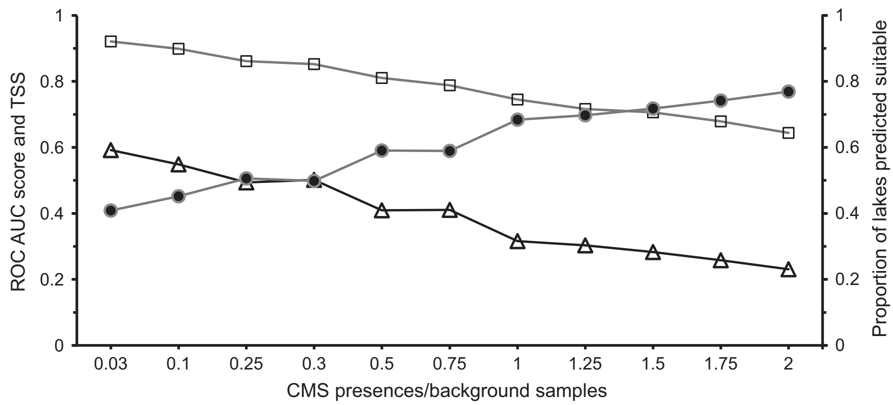


Fig. 6 The effects of simulated decreasing background sample sizes on model performance, measured with ROC AUC (square symbol; values above 0.7 indicate good performance) and TSS (triangle symbol; values above 0 indicate models better than random) and on discriminatory power between suitable and unsuitable lakes, assessed as the proportion of lakes predicted suitable (filled circle symbol). The minimum training presence threshold was used to convert the Maxent continuous suitability values to binary suitable-unsuitable and calculate proportion of lakes predicted suitable. The background samples sizes were selected based on the ratio between the number of known Chinese mystery snail presence records (CMS) and the rest of the lakes.

readily interpretable. To make our predictions for specific lakes available, we have added our assessment of lake suitability from the lake-based model to the Invasive Species Interactive Mapping System for Wisconsin (www.aissmartprevention.wisc.edu). This decision support tool is designed to help resource managers and lake associations in their ongoing efforts to prioritise and prevent the spread of freshwater invasive species (Papeş *et al.*, 2011).

Overall, there were no obvious spatial patterns in the lake suitability predictions (Fig. 3a). This result suggests that lake-specific environmental conditions have a role in determining predicted suitability to CMS. While two climate variables (precipitation in the wettest quarter and mean diurnal temperature range) contributed to the grid-based model, the lake-based model was mainly influenced by local environmental variables (conductivity and lake area).

There are three novel aspects in our estimation of an invasive species potential distribution in lakes: (i) we considered lake-specific variables (conductivity and lake area) in addition to climate variables; (ii) we restricted the grid format of the variables to lakes and (iii) we compared lake-based models to the commonly used grid-based models (excluding terrestrial cells). Lake-based models present the challenge of relying on environmental information for waterbodies that is difficult to obtain at broad scales. In terrestrial systems, the use of maximum entropy algorithm Maxent to estimate potential distributions of species is extensive because large scale climate data sets are freely available (e.g. WorldClim, PRISM). In lakes, environmental information is more often summarised as single observations per waterbody than a gridded surface. The availability of lake-specific information affects the amount of background sampling necessary to run Maxent. The implications of background sampling selection have been comprehensively examined in recent literature, but mostly using terrestrial species (Anderson & Raza, 2010; Merow, Smith & Silander, 2013) or virtual species (Barve *et al.*, 2011; Lobo & Tognelli, 2011; Barbet-Massin *et al.*, 2012). Thus, our study adds to this discussion the effects for predicting potential distributions of aquatic species.

Our study indicates that Maxent can produce models with good performance (as measured by ROC AUC, omission error, and TSS) using background sample sizes smaller than the default 10 000 points, but that model accuracy declines as background sample size decreases, particularly beyond sample sizes of 1000. In addition, discrimination between suitable and unsuitable lakes becomes questionable for models with background samples lower than 1000. We presume that a data set with fewer background samples decreases the discrimination power between suitable and unsuitable lakes because the models are trained on less heterogeneous background data and environmental conditions are more similar between presence and background data.

The environmental data set format (lake versus grid) influenced model performance measures, but not greatly. The lake-based model had lower omission error and higher ROC AUC than the grid-based models; thus the former can be considered more reliable than the latter. Nevertheless, the omission error, TSS, and ROC

AUC scores indicated good performance for both models. We attribute the good performance of the two models to large background sample sizes (default 10 000 for the grid-based model and 7703 for the lake-based model). Thus, in light of this comparison and the background simulation experiments, we propose that, if background sample sizes are above 1000, the data set format (lake or grid) may not have a major effect on model performance for predicting environmental suitability for invasive species in lakes.

The main goal of estimating environmental similarity of a large number of locations to locations supporting an invasive species is to generate a potential distribution map that can help with species prevention and containment efforts (Stewart-Koster, Olden & Johnson, 2015; Uden *et al.*, 2015). Our CMS consensus map between the two models generated using the lake and the grid data set formats indicated model disagreement of the suitability or unsuitability of 11% of the lakes. Depending on the species and prevention or containment situation, this level of discrepancy may or may not be acceptable.

Upon further analysis of the consensus map that considered environmental dissimilarity between lakes with and without known CMS presences, the models predicted that dissimilar lakes were mostly unsuitable for CMS (75% of lakes). On the contrary, environmentally similar lakes were largely predicted to be suitable for CMS (86% of the lakes). Thus, it seems that the modelling algorithm is more likely to associate environmentally dissimilar conditions to unsuitability than to suitability predictions. While this outcome may be expected given that Maxent attempts to estimate a species' ecological niche based on environmental associations with known presences of species, we note that limited knowledge of an invasive species' presence affects model accuracy and potential distribution estimates. In the context of invasion biology, previous studies using various modelling techniques have investigated the effects of model transferability on accuracy measurements (Randin *et al.*, 2006; Peterson *et al.*, 2007; Fernández *et al.*, 2012; Gies *et al.*, 2015). The reality of working with invasive species is that the incomplete nature of presence information, either due to sampling bias or invasion stage (undersaturated landscapes), will generally reduce the transferability of model predictions to broad geographic areas. However, monitoring and prevention efforts would still need to consider lakes or regions with high environmental dissimilarity, to account for the possibility of underestimated potential distributions.

Conclusions

We investigated the applicability of Maxent, an ecological niche modelling algorithm frequently used in terrestrial systems, to estimate the potential distribution of an invasive species in Wisconsin lakes. We found that environmental conditions summarised as individual lake observations (lake data set format) produce lower accuracy Maxent models when the background sample sizes are below one order of magnitude lower than the algorithm default of 10 000 points. Our study also highlighted that the models tended to predict as unsuitable lakes that are environmentally distinct from lakes with the invasive Chinese mystery snail presence records. Thus, potential distribution predictions may underestimate environmental suitability for the species of interest when the presence data set is small or environmentally biased.

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