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ORIGINAL PAPER

Comparative ecological niche models predict the invasive spread of variable-leaf milfoil (*Myriophyllum heterophyllum*) and its potential impact on closely related native species

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Abstract Invasive species can alter patterns of biodiversity by displacing closely related native species that occupy similar habitats. We used multivariate ecological niche modeling to determine the potential spread and displacement of native congeners by the invasive aquatic plant, variable-leaf milfoil (VLM, *Myriophyllum heterophyllum*) in New Hampshire, USA. We show that VLM occurs almost exclusively in "higher order" lakes characterized as large, low elevation systems with relatively high pH, alkalinity and conductivity. In contrast, native milfoils occur across a broad range of lake orders. The strong association between lake order and VLM invasions suggests that VLM is most likely to displace native milfoils in higher order lakes. However, the mechanism by which VLM occurs in higher order lakes—higher propagule pressure versus higher growth and survivorship—is unclear. We therefore caution that native species may ultimately be susceptible to displacement from lower order lakes if the current distribution of VLM reflects higher propagule pressures. Our model provides a valuable tool for the prioritization of monitoring efforts.

Keywords Competitive exclusion · Environmental filtering · Environmental gradient · Landscape position · Multivariate analysis · Propagule pressure

Introduction

Predicting the spread and impacts of invasive species is a central focus of invasion biology and has practical management implications. The impact of an invader on closely related native species will depend on their degree of niche overlap. When niche overlap is low, invaders should have minimal impacts on natives. However, when niche overlap is high, invaders have the potential to displace closely related native species. The development of comparative ecological niche models using available data offers an efficient means for estimating the degree of niche overlap between invaders and closely related native species. Such models can be used to predict the potential spread and impact of invaders.

Invasive aquatic plants pose serious threats to the functioning and effective management of aquatic

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ecosystems. For example, aquatic plant invasions often lead to a loss of native plant diversity (e.g., Boylen et al. 1999; Madsen et al. 1991), decreased property values (Halstead et al. 2003), high economic costs (Pimentel et al. 2000, 2005), alteration of sediment and nutrient processing (Ravit et al. 2003; Windham and Lathrop 1999), disturbance to natural wildlife habitat, and interference with recreation. As such, considerable efforts are undertaken to control invasive aquatic plants. From a practical standpoint, early detection and treatment is critical for limiting the spread of invasive aquatic plants because of the relative difficulty of eradicating established versus nascent invasions (Moody and Les 2007). However, the number of water bodies that can be monitored in any given time period are limited by time and cost. Thus, models that predict the likelihood of invasion in particular lakes and geographic areas are required to aid the prioritization of monitoring efforts.

Early detection and treatment of invasive aquatic plants is hampered by difficulties in distinguishing invasive species from morphologically similar and evolutionarily related native species. For example, several invasive species in New England, USA can be commonly misidentified as related native species (e.g., invasive *Myriophyllum spicatum* vs. native *Myriophyllum sibiricum*; invasive *Myriophyllum heterophyllum* vs. native *Myriophyllum verticillatum*, *Myriophyllum farwelli*, and *Myriophyllum humile*; invasives *Hydrilla verticillata* and *Egeria densa* vs. native *Elodea canadensis*; and invasive *Najas minor* vs. native *Najas flexilis*; see http://www.ct.gov/caes/lib/caes/Aquatics_Guide.pdf). While studies are underway to improve the taxonomic identification of morphologically similar native and invasive species (e.g., Thum et al. 2006), comparative ecological niche models for similar native versus invasive species could be useful for determining the likelihood that natives will be displaced by invasives in particular habitats.

The variable-leaf watermilfoil (VLM, *M. heterophyllum*) has become a high-profile invasive aquatic plant in New England (Les and Mehrhoff 1999). However, factors that facilitate establishment, growth, and spread of VLM remain unknown. Heterosis, or hybrid vigor, has been hypothesized as a major factor contributing to invasive growth (Moody and Les 2002). However, genetic analyses did not identify invasive VLM populations in New Hampshire (NH) as hybrids, suggesting that other factors also play an important role in facilitating invasions (Thum and Lennon 2006). One possibility is that the abiotic and biotic environment plays an important role in whether VLM lineages successfully establish and grow in lakes after initial colonization. However, very little is known about how similar the niches of VLM and native milfoils are (but see Gerber and Les 1996). As such, it remains difficult to predict where VLM is likely to spread, and whether native milfoils are susceptible to displacement by VLM.

