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Range expansion risk for a newly established invasive duckweed species in Europe and Canada

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Research Article

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Abstract

Landoltia punctata is an invasive aquatic plant that has spread across the United States. Unlike native duckweeds, this species has developed herbicide resistance. As a result, invasion can lead to high management costs and the loss of recreational areas and natural habitats. The species has been recently found in Europe, and is also approaching the northern US border with Canada. We predicted the potential distribution of *L. punctata* in western Europe and Canada using presence-only data from the Global Biodiversity Information Facility as well as other literature records. We fit predictive models to this data using a Maxent approach. Since climate data based on surface lake water conditions are often more relevant to macrophytes than air temperature metrics, our models included both water and air temperature bioclimatic variables related to the life history of the species. Model comparisons confirmed a superior fit of lake temperatures to duckweed distribution records. The best fit model suggests a high habitat suitability for the species in most Western European countries and Western Canada. A moderate emission scenario suggests that in 2070 currently compatible areas will still be suitable, and that the Great Lakes region will become suitable. Preventive measures to avoid future spread of *L. punctata* are recommended in these locations to avoid impacts associated with this and similar duckweed species in Europe and the US.

Introduction

Dotted duckweed (*Landoltia punctata*) is an invasive alien species of concern which has spread in the United States in the last few decades. As the climate warms, this species is moving north (Jewitt, 2021). It has been recently observed in US states bordering the Great Lakes region (US Army Corps of Engineers, 2013), and invasion of Canada seems imminent. In addition, the species has also been recently documented in Europe (European and Mediterranean Plant Protection Organization – EPPO, 2015). The continental spread of dotted duckweed in the US, and subsequent ecological and economic consequences, suggests that an examination of invasion risks for dotted duckweed in Europe and Canada may be beneficial.

Globally, aquatic invasive alien species have cost US$23 billion in 2020, although this estimate is likely higher due to underreporting (Cuthbert et al., 2021). Aquatic weeds have an annual economic cost of US$110 million in the US (Pimentel et al., 2000), although we did not find studies estimating the economic costs of *L. punctata* specifically. For controlling duckweed overgrowth in general, an assessment of repeated herbicide application and water quality monitoring program conducted in duckweed infested Maskinonge River, Ontario, Canada, estimated an approximate cost of US$10,400/ha (cost corrected to November 2023 inflation rates; Warren & Neil, 1992). However, because dotted duckweed has developed resistance to herbicides (Koschnick et al, 2006), increased costs associated with herbicide research and development, and management costs from mechanical harvesting can be expected.

Once introduced, dotted duckweed can suppress native duckweeds (Center for Aquatic & Invasive Plants, 2023; Koschnick et al, 2006). Unlike its native counterparts, this species has developed resistance to diquat (Koschnick et al, 2006), one of the most frequently used herbicides to control duckweeds (Wersal and Madsen, 2009). It can form dense mats which cover the surface of water bodies, negatively affecting ecosystems and aesthetic features of recreational areas (Center for Aquatic & Invasive Plants, University of Florida, 2023). Duckweed mats can reduce light and oxygen levels in the water column, resulting in mortality of fish and other organisms. They can also disrupt recreational activities, such as fishing, canyoning, boating, and swimming (Jewitt, 2021).

Previous studies considering the risk of dotted duckweed invasion in Europe concluded that there is a low risk of negative consequences, as this invasive species is ecologically similar to native species, such as common duckweed (*Lemna minor*) (LCH van Valkenburg & Pot, 2008; Branquart, 2016). This assessment may be accurate; however, we note that Europe has been facing severe consequences from the invasion of a similar non-native duckweed species: least duckweed (*L. minuta*). Least duckweed has been clearly capable of quickly spreading (Appendix 1) and occasionally replacing the native common duckweed (Paolacci, Jansen, & Harrison, 2018b). Least duckweed invasions have also been associated with mat formations leading to waterway clogging (Duenas, 2022); reduction in light and oxygen resulting in lower plant and invertebrate richness (Ceschin, 2020); and loss of recreational areas (Paolacci, Harrison, & Jansen, 2018b).

Dotted duckweed is native to Southeastern Asia and Australia (Landolt, 1986), was accidentally introduced to the US state of Missouri around 1930, likely during aquarium supply transportation, and has expanded to several states ever since (Jacono & Pfingsten, 2023). It is considered as noxious in Texas and Lousiana, as a species of high concern in Alabama (Alabama Aquatic Nuisance Species Task Force, 2021), and it has a status of “cautious” in Florida, Minessota, Oklahoma, and Wisconsin (Foster et al., 2009; Cornell Legal Information Institute, 2009; Florida Invasive Species Council, 2019; Texas Invasive Species Institute, 2021; Midwest Invasive Plant Network, 2022). Occurrence records for this species in the US show a range expansion northward, approaching the Canadian borders in the Great Lakes Region (Fig. 1). Dotted duckweed is present in the Mississippi River, about 110 km from the Great Lakes basin, with a possibility of transfer to this region via aquatic pathways (US Army Corps of Engineers, 2013).

