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Forecasting the Invasion of Eurasian Watermilfoil (*Myriophyllum spicatum*) at the Northern Edge of Its North American Range

Lars Lønsmann Iversen[1,2] | Morgan Botrel[1,2,3] | Gray Fedirchuk[1,2] | Valérie Langlois[1,2] | Olivier Morissette[2,4] | Marie-Eve Tousignant[5] | Lindsay Trottier[1,2] | Irene Gregory-Eaves[1,2]

[1]Department of Biology, McGill University, Montreal, Quebec, Canada | [2]Groupe de Recherche Interuniversitaire en Limnologie, Montreal, Quebec, Canada | [3]Département de Biologie, Chimie et Géographie, Université du Québec à Rimouski, Rimouski, Quebec, Canada | [4]Département des Sciences Fondamentales, Université du Québec à Chicoutimi, Chicoutimi, Quebec, Canada | [5]Ministère de l'Environnement, de la lutte Contre Les Changements Climatiques, de la Faune et des Parcs, Québec, Quebec, Canada

Correspondence: Lars Lønsmann Iversen (lars.iversen@mcgill.ca)

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ABSTRACT

1. Eurasian watermilfoil (*Myriophyllum spicatum*) is an invasive aquatic plant posing increasing ecological and management challenges in North America. In Quebec, Canada, the species is rapidly expanding northward into uncolonised catchments. Thus, accurate forecasting of invasion risk is essential to guide proactive monitoring and intervention. This study aims to (i) compare the predictive performance of species distribution models (SDMs) trained at different geographic scales; (ii) identify environmental and anthropogenic factors influencing Eurasian watermilfoil presence at its northern range expansion; and (iii) project future invasion risk under scenarios of climate warming and population growth.
2. We developed random forest SDMs using Eurasian watermilfoil occurrence data from Quebec, North America and Europe, coupled with 24 environmental and anthropogenic variables for 11,823 sub-basins in Quebec. Model performance was assessed across regional, continental and global training datasets. Future projections were based on six scenarios combining population and climate change predictions through 2070 and 2100.
3. Models trained on regional data from Quebec yielded significantly higher prediction accuracy than models based on their broader North American invasive range, their native range in Europe, or combined data. Maximum temperature, mean temperature, precipitation, lake volume and population density emerged as the most important predictors. Under high-warming scenarios, the area predicted to be suitable for Eurasian watermilfoil increased nearly fivefold, with invasion hotspots expanding notably in western Quebec and along the St. Lawrence and Saguenay rivers.
4. Regionally calibrated models more accurately reflect the realised niche of Eurasian watermilfoil at its current invasion front. Projected climate and demographic changes are likely to dramatically expand suitable habitat, increasing invasion risk across Quebec's freshwater landscapes.
5. This study highlights the importance of local context in invasion forecasting and provides a scalable, spatially explicit framework to inform monitoring and management strategies in a globally relevant conservation issue.

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1 | Introduction

Biological invasions are a leading driver of biodiversity change in freshwater ecosystems, threatening their ecological integrity, biodiversity and ecosystem services (Havel et al. 2015; Sayer et al. 2025). Among invasive aquatic plants, *Myriophyllum spicatum* L., commonly known as Eurasian watermilfoil, has emerged as one of the most successful and disruptive macrophytes in North America (Les and Mehrhoff 1999; Jacobs and Mangold 2009; Zhang and Boyle 2010). Eurasian watermilfoil was likely introduced to North American waters via ballast water or to serve as an aquarium plant, and initial documentation of its presence dates back to the 1940s in the United States and in the 1950s in Canada (Aiken et al. 1979; Moody et al. 2016; Jacob-Racine and Lavoie 2018). Eurasian watermilfoil has expanded its range across North American lakes and rivers, forming dense, surface-reaching canopies that suppress native vegetation, disrupt food webs, alter water chemistry, sediment composition and impair human use of waterbodies (Lillie and Barko 1990; Schultz and Dibble 2012; Tasker et al. 2022).

Eurasian watermilfoil is especially abundant in nutrient-rich lakes where its rapid vegetative reproduction—via stem fragmentation and auto-detaching internodes—facilitates both local dominance and long-distance dispersal (Smith and Barko 1990). The species' competitive success stems not only from its growth form but also from its ability to modify the environments it invades. By forming dense, monospecific stands, Eurasian watermilfoil has been shown to alter light penetration and oxygen gradients in the water column, leading to hypoxia in bottom layers and changes in nutrient cycling (Kistritz 1978). For example, while surface oxygen concentrations may increase due to photosynthetic activity in the upper canopy, bottom waters can become oxygen-depleted with canopy shading and decomposition of the abundant organic matter produced (Stanley and Naylor 1972; Unmuth et al. 2000; Hoblyn and Iversen 2024). These alterations can have cascading effects on benthic macroinvertebrate communities, fish habitat and overall ecosystem functioning (Lillie and Budd 1992; Wilson and Ricciardi 2009; Schultz and Dibble 2012). Beyond ecological effects, Eurasian watermilfoil also has socio-economic implications. Its presence is known to reduce recreational value, impede navigation and diminish property values along infested shorelines (Jenkins 2001; Olden and Tamayo 2014; Goodenberger and Klaiber 2016). Consequently, a wide array of management interventions has been developed, including hand pulling, application of benthic mats, mechanical harvesting, herbicide applications and biological control—each with varying success but important economic costs (Sheldon and Creed Jr 1995; Kujawa et al. 2017; Gagné and Lavoie 2023). Prevention is thus the most cost-effective approach. A first step is to develop predictive models that provide information about the potential spread and distribution of Eurasian watermilfoil, allowing lake associations and government authorities to deploy containment strategies (e.g., boat cleaning system (Bleitz et al. 2024)) and communication campaigns to inform stakeholders about areas at risk now and in the future.