Here, we analyze a large, public dataset on NH lakes to reconstruct the temporal and spatial spread of VLM throughout the state. We used this dataset to develop comparative ecological niche models for invasive VLM and native milfoils in NH. Specifically, we determine whether lakes with VLM can be distinguished from lakes with native milfoils on the basis of their habitat characteristics (e.g., lake chemistry, hydrology, morphology) in order to identify lakes where native milfoils may be particularly susceptible to displacement by VLM. In addition, we use our ecological niche models to predict the spread of VLM throughout the state by identifying individual lakes and geographic regions that may be particularly susceptible to invasion by VLM.

Methods

Background on VLM in NH lakes

Variable-leaf milfoil is the most commonly occurring invasive aquatic plant in NH. The first documented occurrence of VLM in NH was in Lake Winnipesaukee in 1970. Since then, it has spread to over 60 water bodies (Fig. 1a). The majority of VLM populations occur in NH's largest watershed, the Merrimack River watershed (77%; Fig. 1b). In contrast, VLM has not been found in NH's smallest watershed, the Androscoggin. However, VLM invasions have increased in all four major watersheds where they have been found over the past 30+ years (Fig. 1b).

Overview of the NH lakes database

We obtained a large database from the New Hampshire Department of Environmental Services (NH DES). The database contained several datasets from