In Europe, this new invader was recently identified in several western countries. For instance, in 2022 it was found for the first time in a yearly survey as a stowaway plant in Belgian garden shops, indicating an early stage of invasion (Neucker & Scheers, 2022). Previous studies suggested a low invasion risk due to frost sensitivity (van Valkenburg & Pot, 2008; Branquart, 2016). However, more recent investigations indicate that both dotted and common duckweed resting fronds may have the ability to overwinter in between ice layers (Ziegler, Appenroth, & Sree, 2023). In fact, common duckweed overwintering capability was demonstrated in Quebec, Canada (Jewell & Bell, 2023). Although dotted duckweed overwintering has not been tested yet, frost sensitivity may not be a restrictive factor, considering physiological and ecological similarities between common and dotted duckweed which we will discuss in more detail subsequently.

Duckweed species can be spread by waterfowl, boats, aquarium trade, and as a stow-away from water garden trading (Landolt, 1986, Jewitt, 2021; Van den Neucker & Scheers, 2022; Jacono & Pfingsten, 2023). In addition to attachment to waterfowl body parts, living duckweed fronds were recently found to survive for several days and reproduce in duck feces. Considering the high mobility of ducks in short distances, such as roaming between water bodies, and long distances, such as in continental fall migrations, along with the high frequency of duck fecal events, endozoochory may be a major duckweed spread mechanism (Paolacci et al., 2023). The usual pathways for *L. punctata* introduction, namely aquarium trade, as a stowaway plant, and animal and boat transportation indicate the potential for multiple introductions, which makes widespread invasions such as that seen in the US more likely, as a result of propagule pressure (Lockwood, Cassey, & Blackburn, 2009).

As with other duckweeds, temperature is a key factor determining dotted duckweed distribution (Crawford et al., 2006), as it affects growth, survival, and reproductive success (Rejmánková, 1975; Mcilraith, Robinson, & Shay, 1989; Echelpoel, 2020). With the exception of some documented opportunistic behaviour resulting from environmental changes (Njambuya, Stiers, & Triest, 2011; Gérard & Triest, 2014; Paolacci, Jansen, & Harrison, 2016, 2018a), dotted duckweed, least duckweed, and common duckweed have similar habitat preferences (e.g., indistinguishable responses to environmental conditions found in Echelpoel, Boets, & Goethals, 2016), such as stagnant, nutrient-rich waters, temperature optima between 25–29°C, and intermediate levels of annual precipitation (Jacono, 2002; Paolacci, Jansen, & Harrison, 2018b). We did not find thermal performance divergences between dotted and common duckweed (Appendix 2). Due to these ecological similarities, it is possible that the range expansion of the invasive dotted duckweed may achieve similar dimensions as its native counterpart common duckweed or the invasive least duckweed.

In addition to current threats posed by invasive species such as dotted duckweed, future invasion scenarios will depend on climate change intensification. In the US, dotted duckweed invasion is moving northwards as a result of a warming climate (Jewitt, 2021). Thus, predictions of invasion risks for dotted duckweeds should consider both present and future environmental conditions to enable short term and long term invasive species management.

Recent findings of duckweed frost resistance, dotted duckweed herbicide resistance, and multiple introduction pathways (e.g., waterfowl dispersal by endozoochory and as a stow-away plant) lead us to hypothesize that dotted duckweed has a potential range similar to that of least duckweed and common duckweed in Canada and in Europe. Secondly, we predict that dotted duckweed range expansion to more Northern regions of Europe and Canada will become more likely in future climate scenarios. To test these predictions, we selected dotted duckweed life history information connected with temperature dependency and precipitation, and predicted the species' possible distribution in Europe and Canada.

Methods

To model current and future habitat suitability for dotted duckweed in Canada and Europe, we used maximum entropy distribution models (Maxent), a widely used approach due to its high prediction power (Elith et al., 2006, Elith et al., 2011). We retrieved occurrence records of dotted duckweed from the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/) and from published papers (Appendix 3). The environmental predictors selected for modeling distribution were based on satellite-derived lake water temperatures, which better represent duckweed habitat conditions than the customarily used air temperature-derived variables (Armitage, 2023). Additionally, we compared Maxent models using air versus lake water temperatures. Finally, future climate scenarios based on air temperatures projected by the Intergovernmental Panel on Climate Change (IPCC) were used to evaluate future habitat suitability for dotted duckweed in Canada and Europe.

Species information

Dotted duckweed is among the smallest flowering plants known (Tippery & Les, 2020). It has the typical simplified body plan of duckweeds, with floating fronds consisting of both leaf and stem cells. The species is characterized by several roots attached to the abaxial side of the fronds. Flowering is rare, as duckweeds preferentially reproduce asexually. As with other duckweeds, reproductive rates are among the highest in the plant kingdom (Ziegler et al., 2015).

Types of climatic data

We used 3 different types of climatic variables to create and compare candidate distribution models, namely bioclimatic predictors based on current air temperatures, predictors based on current lake temperatures, and predicted future temperature variables. These 3 categories are composed of 19 bioclimatic variables. Commonly used current air temperatures were obtained from the WorldClim database (https://www.worldclim.org; Merow, Smith, & Silander Jr, 2011; Fick & Hijmans, 2017).

Lake water temperature predictors were calculated by Armitage (2023) and are based on GloboLakes, a global database of satellite-calculated daily temperatures of lake surfaces (www.laketemp.net/home_GL). The author adjusted the relationship between these lake temperatures and air temperatures using machine learning models based on various atmospheric and geographical factors. Bioclimatic layers were then developed in a similar fashion to air temperature bioclimatic variables.

To predict habitat suitability under a climate change scenario, we used air temperatures from the Intergovernmental Panel on Climate Change (IPCC) climatic predictions for 2070 under a moderate scenario (RCP45), which considers slow carbon emissions across time. These future temperature predictions are also available from the WorldClim database.