To predict and manage the future spread of Eurasian watermilfoil, particularly at the margins of its current range, species distribution models (SDMs) have become increasingly important tools (Guisan and Thuiller 2005). SDMs infer environmental suitability for a species based on observed occurrences and associated spatial variables. To date, SDMs have been widely applied to forecast invasion fronts as well as prioritise invasive species surveillance and control (Worner et al. 2014; Mainali et al. 2015). For Eurasian watermilfoil, environmental lake predictors such as growing degree days, lake size, nutrient availability and human-mediated connectivity (e.g., road density, boat launches) have consistently emerged as important drivers of presence and abundance in the United States (Roley and Newman 2008; Mikulyuk et al. 2020; Thomas et al. 2024). However, little is known about how realised niche preferences relate to the potential distribution of Eurasian watermilfoil across catchments in North America, or how the broadscale spread of the species will evolve under different scenarios of future climate and human population change. Furthermore, the predictive accuracy of SDMs depends strongly on data quality, spatial scale and the inclusion of ecologically relevant variables (Elith and Leathwick 2009; Guisan et al. 2017). For instance, models trained on global or native-range data may underestimate suitability in invaded regions due to niche shifts or biotic interactions (Elith and Leathwick 2009; Nguyen et al. 2022), while regionally trained models may lack generality and underperform in forecasting future expansion (Jarnevich et al. 2022).

Here, we address these challenges by constructing a suite of predictive SDMs for the current and future distribution of Eurasian watermilfoil in the freshwater basins of Quebec, Canada. In Canada, and specifically in the province of Quebec, Eurasian watermilfoil is currently expanding northward into previously uncolonised regions (Jacob-Racine and Lavoie 2018), now invading regions that contain the largest volume and density of freshwater systems on the continent (Messager et al. 2016). Given the heterogeneity of limnological conditions across Quebec, from highly urbanised southern catchments to remote northern systems, identifying the environmental and anthropogenic factors associated with Eurasian watermilfoil presence can inform targeted interventions and long-term monitoring strategies. Moreover, the anticipated effects of global change in the region—through warming temperatures, increased human mobility and changing land use—further underscore the importance of developing robust predictive frameworks.

Our study integrates a large geospatial dataset comprising 11,823 catchments with occurrence records of Eurasian watermilfoil from both regional and global sources. Using a random forest machine learning approach, we quantify the role of climatic, limnological and anthropogenic factors in determining Eurasian watermilfoil presence. Our objectives are to: (1) Evaluate the accuracy of regional vs. global training data, when predicting the distribution of Eurasian watermilfoil in Quebec, Canada.; (2) Identify the relative importance of climate, habitat availability, catchment characteristics and human presence on the presence of Eurasian watermilfoil at the basin level. (3) Estimate and compare projected range expansion of Eurasian watermilfoil based on future climate and population density scenarios. Answering these objectives will enhance our understanding of the ecological and

anthropogenic constraints shaping the current distribution and future spread of Eurasian watermilfoil in North America. This work also provides a spatially-explicit framework for anticipating invasion risk and informing targeted management across Canada's freshwater landscapes.

2 | Methods

2.1 | Data Collection

2.1.1 | Species Occurrence Data

Regional data on Eurasian watermilfoil occurrences were acquired from the Gouvernement du Québec (MELCCFP 2023) that gathered data from Jacob-Racine and Lavoie (2018), citizens' sightings, and local organisations conducting aquatic plant surveys, as well as from occurrences documented in the Global Biodiversity Information Facility (GBIF). The two regional datasets were compared for duplicates according to latitude, longitude and year. The regional dataset captures 1951 occurrences of Eurasian watermilfoil in Quebec between 1958 and 2023. Contemporary occurrence data from across North America and Europe observed between 1995 and March 2023 were accessed from GBIF, resulting in 83,244 occurrences in total. These site-specific occurrence records of Eurasian watermilfoil were spatially aggregated to catchment sub-basins with each sub-basin treated as a single observational unit and classified as presence when ≥ 1 confirmed record occurred within its boundaries.

2.1.2 | Spatial Data

First, the province of Quebec was divided into 11,823 sub-basins delineated by the HydroBASINS dataset (Lehner and Grill 2013). The sub-basins that have the highest spatial resolution offered by HydroBASINS are known as level 12 sub-basins, and these had average size in Quebec of 131.6 km^2 (minimum = 0.1 km^2, maximum = 473.1 km^2). The total area upstream of the Level 12 sub-basins pour point was, on average, 6716.5 km^2 (minimum = 0.2 km^2, maximum = 1,053,294 km^2). Using the species presence data described above, each sub-basin was assigned a value of 1 or 0 based on the presence or pseudo-absence (see following section for details), respectively, of Eurasian watermilfoil in the sub-basin. This resulted in 187 sub-basins in Quebec containing Eurasian watermilfoil, and 11,363 sub-basins where Eurasian watremilfoil has not been observed.

Next, the average bicarbonate concentration in each sub-basin was calculated using a global bicarbonate raster (Iversen et al. 2019). Bicarbonate concentration is expected to be highly correlated with alkalinity in Quebec freshwaters because, at the observed regional pH values (< 9, Guerin et al. 2024), alkalinity is overwhelmingly dominated by bicarbonate ions. Finally, 23 environmental variables calculated at the level 12 sub-basin scale from the BasinATLAS dataset (Linke et al. 2019; Lehner et al. 2022) were appended to each sub-basin. Of these 23 variables, only wetland extent (percent cover) was calculated as a sum of multiple BasinATLAS variables. In this paper, wetland extent refers to the sum of the percent cover in the sub-basin classified by BasinATLAS as: (A) bog, fen, mire; (B) swamp forest, flooded forest; or (C) freshwater marsh, floodplain. The remaining 22 variables were obtained directly from BasinATLAS, without further calculation. Rationale for the selection of these 24 environmental variables (23 variables from BasinATLAS, plus bicarbonate concentration) is provided in Table S1.