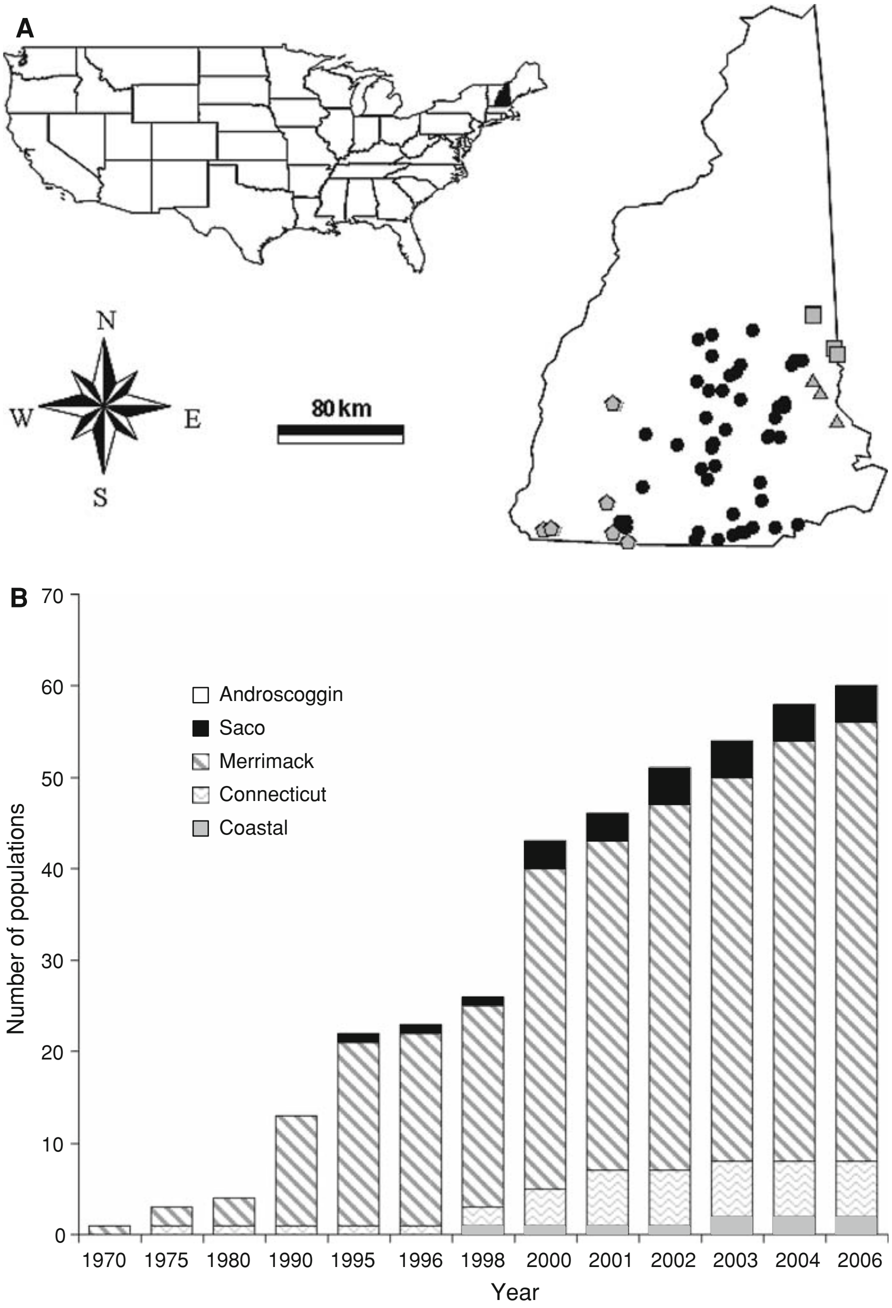

Fig. 1 **a** Geographic locations of lakes invaded by *M. heterophyllum* populations in five major watersheds in New Hampshire. *Black circles* Merrimack, *Gray pentagons* Connecticut, *Gray squares* Saco, *Gray triangles* Coastal. **b** Number of *M. heterophyllum* invasions (including lakes and rivers) through time for each of the five major NH watersheds. Note that the years are not consecutive

various lake surveys conducted between 1976 and 2004, including a lake chemistry dataset (e.g., pH, alkalinity, total phosphorus [TP]), a morphological/hydrological features dataset (e.g., size, elevation, watershed area, flushing rate), a trophic characteristics dataset (e.g., chlorophyll *a*, dissolved oxygen), and a dataset containing presence/absence information for macrophyte species. Throughout this paper, we refer to the chemical, morphological/hydrological, and trophic variables collectively as 'environmental variables'. Many lakes were sampled on multiple occasions (1,646 total samples), and not all environmental variables were collected on any given sampling date. We used only the most recent data available for each lake since it is inappropriate to treat each sample date within a lake independently. In addition, we considered only one of eight bays (Moultonboro Bay, chosen at random) that were sampled in New Hampshire's largest lake, Lake Winnepesaukee, since the bays are not independent.

After merging the four datasets and retaining only the most recent data from each lake, our dataset included 34 environmental variables for 782 lakes (see Appendix). In addition, we calculated 'macrophyte richness' as the sum of all macrophyte taxa minus milfoils from the macrophyte dataset. However, we excluded from our analyses several environmental variables that were missing data for a substantial percentage of lakes. In addition, we excluded several variables from our analyses because of high correlations with other variables ($r > 0.7$). In general, when two or more variables were highly correlated, we retained the variable that was most commonly or easily measured since one of our underlying practical goals was to determine a subset of accessible environmental variables useful for predicting future invasions. We transformed variables when necessary to satisfy assumptions of normality.

Principal components analysis

We performed a principal components analysis (PCA) using the correlation matrix from 17 environmental variables to identify the major environmental gradients in lakes across the entire state ($n = 255$ lakes after removing lakes with missing environmental data, as implemented in Statistica version 8.0 (Statsoft, Inc.). We then plotted factor scores for the first two Principal Components Axis for each lake to gain qualitative insight into environmental characteristics of lakes occupied by VLM relative to those occupied by native milfoils as well as the total range of environmental variation among lakes across the state.

Discriminant function analysis

We used discriminant function analysis (DFA), as implemented in Statistica version 8.0 (Statsoft, Inc.), to compare the environmental characteristics of lakes occupied by VLM and native milfoils. We included only two groups in our analysis: those lakes with only VLM and those lakes with only native milfoils. Four species of *Myriophyllum* are native to NH (*M. humile*, *M. farwelli*, *M. tenellum*, *M. verticillatum*). While the vast majority of lakes with native species were recorded as having *M. humile* (91 lakes vs. 3, 3, and 1 for *M. farwelli*, *M. verticillatum*, and *M. tenellum*, respectively), *M. farwelli* is commonly misidentified as *M. humile* in NH (Thum et al. 2006). In addition, 12 lakes did not contain species information but were listed only as containing native milfoils. Thus, we grouped all lakes with native milfoils into a single category. The qualitative results from our analyses did not differ when using the combined 'native milfoils' versus only the most common species *M. humile*. We excluded five lakes from this analysis that contained both native milfoils and VLM.