All climatic layers were adjusted to correspond to a spatial resolution of 1.56 arc second spatial resolution, which is fine enough to capture an adequate number of samples in the test region.

Determination of predictors informed by life history

In order to reduce model complexity and improve accuracy, we pre-selected biologically relevant predictors within each climatic data type. These candidate predictors were selected based on factors impacting dotted duckweed life history.

Ambient temperatures are a major factor impacting ectothermic organisms such as plants, as their body temperatures depend on external heat sources (Huey & Kingsolver, 1989). As previously mentioned, temperature changes affect duckweed growth, survival, and distribution (Rejmánková, 1975; Mcilraith, Robinson, & Shay, 1989; Echelpoel, 2020). We selected the bioclimatic predictors BIO 1 (mean annual temperature) and BIO 7 (annual range of temperature) to describe the thermal-dependency of dotted duckweeds. Such predictors were previously used in Maxent models describing the distribution of similar duckweed species, and are also known to be good predictors of duckweed thermal performance (see Armitage, 2023).

The bioclimatic variable BIO 10 (mean temperature of the warmest quarter) was included to reflect dotted duckweed optimal growth in warm months. The optimal temperature maximizing dotted duckweed photosynthesis is 25°C (Wisconsin Department of Natural Resources, 2018), which more closely corresponds to summer average temperatures in Europe and southern Canada (around 20°C; Copernicus, 2023, Environment Canada, 2023) in comparison with other seasons of the year.

As previously discussed, duckweeds are rare in places with high or very low precipitation (FNA, 2000). The bioclimatic variable BIO 19 (mean annual precipitation) was selected to determine if habitat suitability reflected a need for moderate levels of precipitation. However, dotted duckweeds display drought tolerance, and are found in dry regions of Australia. The species can produce drought-resistant seeds (Jacono, 2002). The bioclimatic variable BIO 17 (precipitation of driest quarter) was added to determine if dotted duckweed can be found in drier regions.

Species occurrence data

The majority of the occurrence records used in our models were collected from the Global Biodiversity Information Facility (https://doi.org/10.15468/dl.e8qy3r). Sixteen European records described in research papers were also added (Appendix 3). We removed duplicate records and records missing geographic coordinates, resulting in 2,784 observations. To reduce bias from heavily sampled regions, we thinned the data by selecting a single datapoint per 1.56 arc seconds. Our final thinned dataset was composed of 709 observations.

Maxent species distribution models

For each of the 3 climatic data types used (current air temperatures, lake water temperatures, and future air temperatures), we created and compared candidate Maxent models (Maxent 3.4.4: https://biodiversityinformatics.amnh.org/open_source/maxent; Phillips et al. 2017) using the R (R Core Team, 2021) package ENMeval package (Muscarella et al., 2014). We constrained the functional forms used to predict occurrence from climate variables to linear and/or quadratic features that might reflect

known biological responses and/or life history characteristics which depend on climatic factors, such as unimodal thermal dependence (Merow et al. 2013).

We divided our final thinned dataset into training and testing datasets. The training dataset consisted of global records except Europe (668 observations), while our testing dataset was composed of European records (41 observations). We designated a study area encompassing 600km around occurrence records, and selected 709 background points within this study area using a 1.56 arc second spatial resolution. To account for spatial autocorrelation, we performed cross validation by dividing the training data into 4 spatial blocks (Roberts et al., 2017).

We performed a preliminary model fit using lake water temperature predictors to obtain variable contribution and correlation. Those predictors which had the lowest contribution and which were highly correlated with the largest contributing predictors were removed (Table 1). Correlation between predictors was determined using Pearson's correlation coefficients. The final variable selection included mean annual temperature (BIO 1), annual temperature variation (BIO 7), and mean annual precipitation (BIO 19).

Table 1

Variable percent contribution and Pearson correlation coefficients of preselected variables for the preliminary model fit. The variables designated for subsequent model fits were selected based on highest contribution and lowest correlation values. Selected predictors were BIO1 (mean annual temperature), BIO7 (annual range of temperature), and BIO19 (mean annual precipitation).

		Pearson correlation coefficients				
Preliminary variables	Variable contribution	BIO 1	BIO 7	BIO 19	BIO 17	BIO 10
BIO 1 (mean annual temperature)	36.92%	1	-0.65	0.18	0.05	0.94
BIO 7 (annual range of temperature)	20.44%		1	-0.38	-0.3	-0.35
BIO 19 (mean annual precipitation)	19.41%			1	0.8	0.07
BIO 17 (precipitation of driest quarter)	15.33%				1	-0.05
BIO 10 (mean temperature of the warmest quarter)	7.9%					1

We then created several candidate Maxent models using these 3 climatic variables and a range of regularization parameters to produce models with different levels of complexity. These models were evaluated using the Area Under the Curve (AUC) approach, which gives the probability of telling apart a given presence observation in the testing dataset from a random background point in the study area (Merow, Smith, & Silander Jr, 2013). We also estimated the True Skill Statistic (TSS), which compares model predictions to a validation dataset. It is calculated as the proportion of presences correctly predicted (sensitivity) + the proportion of absences correctly predicted (specificity) -1. (Allouche, Tsoar, &

Kadmon, 2006; Ruete & Leynauld, 2015). The Akaike information criterion (AIC) was also calculated for each model. The permutation importance of each predictor was determined by randomly rearranging the values of variables across training points and assessing the subsequent reduction in AIC values. Finally, we analyzed if tolerance ranges from response curves are realistic considering climate data in occurrence regions. For BIO 1 (mean annual temperatures), we verified the adequacy of response curves to experimentally-obtained performance curves reflecting the life history of dotted duckweeds.