Across North America and Europe, the HydroBASINS dataset delineates 306,791 level 12 sub-basins (169,133 in North America; 137,658 in Europe). The average sub-basin size in this dataset was 130.7 km^2 (minimum = 0.1 km^2, maximum = 1214.0 km^2). The mean upstream area of the North American and European sub-basins was 10,273 km^2 (minimum = 0.1 km^2, maximum = 3,179,500 km^2). The presence of Eurasian watremilfoil across North America and Europe was mapped according to the GBIF occurrences described above. This resulted in 8366 sub-basins in North America (2495 sub-basins) and Europe (5871 sub-basins); Eurasian watremilfoil is native to Europe. Following the process described above for sub-basins in Quebec, the 24 environmental and anthropogenic variables were appended to the North American and European sub-basins (Table S1).

To support our regional predictive model, future projections for population density and climate scenarios were calculated for each of the 11,823 sub-basins in Quebec. Population density across Quebec municipalities in 2021 and 2041 was estimated according to population projections made by StatisticsQC (Institut de la Statistique du Québec 2022), then divided by the total area of each municipality (Ministère des Ressources naturelles et des Forêts 2024). The 2021 and 2041 projected population densities were then averaged for each sub-basin.

To check for consistency between population datasets, we calculated Pearson's correlation coefficient between the 2010 population density estimate from BasinATLAS and the sub-basin 2010 population density estimate from StatisticsQC (Institut de la Statistique du Québec 2024) at the sub-basin level. The two population density estimates for 2010 are highly correlated ($r = 0.858$), which supports our use of the BasinATLAS estimate in the subsequent SDMs.

Finally, we obtained climate projections from CHELSA (Karger et al. 2017, 2023) for mean annual temperature (defined as the annual daily mean air temperatures averaged over 1 year; °C), maximum annual temperature (defined as the highest temperature of any monthly daily mean maximum temperature; °C), and total annual precipitation (defined as the accumulated precipitation amount over 1 year; kg m^{-2} $year^{-1}$). These projections were made under three warming scenarios using the Sixth Phase of the Coupled Model Intercomparison Project (CMIP6): (1) SSP1-2.6 (warming by 1.8°C by 2100); (2) SSP3-7 (warming by 3.6°C by 2100); and (3) SSP5-8.5 (warming by 4.4°C by 2100), as modelled by the National Oceanic and Atmospheric Administration, Geophysical Fluid Dynamics Laboratory's Earth System Model (GFDL-ESM4). Each of the climate parameters was estimated for every level 12 sub-basin in Quebec over two time periods: 2041–2070 and 2071–2100.

2.1.3 | Predicting Eurasian Watermilfoil Distributions

We used a random forest machine learning approach to predict landscape-level factors and the probability of Eurasian watermilfoil occurrences in Quebec. Based on the expected relationship between Eurasian watermilfoil presence and climatic, spatial, and anthropogenic factors (See Table S1), we established a model structure to evaluate: (i) the prediction power of local vs. large scale occurrence data of Eurasian watermilfoil when training the random forest algorithm; (ii) the relative importance of the selected factors when predicting Eurasian watermilfoil presence and the directional patterns of these factors; (iii) changes in potential Eurasian watermilfoil occurrence based on future climate and population density scenarios.

In the modelling framework we integrated two components of known biases when estimating range expansion of invasive species and species range shifts. For invasive species, prediction accuracy can be inconsistent when different baseline sources are used to parameterise the relationship between effect variables and species occurrences. In particular, training data based on species' native ranges has yielded suboptimal model performance when predicting occurrences in invaded regions (Broennimann and Guisan 2008; Nguyen et al. 2022). However, estimating species occurrences solely based on regional data can, on the other hand, lead to poor prediction accuracy when forecasting occurrences into novel environments (Liu et al. 2022; Larson 2025).

To evaluate the effect of training data used, we collected known observations of Eurasian watermilfoil at different scales: across catchments within Quebec, its entire invasive range in North America, and its native range in Europe. We then compared the prediction accuracy of models trained on regional (Quebec), invasive, native, and total occurrence data.

For absence data, we estimated pseudoabsence from catchments with no known records of Eurasian watermilfoil. It has been argued that species distribution models derived from observational data in Canada can be biased due to an overrepresentation of observations in the south relative to the northern part of the country. Thus, when sampling pseudoabsence data, artificial contrasts might arise between known presence occurrence and random pseudoabsence draws of the entire region of interest (Phillips et al. 2009). To correct for such sampling bias, we selected absence catchments based on existing macrophyte observations in a catchment. For catchments without any Eurasian watermilfoil presence, we used GBIF observations of all known macrophytes in the region to calculate the proportion of GBIF records in a catchment relative to other catchments in the province. These proportions were then used as a probability weight when creating random samples of catchments with at least one existing macrophyte record. This procedure integrates two levels of information in the development of pseudoabsence datasets: (i) for catchments without Eurasian watermilfoil, a catchment that has some preexisting data of macrophyte presence is more likely a true absence and (ii) when there exist many macrophyte observations, a catchment is more likely a true absence compared to a catchment with few observations.

We chose a balanced sampling design for presence and pseudoabsence across the different datasets. Specifically, we had a 1:1 ratio between presence–absence data and conducted random sampling of the continental datasets so that they would match the sample size of the Quebec presence datasets (184 basins).

For each random forest model, the catchment datasets were randomly split into quarters and used as independent data for model training (75% of the data) and prediction accuracy (25% of the data). An initial random forest model structure was created including 24 environmental variables (combining information at the sub-watershed and full catchment level) as explanatory variables and Eurasian watermilfoil presence/absence in each catchment as the response variable. This initial model was trained across a range of different fitting parameters for all four combinations of training datasets (Quebec, North America, Europe, and all occurrence datasets), and within this framing, the optimal minimum node size was set to five, the number of variables randomly sampled as candidates at each split was set to 15, and the number of split trees to 500. Sampling uncertainty was integrated by performing 1000 simulations of the sampling procedures for all random forest models generated. Differences in prediction accuracy between datasets were evaluated based on group mean prediction accuracy and the 95% confidence of these predictions.