We ran the DFA using only those lakes located in the Merrimack watershed, which is the largest watershed with the most lakes in NH. We chose to restrict the DFA to Merrimack lakes for three reasons. First, VLM invasions are disproportionately more frequent in the Merrimack River watershed compared to other four major watersheds (77% of all invasions; $\chi^2_4 = 14.1$, $P = 0.007$; see section "Results" for details) whereas native milfoils occur in relatively even frequencies among the five major NH watersheds ($\chi^2_4 = 5.4$, $P = 0.25$). Thus, restricting the DFA to only those milfoil populations occurring in the Merrimack reduces potential bias in comparing VLM to native milfoil habitat in geographic regions where the former does not occur solely as the result of dispersal limitation. Second, restricting our analysis to the Merrimack watershed resulted in relatively even sample sizes for VLM and native milfoils, whereas the total number of native milfoil populations is roughly three times the number of VLM populations. Finally, restricting the analysis to the Merrimack allowed us to evaluate the accuracy with which the DFA predicted occurrences of VLM and native milfoils in other watersheds, and therefore provides a method to verify DFA accuracy. In addition to restricting our analysis to the Merrimack watershed, we excluded the four Merrimack lakes where both VLM and native milfoils were listed as co-occurring.

We ran an initial DFA using all 17 environmental variables included in the PCA (see Table 1; Appendix) to explore for each variable the partial λ, tolerance, and 'loadings' (standardized canonical coefficients and factor structures). We used a forward selection procedure to identify the subset of environmental variables that entered significantly into the model ($\alpha = 0.05$).

Table 1 Factor loadings for 17 environmental variables used in a principal components analysis of NH lakes

	PC1	PC2
Alkalinity	0.05	0.74
Conductivity	0.15	0.69
Watershed area	−0.43	0.66
pH	−0.17	0.64
Area	−0.70	0.53
Macrophyte richness	−0.02	0.45
% Ponded	−0.21	0.34
Flushing rate	0.52	0.27
Chlorophyll *a* concentration	0.77	0.14
Total kjehldahl nitrogen	0.64	0.09
Depth of thermocline	−0.84	0.03
Total phosphorus	0.72	0.03
Mean depth	−0.80	−0.06
Summer dissolved oxygen concentration	−0.61	−0.15
Secchi depth	−0.85	−0.16
Elevation	−0.27	−0.62
Relative depth	0.06	−0.67

Environmental variables are sorted by their loadings on PC2 as it is the major axis distinguishing VLM from native milfoils

Backwards selection identified a similar subset of variables. We evaluated the accuracy with which the discriminant function successfully classified lakes with VLM versus native milfoils in the remaining four watersheds that were not included in the DFA using percent correctly classified based on Mahalanobis distances. We used the discriminant function to predict the potential spread of VLM across NH by assigning each lake where VLM and native milfoils have not been found to either the VLM or 'native' group based on posterior probabilities calculated from Mahalanobis distances between the discriminant function score for each lake and the VLM and 'native milfoils' centroids in the DFA. In addition, we used the DFA to identify those lakes with native milfoils that may be particularly susceptible to displacement by VLM, as indicated by assignment of these lakes to VLM instead of native milfoils.

Results

The first two axis in the PCA explained 50% of the environmental variation across all lakes in the