For each selected maxent model, the AUC and TSS were estimated for 4 datasets: the training data which consisted of global records excluding Europe; the test data including European records; European records with exact geographic coordinates from GBIF; and literature records containing both exact and approximate European geographic coordinates. These latter two groups were assessed to investigate if using records with inexact geographic coordinates would reduce the predictive power of the selected model.

Results

Distribution models

In order to predict current and future distribution scenarios for dotted duckweed, we selected the best model (highest test data average AUC and lowest AICc) among candidate models fit with linear or linear and quadratic terms, and several options of regularization parameters. We repeated this process for models created using current lake water temperatures, current air temperatures, and future scenarios based on air temperatures (see Appendix 4 for information on all candidate models). We selected the best model for each set of the three climatic data types. For all cases, the selected model was fitted with both linear and quadratic terms, 0.5 regularization multipliers and 5–6 parameters (Table 2).

Table 2

The best models for each of the 3 types of climatic data (current lake water, current air, future air temperatures). Each of these models was selected amongst 16 candidate models (Appendix 4). Model features (linear or linear and quadratic together), regularization multipliers, Area Under the Curve (AUC) metric for the data used in training, average AUC considering the 4 testing spatial blocks, AICc values, delta AICc, and number of parameters used in each selected model. The selected models have the lowest AICc and the highest average testing AUC.

Model	Features	Regularization multiplier	Training AUC	Mean testing AUC	AICc	Number of parameters
Current lake	LQ	0.5	0.89	0.81	15,485	6
Current air	LQ	0.5	0.87	0.77	20,218	5
Future air	LQ	0.5	0.88	0.78	20,178	6

All selected models had good predictive power. For the current lake temperature model, the 10th percentile training presence threshold was 0.41; for the current and future air models, this threshold was 0.46. The global training data had AUC ranges of 0.87–0.89 and TSS of 0.62–0.64 when applying the maximum training sensitivity plus specificity threshold (current lake = 0.56, current air = 0.60, future air = 0.58). The European test data had AUC ranges of 0.85–0.94 and TSS of 0.70–0.80 when considering this same threshold (Table 3). The model using lake water temperatures had the highest predictive power, while the model using current air temperatures had the lowest predictive power. Model transferability was only slightly affected by the addition of records with inexact coordinates, as TSS values are not greatly reduced when comparing datasets including versus excluding inexact occurrences (Table 3).

Table 3

Accuracy metrics for models based on different temperature variables. The training dataset is composed of global dotted duckweed records except European; the testing dataset is composed of European observations from GBIF and both exact and inexact European records found on research papers. The “exact locations” dataset is restricted to GBIF and literature observations with exact coordinates.

	TSS			AUC		
Model	Train	Test	Exact locations	Train	Test	Exact locations
Current lake	0.64	0.80	0.80	0.89	0.94	0.95
Current air	0.62	0.73	0.79	0.87	0.85	0.87
Future air	0.63	0.71	0.74	0.88	0.85	0.86

The percentage contribution and permutation importance for each climatic variable was obtained across models. Overall, BIO 1 (mean annual temperature) and BIO 7 (annual temperature variation) variables have the highest permutation importance across models, while BIO 19 (mean annual precipitation) has the lowest importance. However, while BIO 7 is the most important variable for the model based on lake temperatures (49%), BIO 1 is the most relevant predictor for the models based on air temperatures (60.1% and 51.5% for models based on current and future temperatures, respectively).

Table 4

Percentual contribution and permutation importance for predictors used across models. Values for variables with the highest permutation importance are in bold. BIO 1 (mean annual temperature); BIO 7 (annual temperature variation); BIO 19 (mean annual precipitation).

	BIO 1		BIO 7		BIO 19	
Model	% contr.	Permut. import.	% contr.	Permut. import.	% contr.	Permut. import.
Current lake	46.8	38.7	40.2	**49.0**	13.0	12.2
Current air	47.7	**60.1**	45.0	39.5	7.3	0.4
Future air	55.9	**51.5**	37.0	45.9	7.1	2.7

Response curves

The fitted response curves for the climatic variables are unimodal (Fig. 2). Overall, responses are realistic, as their values are within climate data from occurrence records, as indicated by optimal suitability values and range (Table 5). Within the 3 bioclimatic variables, BIO 7 (annual range of temperature) responses are the most divergent among models, as the lake-based temperature model predicts a much narrower response curve that reflects a narrower range of temperatures in relation to the air temperature models. For BIO 19 (mean annual precipitation), the model based on air temperatures estimated a decreasing function with much less variability across temperatures in relation to the other models. Optimal suitability estimated by the current air temperature model also occurs at much lower precipitation conditions in comparison with the other models (Table 5).

Table 5

Suitability values given by response curves of each Maxent model.