Variable importance was estimated as the mean variable contributions across the 1000 individual model runs. The directionality of the 5 most important variables was visualised by plotting the estimated probabilities from the model against the gradient of observed values of the specific factor.

Using the same simulation process as for the regional vs. global dataset comparisons, we estimated three forecasting scenarios for Eurasian watermilfoil integrating both expected changes in population density and climate change for a 1.8°C, 3.6°C and a 4.4°C increase in global temperature by 2100 over two time steps: 2040–2071 and 2071–2100.

All results were generated using R (V. 4.2.0). We used the "raster" and "sf" packages for spatial data management and the random forest models were constructed using the randomForest and "ranger" packages. The code and data used to produce the study are available via Zenodo: https://zenodo.org/records/16996797.

3 | Results

3.1 | Predicting the Spatial Distribution of Eurasian Watermilfoil in Quebec

Overall, we find that our model-based predictions of Eurasian watermilfoil presence in Quebec match the expectations from the known observations at the invasive front in the region (Figure 1). High probability of invasion areas are predominantly found in the southern part of the province (Figure 2a). Compared to training datasets from North America and Europe, there was a clear increase in prediction accuracy when developing a predictive model solely based on training

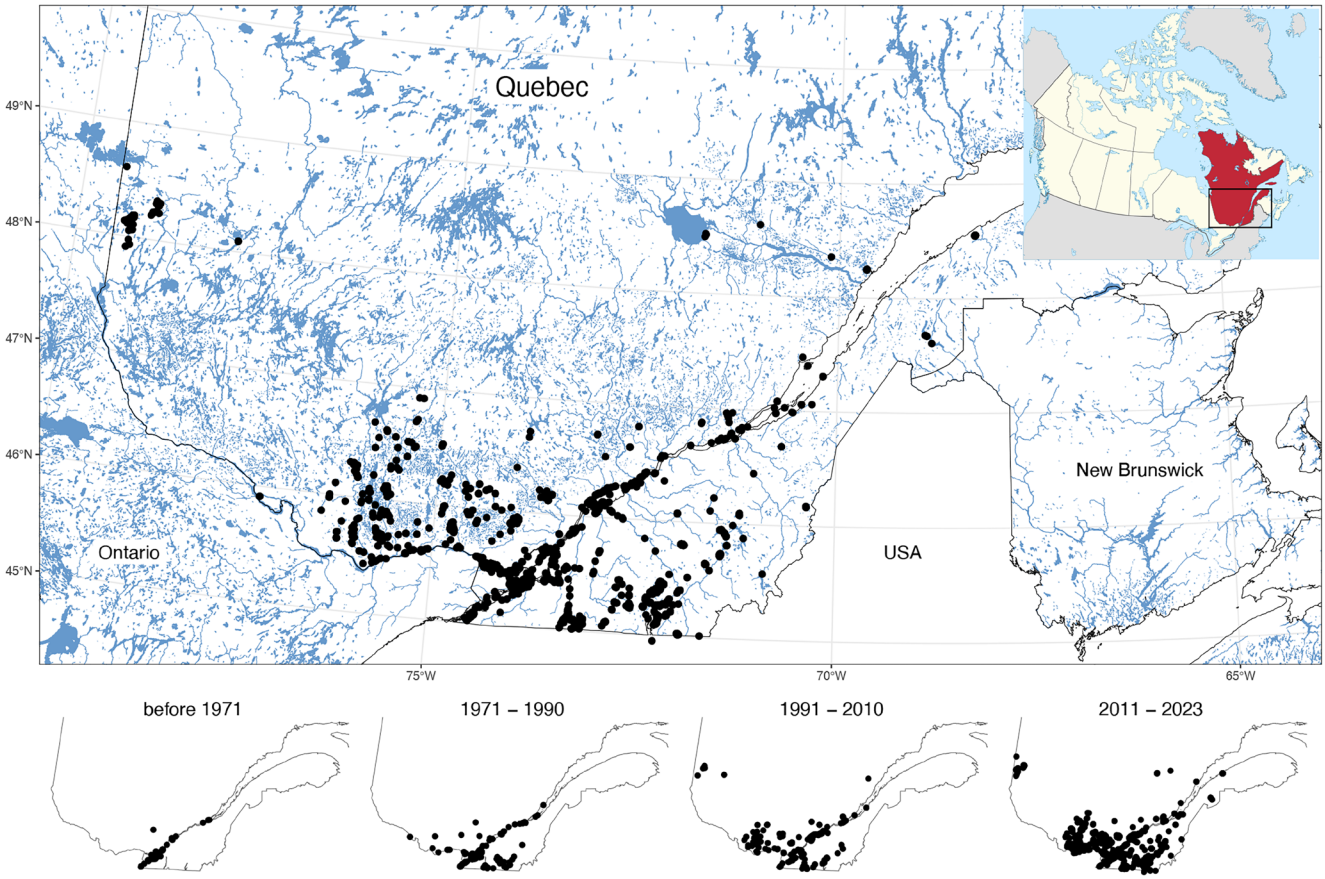


FIGURE 1 | Documented occurrences of the invasive macrophyte Eurasian watermilfoil across southern Québec, Canada. Black dots indicate known contemporary records of the species. The inset map shows the position of the main map within Canada. The lower panels illustrate the temporal progression of the invasion, grouped into four periods (before 1971, 1971–1990, 1991–2010 and 2011–2023), highlighting the species' initial establishment in the St. Lawrence Lowlands and its subsequent spread northward and westward into new catchments (adapted from Jacob-Racine and Lavoie 2018).

data from Quebec. The random forest models trained with the Quebec-restricted data predicted the correct presence of Eurasian watermilfoil with an 82% probability (Figure 2b). The Quebec model was much stronger than when the model was trained using North American (accuracy of 57%) or European datasets (accuracy of 53%) or both regions combined (accuracy of 54%) (Figure 2b).