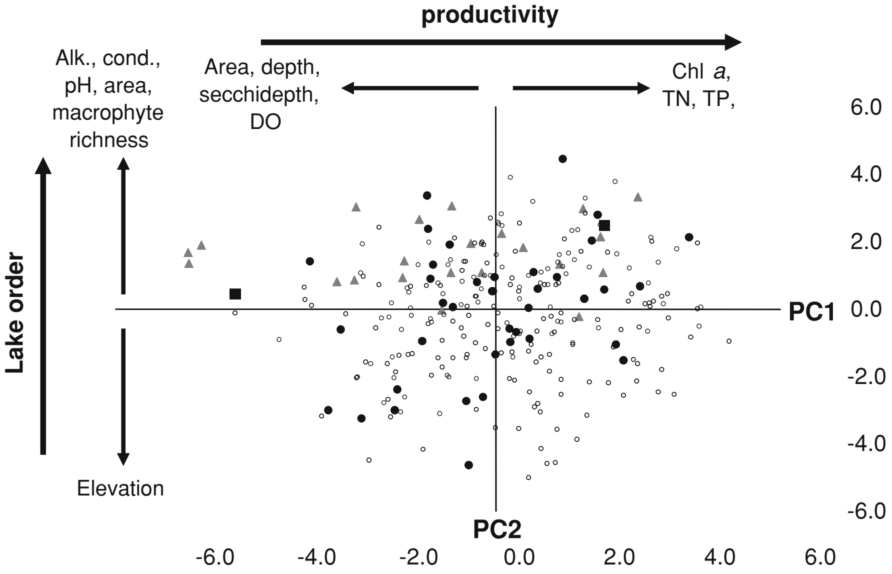

Fig. 2 PCA biplot of NH lakes with and without native milfoils or *M. heterophyllum*. Axis 1 represents a productivity gradient and axis 2 represents a gradient in lake order or landscape position (see text for details on interpretation and Table 1 for loadings of individual variables on each axis). *Chl a* chlorophyll *a*; *DO* dissolved oxygen; *TN* total nitrogen; *TP* total phosphorus; *Alk* alkalinity. *Gray triangles* lakes with VLM; *filled circles* lakes with native milfoils; *filled squares* lakes with both VLM and native milfoils; *open circles* lakes without VLM or native milfoils

NHDES database (Fig. 2). The first axis (30%) can be interpreted as a productivity gradient spanning deep, clear, low productivity lakes to more productive, shallow lakes with high TP, TKN, and chlorophyll *a* concentrations whereas the second axis (20%) illustrates the relationship between lake chemistry and landscape position; namely, lakes that are lower in elevation tend to have higher pH, alkalinity, and conductivity (Fig. 2; Table 1). Macrophyte richness and relative depth were also highly associated with axis 2. Lake size—as indicated by lake surface area and watershed area—exhibited relatively high negative correlations with both PCA axis 1 and 2. While VLM populations occurred across the range of environmental variation along PCA axis 1, they were restricted almost exclusively (with the exception of one lake) to lakes with positive scores on PCA axis 2. Thus, relative to the range of environmental variation in lakes across the state, VLM invasions occurred in larger lakes that are (1) low in elevation, (2) high in pH, alkalinity, conductivity, and macrophyte richness.

The DFA significantly discriminated VLM lakes from those with native milfoils (Wilks' $\lambda = 0.54$, $F_{6,77} = 10.8$, $P < 0.0001$). Six of the 17 environmental variables entered significantly into the DFA using the forward selection procedure (Table 2). Although watershed area and alkalinity entered significantly, we substituted lake area and pH for them, respectively, since the former are more commonly and easily obtained in lake sampling efforts; these substitutions did not qualitatively affect the discriminatory power or relative contributions of variables in our analysis. Similar to the PCA findings, the standardized canonical coefficients and factor structures of the environmental variables in the DFA indicated that, relative to lakes with native milfoils, VLM occurred in lakes that were (1) larger, (2) higher in TP, pH, and flushing rate, (3) lower in elevation, and (4) less species rich in macrophyte composition (Table 2).

The DFA predicted VLM and native milfoil occurrences with high accuracy. The DFA correctly classified a high percentage of VLM and native milfoil occurrences (90.6 and 82.7%, respectively) in the Merrimack watershed. More importantly, however, the discriminant function correctly classified a high percentage of VLM and native milfoil occurrences beyond the Merrimack watershed. Eight of nine VLM lakes located in Coastal (2), Connecticut (3), and Saco (4) watersheds were correctly classified as VLM lakes. In addition, four of the five lakes that were excluded from the DFA (because both VLM and native milfoils occurred there) were classified as VLM lakes. Taken together, the DFA accurately classified 13 out of 15 (87%) VLM lakes that were not included in the original DFA. Similarly, the DFA correctly classified 43 of 49 (88%) lakes with native milfoils that were not included in the DFA.