	BIO 1 (°C)			BIO 7 (Δ°C)			BIO 19 (mm)		
Model	Min	Opt	Max	Min	Opt	Max	Min	Opt	Max
Current lake	4.7	15.7	30.7	5.2	16.8	33.2	-8.6	349.8	1,765
Current air	0.2	15	30.1	7.7	20.7	49.3	-9	-9	1,701
Future air	3.9	17.52	32.6	7.9	22.8	49.5	-10	466.9	1,513

BIO 1 (annual mean temperature) response curves from both water and air models based on current temperatures are very similar. A thermal performance curve for dotted duckweed obtained in laboratory conditions was scaled to maximum BIO 1 response values to enable a comparison with response curves in a similar fashion as in Armitage (2023). This curve was then superimposed to BIO 1 response curves. The response curves fit using lake temperatures, current air temperatures, and future air temperatures are all similarly following the overall shape of a thermal performance curve obtained in the laboratory for

this species. Additionally, the response curve using future air temperatures approaches slightly more the laboratory-obtained thermal performance curve in comparison to curves fit using current conditions (Fig. 2).

Current and future habitat suitability prediction maps

Overall, our models indicate several currently unoccupied regions which are suitable for dotted duckweed in Europe and Canada. Such areas include most of western Europe and some western areas in Canada (Fig. 3). For both Europe and Canada, models based on lake water temperatures predict a much larger suitable area for dotted duckweed in relation to models using air temperatures.

Future dotted duckweed habitat suitability in a moderate emission scenario indicates that Western Europe will continue being highly suitable, while some areas in eastern Canada that are currently unsuitable will become suitable, such as the Great Lakes region (Fig. 3).

Discussion

Our models provide evidence that most areas in Western Europe and some western and eastern areas of Canada are currently suitable habitats for dotted duckweed. Our future predictions indicate that Europe will continue being highly suitable for this species, and that the Great Lakes region in Canada will become a suitable habitat for this invasive species.

Models using lake water temperatures have a lower prediction error than the models using air temperatures across all performance metrics. These results are in accordance with previous research that predicted the distribution of common duckweed and greater duckweed using the same satellite-measured lake water temperature climatic layers as the ones we did (Armitage, 2023). Al-Chokhachy et al. (2013) also found that stream water temperatures improve the performance of models predicting fish distribution. In conjunction with these other studies, our research suggests that using water temperature-corrected predictors more closely reflects thermal niches and leads to more accurate distribution predictions than models based on air temperatures.

In Armitage's (2023) study, response curves for BIO 1 (mean annual temperatures) were found to be similar to thermal performance curves for common and greater duckweed. In our research, model tuning also resulted in response curves that approximate the shape of dotted duckweed thermal performance curves. Thus, the distribution predictions obtained herein and by Armitage (2023) may reflect the thermal physiology of the studied species. The superiority of these predictions in relation to air temperature-based models can be illustrated by observing duckweed range limits in Armitage (2023) and in our research. In both studies, lake water temperature-based models better reflect observed margins (e.g., predictions matching observed records in northern locations such as Sweden and Finland) in comparison to models based on air temperatures. Differently than models based on air temperature, models based on water temperatures also predict high suitability in several western Canadian regions, which match the distribution of ecologically similar common duckweed, as seen in Armitage (2023).

Unlike Armitage (2023), our models based on water versus air temperatures do not result in different annual mean temperature (BIO 1) response curves: both models similarly approach the shape of dotted duckweed thermal performance curves. Thus, for dotted duckweed, variables other than BIO 1 seem to be behind the superior performance of the model based on lake water temperature. This is indeed the case, as BIO 7 (annual temperature variation) has the highest permutation importance in the model based on water temperature, while the models based on air temperature are mostly driven by BIO 1. Considering that the model based on lake water climate factors is the best predictor, we can conclude that dotted duckweed optimal habitats are characterized by lower annual temperature variation than suggested by models based on air temperature.

In addition to BIO 7, mean annual precipitation (BIO 19) is more important for the model using lake temperature than it is for the models using air temperature. Moreover, the unimodal annual precipitation curve resulting from the lake temperature-based model better characterizes the need for moderate precipitation levels reported in the literature for duckweeds in comparison to the decreasing curve obtained in the current air temperature-based model.

Taken together, the divergences identified in models fit using lake water temperature-corrected variables lead to predictions of a much wider suitable habitat for dotted duckweed in Europe and Canada than estimated by air temperatures. Our model with the highest predictive performance based on lake water temperature suggests that the countries at highest risk for dotted duckweed establishment in western Europe are Portugal*, Ireland, UK*, France*, Belgium*, Netherlands*, and Denmark. Such territories are practically 100% suitable for this invasive species. In other countries such as Spain, Italy*, Switzerland*, Germany, Austria, Norway, Sweden*, and Finland*, dotted duckweeds can find a mix of either moderately suitable or highly suitable habitats (countries highlighted with an asterisk have already been invaded by dotted duckweed). Unsuitable regions in Europe include semi-arid areas in Spain and the Alps mountain range.

In Canada, current suitability is mainly restricted to the provinces of British Columbia and Alberta and a few maritime locations. In British Columbia, highly suitable areas include the southern coast and the central interior region. These areas are characterized by more moderate precipitation levels and milder temperatures than mountainous or northern regions of the province (Wang et al., 2016). Additionally, dotted duckweed was observed in Portland, Oregon, US, in 2007, at about the same longitude and around 240 km south from this Canadian region. Thus, risk of invasion is increased in highly suitable habitats in western Canada because of the presence of this invasive species relatively close to the US-Canada border.