3.2 | The Factors Associated With Eurasian Watermilfoil Invasion in Quebec

The mean individual variable importance across the 1000 random forest model iterations showed that temperature is strongly associated with Eurasian watermilfoil presence in the study region. The maximum monthly temperature and mean annual temperature were the most important variables when predicting the presence of Eurasian watermilfoil (Figure 3a). For both temperature variables, there was an increase in predicted watermilfoil presence with higher temperature values (Figure 3b). Beyond temperature, the other important factors included annual precipitation, total lake volume and the human population density at local and catchment scales (Figure 3a). Like with temperature, all these variables were positively associated with the probability of watermilfoil presence.

3.3 | Changes in Eurasian Watermilfoil Distribution Based on Future Climate and Population Density Scenarios

Based on projected changes in population densities and 4.4 degree C climate change scenarios (downscaled to the sub-basin level), we estimate that 13% of all sub-basins in Quebec will have a high likelihood of Eurasian watermilfoil invasion by 2070 (Figure 4). Under this scenario, we are forecasting that Eurasian watermilfoil will have an equal or higher minimum suitability in sub-basins than currently. Comparing current to future predicted distributions across all scenarios, there is an up to 194% Eurasian watermilfoil increase in prevalence in sub-basins that are categorised as being high occurrence probability basins. The invasion front by 2070 is especially evident in regions around the Saguenay River and the lower reaches of the St. Lawrence River, as well as in the western part of the province (Figure 4).

We find that the current potential distribution of Eurasian watermilfoil equals 5.9% of the total area in the province (compared to the 6.1% sub-basins that were classified as current high probability areas—Figure 4). For all three climate change scenarios, there is a significant increase in the potential distribution areas by 2070 and 2100 (Figure 5). The increase in area that is suited for the species is estimated to be as high as 421,354 km^2 in 2100

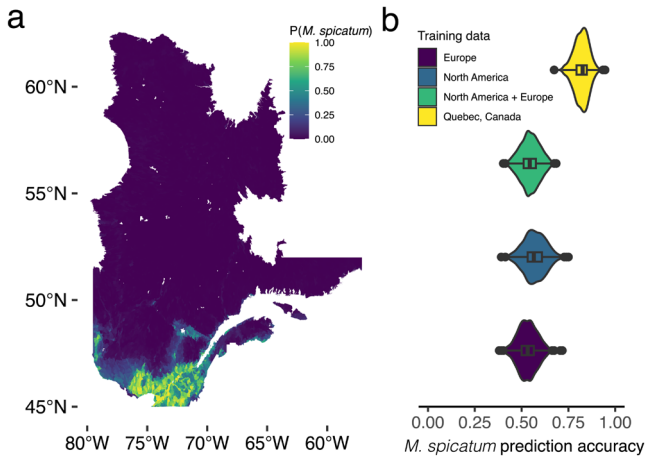


FIGURE 2 | Regional suitability prediction of Eurasian watermilfoil in Quebec, Canada. (a) Predicted probability of occurrence of Eurasian watermilfoil under modern conditions across Quebec, Canada, based on a species distribution model (SDM) trained on regional occurrence data. Warmer colours indicate higher predicted probability, with the highest suitability concentrated in the southern part of the province. (b) Prediction accuracy of SDMs trained on different geographic datasets: Europe (purple), North America (blue), combined North America + Europe (green) and Quebec, Canada (yellow). Accuracy measures are shown as violin plots, with each one summarizing the distribution of prediction scores based on simulations. Models trained with regional data from Quebec outperform those trained on broader geographic datasets, highlighting the value of local information for accurate prediction of invasive species distributions.

for a 4.4°C warming scenario. In comparison to the current potential distribution area (90,679 km^2), this would represent a ~5 times increase in suitable habitat area for the presence of Eurasian watermilfoil in Quebec.

4 | Discussion

Our finding that the regionally trained model outperformed those trained on global, invasive, or native-range data reinforces the growing evidence that prediction accuracy at invasion fronts depends critically on matching the environmental context of training data to that of the target region (Elith and Leathwick 2009; Liu et al. 2022). Low environmental similarity between training and projection areas significantly reduces SDM transferability, particularly when models extrapolate to non-analog climates (Nguyen et al. 2022). It is well accepted that extrapolating SDMs across space must be approached with caution, especially when target environments fall between the environmental domains captured in training data (Guisan and Thuiller 2005; Elith and Leathwick 2009). In our case, training models on global or even North American data failed to capture the specific temperature combinations characterizing Quebec's invasion front, leading to model prediction underperformance (Figure S1). The realised niche at invasion fronts is often less saturated compared to its native range or differences occur due to indirect constraints on the realised niche (Guisan et al. 2014; Tingley et al. 2014). In the case of Eurasian watermilfoil in Quebec, the relatively reduced availability of potential anthropogenic dispersal vectors, along with inadequate temperature, might confine the distribution and the realised temperature niche preference needed for invasion success.

At the basin level, the distribution of Eurasian watermilfoil in Quebec was best explained by a sum of population density, temperature and water availability. This aligns with studies in North America that consistently identify human-mediated dispersal and lake-specific characteristics as key drivers. At the lake level, road density—a proxy for human access—has been shown to be among the strongest predictors of invasion risk of Eurasian watermilfoil, though less so for abundance (Mikulyuk et al. 2020; Thomas et al. 2021). Similarly, the proximity to already invaded lakes, lake size and water clarity as important predictors in Minnesota emphasised the role of both propagule pressure and establishment conditions (Roley and Newman 2008). Our inclusion of climate-related variables echoes findings by (Thomas et al. 2024), who demonstrated that lake temperature critically shapes niche suitability, but is associated with considerable uncertainty under novel conditions. Furthermore, our findings add to the current literature that predicts invasion success at the regional lake level by scaling the probability of Eurasian watermilfoil across basins and catchments. Although the causal link of temperature and human presence can be downscaled from basins to lakes (increased growing degree days and dispersal vectors), the importance of precipitation and total lake volume might be more scale dependent and can be attributed to increased presence of and connectivity between potential habitats.