Discussion

Our multivariate analyses demonstrate that VLM invasions are strongly associated with landscape position, or "lake order". Specifically, VLM were found almost exclusively in higher order lakes

Table 2 Contributions of each variable in the DFA

Variable	Wilks' λ, if removed	Tolerance	Stand. can. coeff.	Factor structure
Elevation	0.61	0.93	−0.50	−0.44
Macrophyte richness	0.59	0.84	−0.44	−0.07
pH	0.55	0.93	0.23	0.28
Flushing rate	0.55	0.83	0.24	0.10
Total phosphorus	0.61	0.75	0.57	0.23
Area	0.77	0.70	0.96	0.54

Wilks' λ is a measure of the discriminatory power of the DFA and ranges from 0 (perfect discrimination) to 1 (no discrimination). 'Wilks' λ, if removed' is the Wilks' λ that would result if the individual variable was removed from the analysis. Tolerance is a measure of the explanatory redundancy of each variable, and ranges from 0 (totally redundant) to 1 (totally independent of other variables). The standard canonical coefficients (stand. can. coeff.) and factor structures are two measures of the contribution of each variable. The former standardizes the canonical coefficient by the variance in the variable whereas the latter reflects the correlation between the value of the variable and the canonical score for each case characterized as large, low elevation systems with relatively high pH, alkalinity and conductivity. In contrast, native milfoils were found across the range of lake orders, including lower order lakes that are characterized as smaller, higher elevation systems with lower alkalinity, conductivity, and pH.

Landscape position, or lake order, influences a number of chemical variables (e.g., Kratz et al. 1997; Soranno et al. 1999; Webster et al. 1996, 2000). Lower elevation lakes (higher lake orders) receive a larger fraction of their water inputs from ion-rich groundwater sources as compared to higher elevation lakes (lower lake orders) that receive the majority of their water inputs from ion-poor precipitation. As a result, higher order lakes have higher alkalinities, conductivities, pH, and flushing rates compared to lower order lakes. At the same time, higher order lakes tend to be much larger than lower order lakes in NH. Thus, while it is clear that VLM populations are strongly associated with higher order lakes whereas native milfoils are not, it is not clear which aspect(s) of lake order—hydrology/morphology versus chemistry—explain this pattern.

The association of VLM with higher order lakes may reflect greater propagule pressure in higher versus lower order lakes. It is well established that propagule pressure plays an important role in biological invasions (Lockwood et al. 2005) and therefore should be considered the null model for invasion success (Colautti et al. 2006). The large size of lower elevation lakes in NH may provide a bigger target for species introductions. Furthermore, the large, low-lying lakes in the Merrimack River watershed where most VLM populations occur have a larger amount of recreational boating activity—a major culprit in the spread of invasive aquatic species (e.g., Johnson et al. 2001)—as compared to the smaller lakes and ponds in higher elevation areas.

While the null hypothesis of differences in propagule pressure cannot be rejected as the explanation for VLM distribution in NH, the strong correlations between landscape position and several water chemistry variables suggests that water chemistry differences among lakes may also play an important role in the growth and survivorship of VLM. For example, VLM and Eurasian watermilfoil (EWM) tend to inhabit lakes with higher pH and calcium levels relative to several other species in Michigan and Wisconsin (Gerber and Les 1996). Similarly, alkalinity and other variables that influence dissolved inorganic carbon (DIC) are important predictors of EWM invasions in Wisconsin lakes (Buchan and Padilla 2000). If VLM is similar to EWM in its response to alkalinity or other correlated chemical variables (e.g., pH, conductivity), then these water chemistry variables may play an important role in the establishment and growth of VLM. Thus, experiments that manipulate lake chemistry variables independently of lake morphology/hydrology are required to determine the relative importance of propagule pressure versus water chemistry in creating the observed association of VLM and lake order.

In addition to landscape position and water chemistry differences, our results suggest that VLM invasions are associated with macrophytes richness. When compared to all NH lakes, our PCA results indicate that lakes containing VLM have higher macrophytes richness than lakes without VLM. However, our DFA indicated that lakes with native milfoils have higher macrophytes richness than lakes invaded by VLM. In a recent study, Capers et al. (2007) also found VLM to be less likely to invade lakes with higher native species richness in Connecticut lakes and ponds. This may indicate that more diverse native aquatic plant assemblages are more resistant to VLM invasion (e.g., Levine 2000). Alternatively, the relatively lower macrophyte richness may reflect extinctions of native plant communities after the establishment of VLM.