In Alberta, Canada, suitability coincides with the Boreal Plains ecozone, characterized by moderate precipitation levels, cold winters, and mild summers (Smith et al., 1998). Cold winters may not be an impeding factor for dotted duckweed establishment, given duckweed frost tolerance (Jewell & Bell, 2023; Ziegler, Appenroth, & Sree, 2023). British Columbia and Alberta were also shown to be highly suitable to common duckweed in previous studies using lake water temperature-based models. Moreover, the

current distribution range of common duckweed includes these and other northern regions in Canada (Armitage, 2023). Therefore, it is plausible to consider that these areas can be invaded by dotted duckweed because these species have very similar thermal performance curves (Appendix 2).

Future distribution predictions based on a moderate emission scenario indicate that most currently suitable areas will still be viable for dotted duckweeds in 2070. Moreover, new suitable areas will become available both in Europe and in Canada. Nordic countries will become more viable than nowadays in Europe, while the Great Lakes region will become suitable in Canada. Because this species is currently abundant across the East of the US, including observations very close to the Canadian border (about 110 km to the Canadian Great Lakes region), climate change preparedness plans for the region should consider this invasion risk in the near future.

One limitation of our study is the lack of future climate predictions for lake water temperature. Predictions based on water temperatures could yield more realistic species distributions across climate change emission scenarios. Such data might also be valuable if applied to other invasive species, such as the new 6 invasive aquatic plants among the recently released list of the 10 prohibited invasive species in Ontario, Canada (Ontario Newsroom, 2023).

Previous studies predict low invasion risks for dotted duckweed in Europe due to life history similarities with its native counterpart common duckweed. However, least duckweed (*L. minuta*), consisting of another ecologically similar duckweed species, has achieved a widespread distribution in Europe. Likewise, dotted duckweed has spread across the US in the last few decades. Our research predicts that dotted duckweed has the potential to achieve wide distribution in North America and West Europe. This wide distribution may lead to significant ecological and economic impacts. Thus, we suggest that dotted duckweed has the potential to be as disruptive as the invasive least duckweed in western Europe.

In addition to ecological damage, waterway clogging, and loss of recreational areas, aquatic invasive species such as dotted duckweed can invade aquaculture breeding tanks and result in economic loss in this industry (e.g., see impacts of invasive tunicates for the mussel aquaculture industry in Canada; Fisheries and Oceans Canada, 2016). In fact, one data record describes dotted duckweed growing as “very vital monocultures found in outdoor breeding tanks” in Belgium (van Valkenburg & Pot, 2008). Aquaculture is a major industry in western Europe, worth €4.2 billion in 2021 (Eurostat, 2021). Thus, considering risks to both natural environments and economic activities, environmental managers both in European countries with a recent dotted duckweed invasion history and in uninvaded countries are recommended to develop surveillance systems and/or early containment programs.

The potential for widespread distribution found in our work highlights the importance of prevention or early containment as the only feasible measures to avoid or reduce negative consequences of invasive dotted duckweed spread. The large regions of potentially suitable habitat predicted by our model indicate the potential for invasion scenarios in Europe and Canada similar to the observed for least duckweed in Europe and dotted duckweed in the US. Future studies could also focus on other

geographic areas currently reporting dotted duckweed invasions, such as eastern Europe, the Middle East, and South America.

Once dotted duckweed spreads, management becomes virtually impossible, as it reproduces asexually and has one of the fastest growth rates seen in higher plants (Ziegler et al., 2014). In addition, there are multiple introduction pathways, such as aquarium and garden trade (Neucker & Scheers, 2022), and deposition through waterfowl feces (Paolacci et al., 2023). Herbicide resistance developed by dotted duckweed (Koschnick et al, 2006) is an additional factor that would hinder management actions. Potential preventive measures include the development of regulations and educational awareness to the garden and aquarium industries.

Declarations

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Author Contribution

D.A.P and K.C. wrote the main manuscript text and D.A.P prepared models and figures. All authors reviewed model analyses and the manuscript.