The predicted 194% increase in high-suitable sub-basins for Eurasian watermilfoil across Quebec represents a substantial potential range expansion, indicating that nearly twice as many catchments could become vulnerable for invasions under expected climatic and population conditions. This level of projected spread is comparable in magnitude to other aggressive aquatic invaders in the region which have also shown rapid expansions facilitated by climate warming and human-mediated dispersal. For instance, zebra mussels (*Dreissena polymorpha*) have spread to hundreds of lakes in Quebec and Ontario within two decades of introduction, with similarly strong associations to boat traffic and hydrological connectivity (Ricciardi 2006).

Species distribution of invasive aquatic plants is often estimated at the scale of individual lakes or waterbodies, where fine-grain physical, chemical and biological attributes can be directly linked to observed occurrences (Roley and Newman 2008; Mikulyuk et al. 2020; Tamayo and Olden 2014). Such site-level approaches are well suited for understanding local establishment processes, but they rely on detailed, consistently sampled lake-specific data. In contrast, our sub-basin–based approach emphasises spatial completeness and regional inference by relying on predictors that are available consistently across the landscape (Linke et al. 2019; Lehner et al. 2022). This necessarily involves trade-offs: air temperature, for instance, is a coarser proxy than in-lake thermal conditions (Armitage 2023), and aggregated hydrological or land-cover variables cannot resolve heterogeneity among individual lakes within a basin. However, these broader predictors still capture large-scale climatic, hydrological and anthropogenic gradients that structure invasion

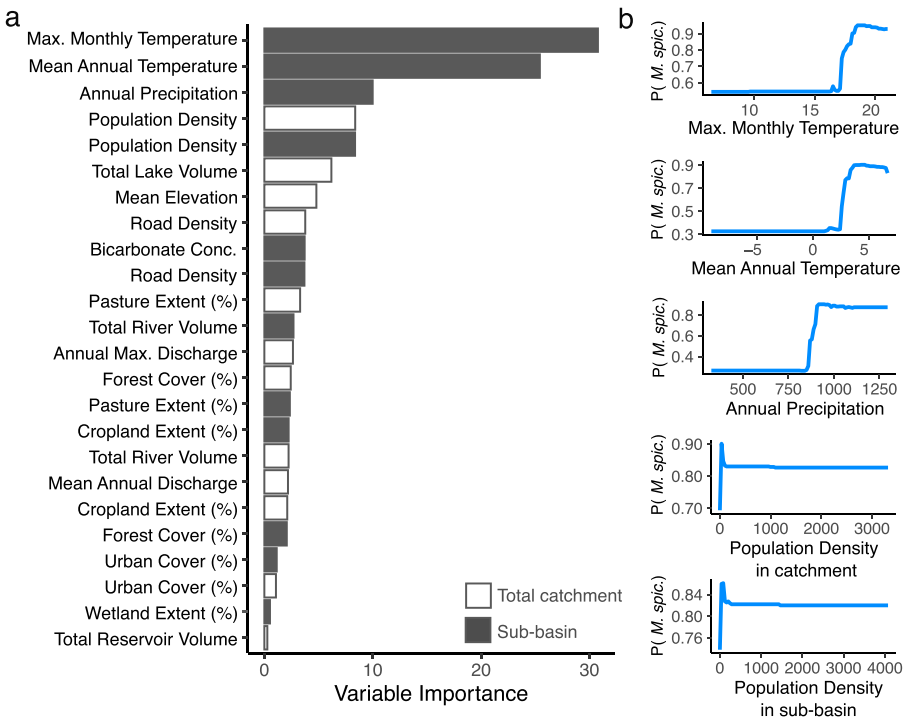


FIGURE 3 | Relative importance and effects of predictors on the distribution of Eurasian watermilfoil. (a) Average variable importance for predicting *Myriophyllum spicatum* presence across Quebec, based on random forest models. Bars represent the contribution of each variable, with darker bars indicating sub-basin scale predictors and lighter bars representing catchment-scale predictors. The most important predictors include maximum monthly temperature, mean annual temperature, annual precipitation and population density at both sub-basin and catchment scales. (b) Partial dependence plots showing the marginal effects of the five most important predictors on the probability of Eurasian watermilfoil occurrence (i.e., P(*M. spic*)). Each plot depicts how predicted occurrence probability changes with increasing values of the given variable, while holding other predictors constant.

pressure and dispersal pathways (Elith and Leathwick 2009; Liu et al. 2022), making them suited for identifying where invasion risk is most likely to emerge at regional scales. Still local ecological effects, such as biotic interactions or lake-specific habitat conditions, remain important for determining the causality between establishment and impact at individual sites and the drivers causing such impacts.

The ecological consequences of Eurasian watermilfoil invasions have been studied for several decades and yet there are still important unknowns. Temporal monitoring has demonstrated that Eurasian watermilfoil can decrease native macrophyte communities' species richness and abundance, likely by outcompeting native species for root space and light (Boylen et al. 1999). A global literature meta-analysis found that, as an invader, Eurasian watermilfoil has a positive impact on macroinvertebrate diversity and abundance (Tasker et al. 2022). It has also been shown that Eurasian watermilfoil can host invertebrate communities with species compositions that differ from their neighbouring native counterparts, which may have indirect effects on higher trophic levels (Wilson and Ricciardi 2009). Invertebrates can also affect the growth of Eurasian watermilfoil. For example, Chase and Knight (2006) demonstrated in the context of a mesocosm experiment that invasive Eurasian watermilfoil increased with nutrient enrichment when native algivorous snails were absent, but were outcompeted by native plants when snails were present. Finally, the direct impact of Eurasian watermilfoil on North American fishes remains unclear and is not generalisable across species or life stages (Kusnierz and Tholl 2024). To fully understand how the expansion of this invader in Quebec will impact native communities, further ecosystem-specific studies are required.