Are native milfoils at risk of being displaced by VLM? We identified three lakes in the macrophyte survey dataset where a native species was recorded in an earlier sample but was not recorded after invasion by VLM. While we cannot rule out sampling error, these results suggest that VLM is capable of displacing native milfoils—either through direct displacement or via extinction of native species through some other mechanism (e.g., habitat modification or changes in water quality) and subsequent colonization by VLM. Regardless of the mechanism, our analyses suggest native milfoils have the greatest risk of being displaced by VLM in higher order lakes. Specifically our DFA identified 20 lakes that are most prone to displacement by VLM and should be given high priority for monitoring efforts: 16 lakes with native milfoils and four of five lakes where both native milfoils and VLM co-occurred in the most recent sample(s) were classified as VLM lakes rather than native milfoil lakes by the DFA. In fact, we recently identified VLM in one of the above 16 lakes with native milfoils that was predicted to be invaded by VLM (Powwow Pond). While this is only one lake, this finding suggests that our model can accurately identify lakes with native milfoils that are at high risk for invasion by VLM. In addition, if the current distribution of VLM is controlled by propagule pressure as opposed to water chemistry or native species richness, then native milfoils may ultimately be susceptible to displacement by VLM in lower order lakes as well.

Our results suggest that the major NH watersheds have different susceptibilities to VLM invasion. Our model predicts continued invasion of lakes throughout the Merrimack River watershed, where VLM is currently most common. However, one surprising prediction from our model is that the Coastal watershed contains more lakes with a high risk of invasion than any other watershed on a per capita basis, and thus that the greatest per capita increase in invasions will be in the Coastal watershed. Our model identified 44% of the lakes in the Coastal watershed to be at ‘high risk’ for VLM invasion (>50% posterior probability of invasion using the DFA) whereas only 31% of the lakes in the Merrimack River watershed were identified as high-risk lakes. Thus, even though the total number of predicted invasions is higher for the Merrimack River watershed because it contains the greatest percentage of all NH lakes, the percentage of lakes predicted to be invaded by VLM is higher in the Coastal watershed. In stark contrast to the preponderance of predicted invasions in the Coastal and Merrimack watersheds, none of the lakes in the Androscoggin watershed have >50% posterior probability of being invaded. Similarly, the Connecticut River watershed contains a relatively low proportion of lakes with >50% posterior probability of being invaded, despite it being the second largest watershed in the state.

Our ecological niche models provide a practical tool for decisions regarding the prioritization of monitoring efforts. The posterior probability of being invaded (i.e., being assigned as a VLM lake) for each lake can be directly included in monitoring strategies. For example, our results suggest that a relatively higher allocation of monitoring resources may be warranted for ‘high risk’ watersheds such as the Coastal watershed whereas comparatively few monitoring resources may be dedicated to ‘low risk’ watersheds like the Androscoggin. In addition, priorities for monitoring efforts can be chosen to match the level of resources available for monitoring at any given time because lakes can be chosen by their individual posterior probabilities of being invaded. For example, our results show that only 34 lakes had a posterior probability of being invaded >90% whereas 138 lakes had a posterior probability of being invaded >50% (Fig. 3). Furthermore, posterior probabilities can be easily considered jointly with