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Figures

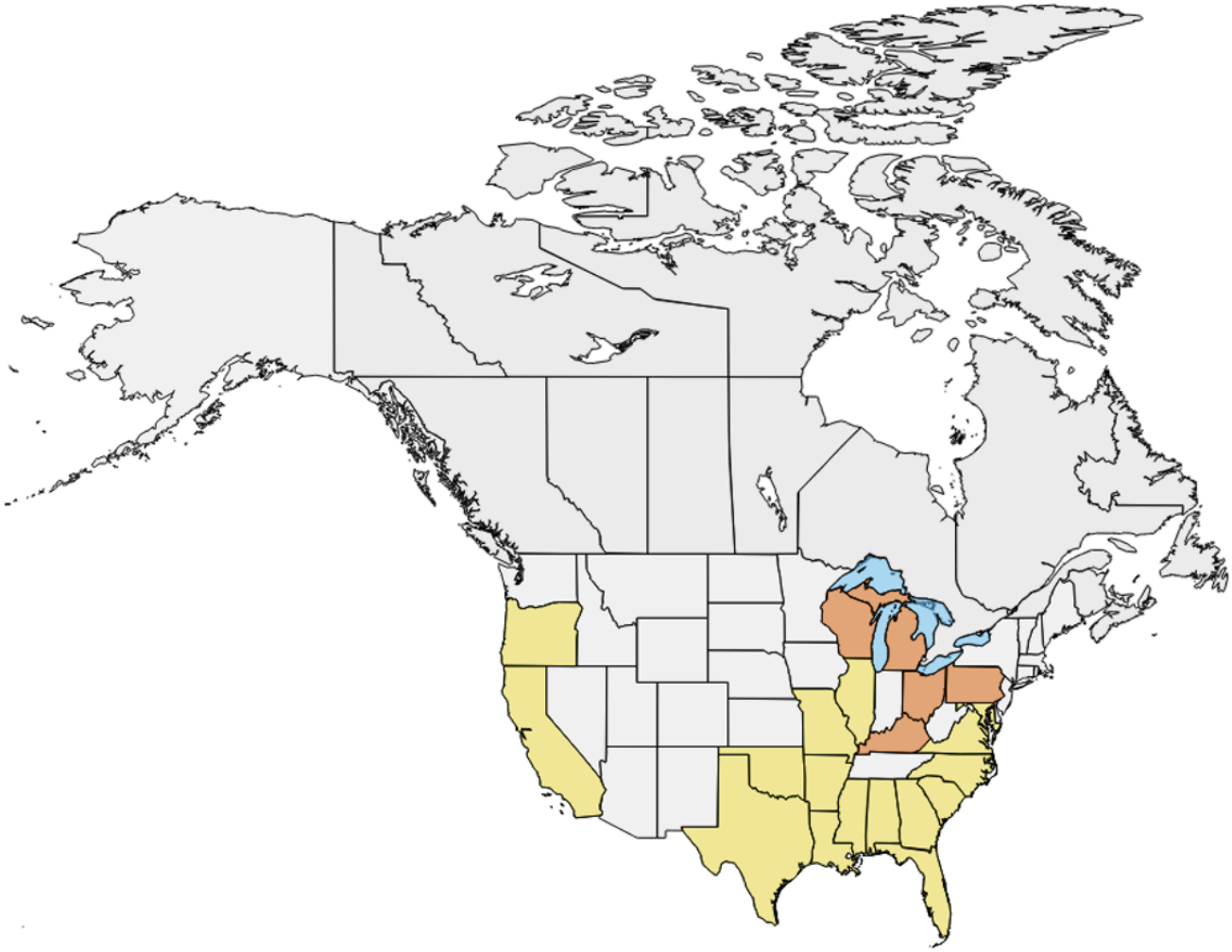


Figure 1

US states where dotted duckweed was identified in past years (yellow: before 2000, orange: after 2000). Year of occurrence refers to the first time this species was recorded in a given jurisdiction. Species occurrence retrieved from GBIF.org on 2023-09-19 (https://doi.org/10.15468/39omei).