There is evidence that Eurasian watermilfoil can facilitate the establishment and spread of other invasive species—as per the invasion meltdown hypothesis. For example, Dreissenid mussels are known to filter large quantities of water, reducing the water turbidity, which in turn can allow Eurasian watermilfoil to establish and expand (Crane et al. 2020, 2022). The plants, in turn, can provide habitat for juvenile Dreissenids. In their study of multiple invaders (Weir et al. 2024) found that the top predictor of Eurasian watermilfoil in data-intensive SDMs set in Upper Mississippi River Basin (USA) was another invasive plant species (*Potamogeton crispus*) and Eurasian watermilfoil was the top predictor of Dreissenid mussels presence. The underlying mechanism behind such co-occurrence was considered linked to increased light availability in the littoral zone due to filter feeding by Dreissenid mussels, thereby supporting macrophyte growth. In future provisional SDM studies, it will be important to consider other biotic factors, including native macrophyte composition that may act as competitors and temper invasion success.

The projected expansion we document herein signals an urgent need for proactive monitoring, prevention and response strategies, particularly in high-risk basins. Some measures

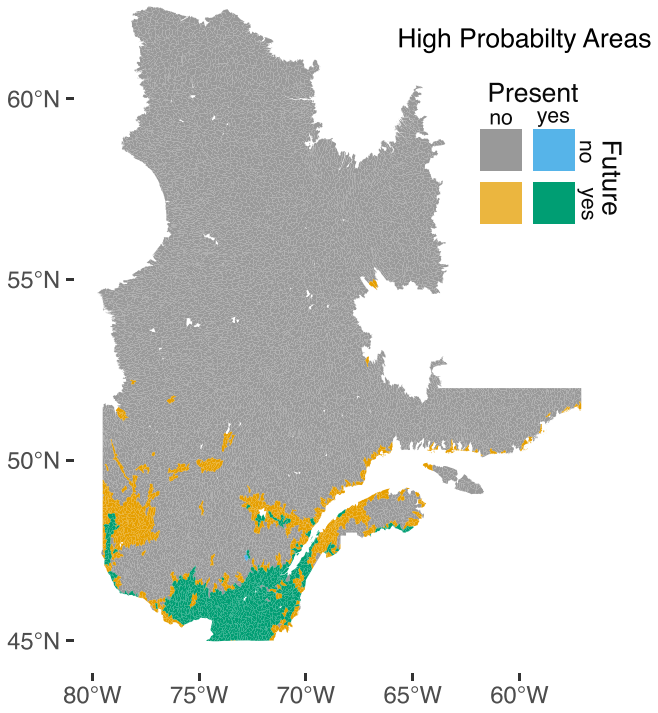


FIGURE 4 | Projected range of Eurasian watermilfoil in Quebec due to global change. Map shows areas with high predicted probability of Eurasian watermilfoil presence under present and future scenarios. Future scenarios are based on predicted 2070 changes in provincial population densities, temperature and precipitation. The climate predictions are based on a 4.4°C warming scenario. The model predicts substantial northward expansion of high-suitability areas, particularly along major river corridors and western regions.

are already in place in multiple water bodies, such as manual removal, installation of benthic barriers, installation of boat cleaning stations, information campaigns and monitoring efforts. Cleaning stations prevent further spread by reducing the number of propagules transported between lakes, therefore reducing the risk of successful introduction (Colautti et al. 2007). Simple manual removal from watercraft by boaters is known to be efficient in removing most of the plant material, and the removal efficacy is even greater when the removal is done by trained employees using dedicated equipment (Angell et al. 2024). As of August 2025, the Gouvernement du Québec listed 183 cleaning stations (MELCCFP 2025), the majority of which were either freely available or at a low cost (below 50 CAD). However, most stations are located in areas where Eurasian watermilfoil is already present, and many of the "at risk" areas we identified are farther north and east of where cleaning stations are commonly found. A proactive step, currently not in place, would be to instal new stations in regions where Eurasian watermilfoil is projected to colonise, thus minimizing its expansion in the most "at risk" areas. The installation of benthic barriers, mechanical harvesting and manual removal of the plants have also been shown to be effective at a local scale in reducing the size of Eurasian watermilfoil beds in invaded lakes (Guitard 2022; Gagné and Lavoie 2023). Facilitating such measures in already invaded lakes not only helps to minimise the impacts of the current invasion, but it is also an option to limit the spread to new locations by reducing the risk for watercrafts to pick up fragments in the first place.

Education campaigns aimed at increasing awareness of invasive species are widely used across Quebec and elsewhere. While most such campaigns don't often reliably track the efficacy and outcomes on the spread and control of invasive species (Haley et al. 2023), those that do show a concrete reduction in the population of targeted species over time when community members actively removes plant material (Love and Genovese 2019). Education campaigns may also lead to an increase in the number of reported sightings (Keiter and Beasley 2017), which facilitate early detection in newly invaded areas and enable the roll out of a faster, cheaper, and more efficient response (Vander Zanden et al. 2010). Along with increased awareness, tools that allow citizens to easily report sightings of invasive species, or detection programs using new technologies like environmental DNA, can greatly increase the ability of municipalities to respond to the projected invasion by Eurasian watermilfoil (Newton and Sylvester 2016).

While exploring prevention and control measures is crucial to address the future spread of Eurasian watermilfoil, the financial cost associated is considerable (Guitard 2022; Gagné and Lavoie 2023) and might constitute a significant barrier to justify more preventative measures in previously unaffected regions. On the other hand, the dense surface canopies created by the species have been shown to impair recreational access and lower property values, generating substantial economic costs for lakefront communities (Olden and Tamayo 2014). Because much of the cost of implementing these measures falls on municipalities and local citizens' groups, the economic impact of the invasion is often one of the main arguments used to justify the investment. The projections shown here could help in this regard by making the risk of invasion more concrete for stakeholders. Additionally, continued financial support from governments towards control of existing Eurasian watermilfoil populations and the installation and maintenance of cleaning stations would be an important tool to increase the feasibility of prevention or control plans.