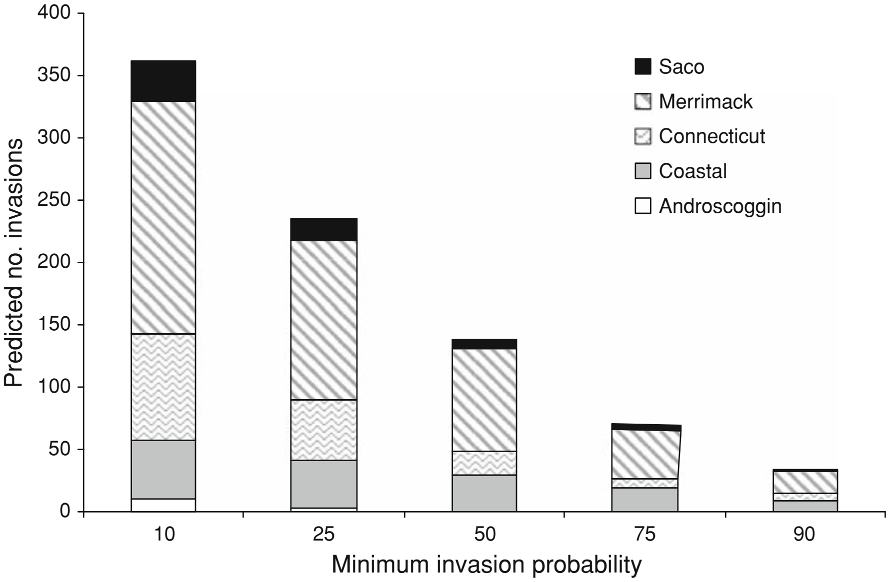

Fig. 3 Number of New Hampshire lakes predicted to be invaded by *M. heterophyllum*, and their geographic distribution among watersheds, for a given minimum posterior probability from the DFA. For example, the minimum invasion probability of 50 identifies all lakes with >0.5 posterior probability of being assigned as an *M. heterophyllum* lake in the DFA

other factors related to management decisions, such as conservation goals (e.g., protecting native milfoils where they may be threatened by VLM invasions) or recreational value of water bodies. As such, our DFA provides a quantitative way for informing monitoring decisions.

Conclusions

We have shown that routinely measured physical, hydrological, and chemical variables can accurately distinguish VLM lakes from those occupied by closely related and morphologically similar native milfoil species, and can therefore be used to predict susceptibility of lakes to invasion by VLM, as well as susceptibility of native milfoils to displacement by VLM. Thus, our analyses simultaneously provide important insight into the invasive potential of VLM and a practical tool for lake monitoring, conservation, and management efforts throughout its non-native range.

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Appendix

See Table 3.

Table 3 Environmental variables obtained from NH DES lakes database

Environmental variable	Original database	Notes
Alkalinity (mg/l)	Chemistry	
Apparent color (cholorplatinate units)	Chemistry	Excluded—correlation with secchi depth (−0.74)
Conductivity (μmhos/cm)	Chemistry	
pH	Chemistry	
Total kjeldahl nitrogen (TKN; mg/l)	Chemistry	
Total phosphorus (TP; mg/l)	Chemistry	
Calcium (mg/l)	Chemistry	Excluded—correlation with alkalinity (0.87) and conductivity (0.78)
Chloride (mg/l)	Chemistry	Excluded—correlation with conductivity (0.96)
Magnesium (mg/l)	Chemistry	Excluded—correlation with alkalinity (0.71) and conductivity (0.89)
Nitrate (mg/l)	Chemistry	Values suspect because below detection limit in most cases
Potassium (mg/l)	Chemistry	Excluded—correlation with conductivity (0.78)
Sodium (mg/l)	Chemistry	Excluded—correlation with conductivity (0.94)
Sulfate (mg/l)	Chemistry	Excluded—missing data (16% missing)
Turbidity (NTU)	Chemistry	Excluded—missing data (not measured after 1982)
Elevation (ft)	Morphology	
Area (ha)	Morphology	
Maximum depth (m)	Morphology	Excluded—correlation with mean depth (0.93)
Mean depth (m)	Morphology	
Relative depth (%)	Morphology	
Shorelength (m)	Morphology	Excluded—correlated with area (0.93)
Shoreline configuration	Morphology	Excluded—correlated with shorelength (0.75)
Volume	Morphology	Excluded—correlated with area (0.90)
Watershed area	Morphology	
Percent ponded	Morphology	
Areal water load	Morphology	Excluded—correlated with flushing rate (0.92)
Flushing rate	Morphology	
Phosporus retention	Morphology	Excluded—correlated with flushing rate (−0.91)

Table 3 continued

Environmental variable	Original database	Notes
Depth of thermocline	Trophic	
Hypolimnion volume	Trophic	Excluded due to missing data (23% missing)
Anoxic zone volume	Trophic	Excluded due to missing data (42% missing)
Summer dissolved oxygen	Trophic	
Winter dissolved oxygen	Trophic	Excluded due to missing data (20% missing)
Chlorophyll *a* concentration	Trophic	
Secchi depth	Trophic	
Macrophyte richness	Macrophytes	

The category for each environmental variable is given under "original database". Many of the original variables were excluded from the analysis either because they were missing a large fraction of data for lakes or because they were highly redundant/correlated with other variables (see text for details)

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