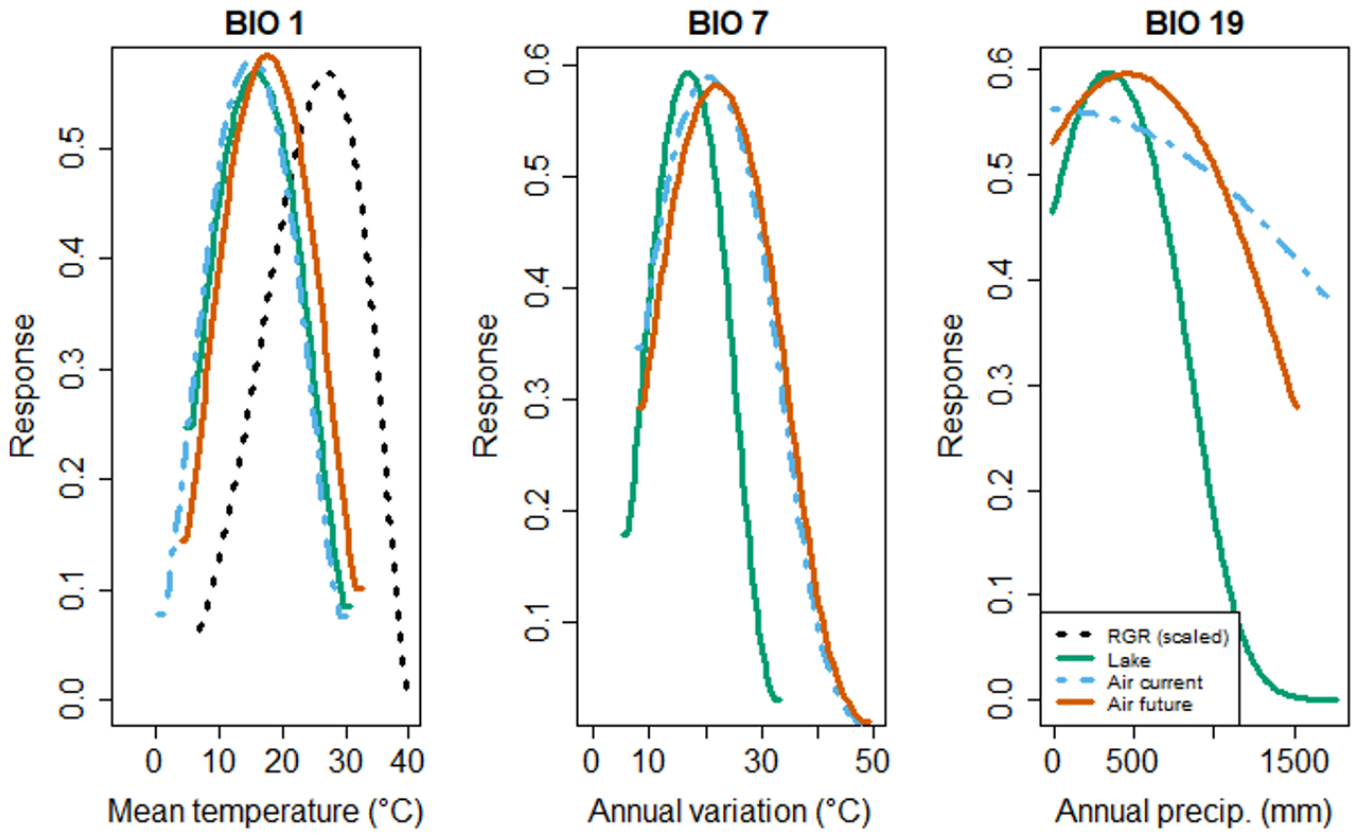


Figure 2

Response curves obtained from the selected Maxent models for BIO 1 (mean annual temperature), BIO 7 (annual range of temperature), and BIO 19 (mean annual precipitation). For BIO 1, a thermal performance curve for dotted duckweed was added for comparison with Maxent response curves. Performance is based on relative growth rates (RGR) obtained by counting final populations of individual fronds across several constant temperatures after a 5-day experiment period. The curve is based on the Ratkowsky model (Ratkowsky, 1983).

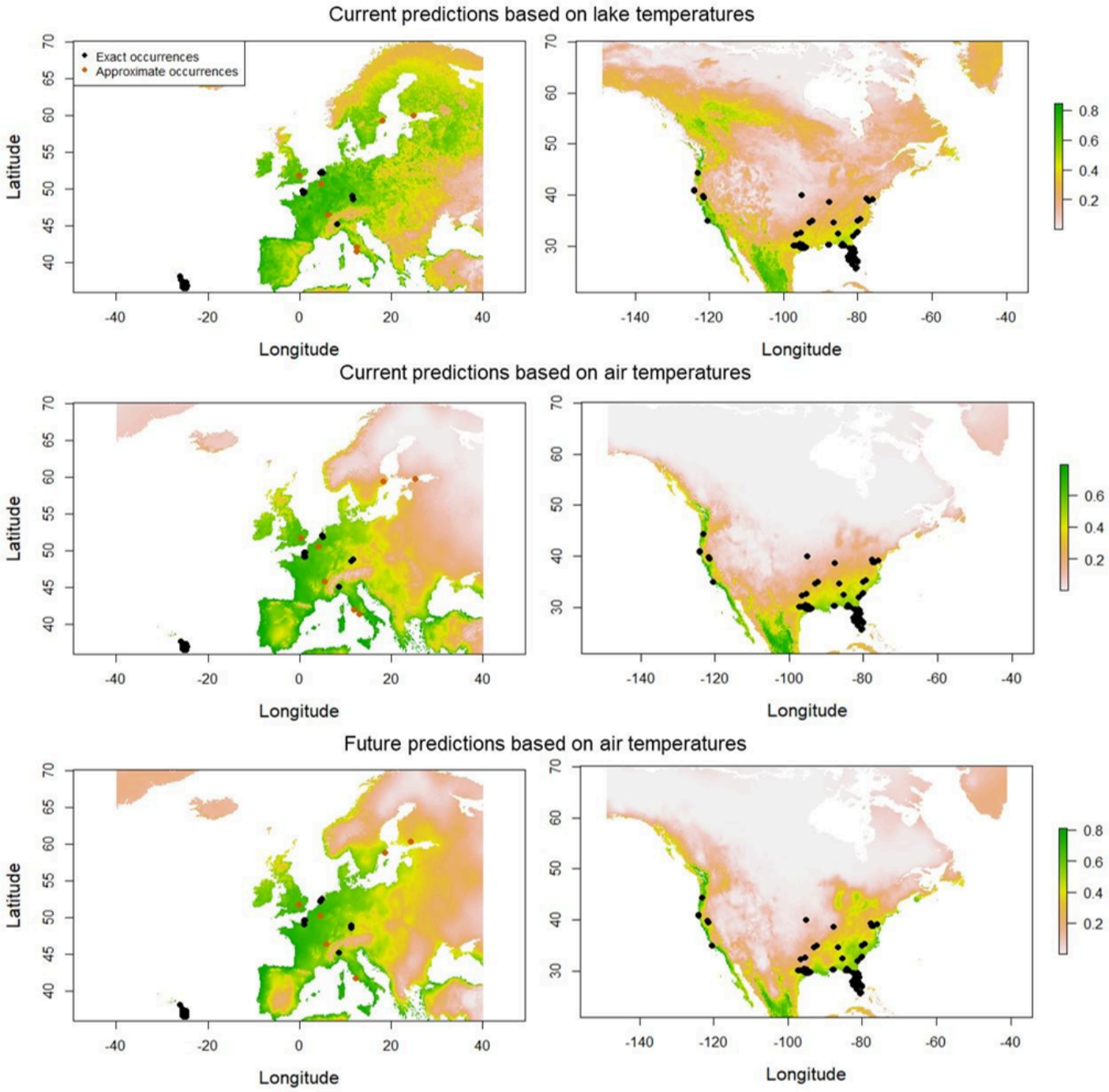


Figure 3

Predicted habitat suitability for dotted duckweed in western Europe and North America. Habitat suitability is in a scale of 0 to 1 and results are shown for the best models based on BIO 1 (mean annual temperature), BIO 7 (annual range of temperature), and BIO 19 (mean annual precipitation) environmental variables from Armitage (2023) (lake water temperatures) and https://worldclim.org (current and future predictions based on air temperatures).

Supplementary Files

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