In conclusion, our findings demonstrate that the expansion of Eurasian watermilfoil in Quebec is poised to accelerate under projected climate and population change scenarios, with a potential fivefold increase in suitable habitat by 2100. This underscores the urgent need for regionally calibrated predictive models and monitoring frameworks to inform proactive management. The superior performance of the locally trained model highlights the importance of spatial context when forecasting invasion risk based on species' realised niches, particularly at dynamic range margins. Given the substantial ecological and socio-economic costs associated with Eurasian watermilfoil invasions—ranging from altered ecosystem functioning and biodiversity loss to reduced recreational value—our spatially explicit forecasts offer a valuable tool for prioritizing intervention in high-risk areas. As climate warming and human disturbance continue to reshape aquatic landscapes, integrative approaches that combine predictive modelling, on-the-ground surveillance and adaptive management will be essential for mitigating the long-term impacts of aquatic plant

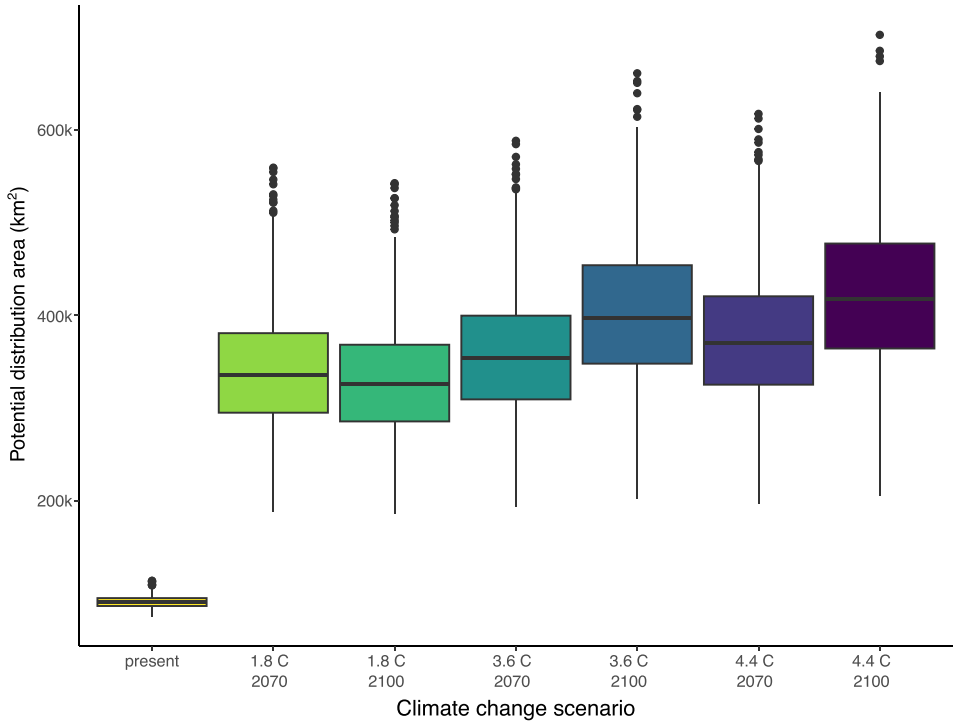


FIGURE 5 | Current and projected expansion of Eurasian watermilfoil distribution area under future climate change and population growth scenarios. Boxplots show the predicted potential distribution area (km^2) of Eurasian watermilfoil in Quebec under present-day conditions and six future climate scenarios, based on combinations of three levels of global warming (1.8°C, 3.6°C, 4.4°C), two future time horizons (2070 and 2100) with predicted changes in population densities. All future scenarios project substantial increases in suitable area relative to present conditions, with median predictions ranging from ~330,000 to over 420,000 km^2. Higher warming levels are associated with greater expansion, indicating strong sensitivity of range size to climate forcing. Boxes indicate the interquartile range (25th to 75th percentile); the horizontal line denotes the median, and whiskers extend to 1.5× the interquartile range. Points represent outlier predictions across model replicates.

invasions at both the regional scale and across freshwater ecosystems worldwide.

Author Contributions

Conceptualisation: Lars Lønsmann Iversen, Morgan Botrel and Irene Gregory-Eaves. Developing methods: Lars Lønsmann Iversen. Conducting the research: Lars Lønsmann Iversen, Morgan Botrel, Marie-Eve Tousignant, Lindsay Trottier. Data analysis: Lars Lønsmann Iversen, Data interpretation: Lars Lønsmann Iversen, Morgan Botrel, Gray Fedirchuk, Valérie Langlois, Olivier Morissette, Lindsay Trottier and Irene Gregory-Eaves. Preparation of figures and tables: Lars Lønsmann Iversen, Morgan Botrel and Lindsay Trottier. Writing: Lars Lønsmann Iversen, Lindsay Trottier, Morgan Botrel, Gray Fedirchuk, Valérie Langlois, Olivier Morissette, Marie-Eve Tousignant and Irene Gregory-Eaves.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All code and data needed to recreate the study are available via Zenodo: https://zenodo.org/records/16996797.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Realised niche differences among Eurasian watermilfoil presence records across regions. Density plots show the distribution of maximum monthly temperature values in watersheds where species has been recorded, based on presence data from Europe (EU, purple), North America (NA, teal) and Quebec (QC, yellow). The distributions highlight regional differences in the realised thermal niche of the species. Presence records from Quebec are concentrated within a narrower and cooler temperature range compared to North America overall, while European occurrences are centered at slightly lower temperatures. **Table S1:** Description of environmental and anthropogenic variables included in the random forest model.