Predicting Eurasian watermilfoil invasions in Minnesota

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Abstract

Eurasian watermilfoil is an invasive aquatic macrophyte that can be difficult to control once established in a lake. Identifying characteristics of lakes susceptible to Eurasian watermilfoil establishment can aid management by allowing managers to focus their education and monitoring efforts on susceptible lakes. Using linear discriminant function analysis and logistic regression to analyze known occurrences of Eurasian watermilfoil, we developed models to predict susceptible lakes in Minnesota. The most reliable predictors of Eurasian watermilfoil invasion were distance to the nearest invaded lake and duration of that invasion, indicating that transport (exposure) is an important variable. However, exposure is not a guarantee of establishment: lake size, alkalinity, Secchi depth, and lake depth were also significant predictors of invasion. Specifically, large deep lakes with moderate to high alkalinity and moderate Secchi depth were more likely to be invaded. Models predicted an additional 2,100 to more than 4,700 of Minnesota’s more than 12,000 lakes could be invaded by Eurasian watermilfoil.

Key words: Eurasian watermilfoil, invasive species, Minnesota, predictive models

Eurasian watermilfoil (Myriophyllum spicatum L.; hereafter milfoil) is an invasive aquatic macrophyte introduced to North America from Eurasia. It grows quickly, often forming dense mats of vegetation concentrated at the water’s surface, enabling it to outcompete many native macrophytes. Its dense growth is associated with reduced native plant and invertebrate abundance and diversity and altered fish communities (Keast 1984, Madsen et al. 1991, Cheruvellil et al. 2002), and it can make boating, swimming, and other recreational activities difficult.

Reproduction is primarily asexual, and plants spread by runners and fragmentation (Madsen et al. 1988). Milfoil fragments can get caught on boats and boat trailers and be transported to other water bodies (Buchan and Padilla 2000, Invasive Species Program 2005), where the milfoil establishes a new population. It can also spread to connected waterbodies through channels, but its primary mechanism of transport is by boat (Smith and Barko 1990).

Since its introduction to North America in the 1940s, milfoil has spread to 46 states. It was first found Minnesota in 1987 in Lake Minnetonka and had been observed in 152 water bodies in the state in 2003 (Invasive Species Program 2005; Fig. 1). Once established, milfoil can be difficult to control. Establishment may be prevented by managing for an invasive weed early in the invasion process, such as by preventing introductions or eradicating small populations (Lodge et al. 2006). This may be facilitated through boater education and lake monitoring efforts (Invasive Species Program 2005).

Given the large number of lakes in Minnesota, prevention and monitoring efforts may be improved by focusing on lakes susceptible to milfoil invasion. Previous studies have found that milfoil abundance and presence can be explained by lake-specific traits (Madsen 1998, Buchan and Padilla 2000, Van den Berg et al. 2003). Such variables can be used to develop statistical models that predict future invasions (Ramcharan et al. 1992, Buchan and Padilla 2000). The goal of this project was to identify lakes susceptible to milfoil invasion in Minnesota based on simple, broadly available variables. To address both the spread of milfoil and its ability to establish in a given lake, we considered both human transport and physicochemical variables: the likelihood of

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milfoil introduction (*i.e.*, lake exposure), and its likelihood of establishment.

**Materials and methods**

We compiled data for 6,350 Minnesota lakes from the Minnesota Department of Natural Resources (MDNR) data warehouse and the Minnesota Pollution Control Agency (MPCA) STORET database. These data were collected by state and local agencies as part of regular water quality monitoring, fisheries inventories, or other lake assessment efforts. Lakes known to be invaded were obtained from the MDNR (2005). The list of invaded lakes likely does not include all invasions, because invasions are discovered haphazardly by state agency staff or citizens. Some are discovered while the milfoil population is still low, and many are discovered after the milfoil has become widespread (Invasive Species Program 2006). Suspected invasions are confirmed by MDNR Invasive Species Program staff, and hybrid watermilfoil (*M. sibiricum × M. spicatum*) is recorded as Eurasian watermilfoil. Plants from questionable populations were genetically tested to be sure they were not native watermilfoils.

Exposure variables in the data set included distance to the nearest invaded lake and duration of nearest invasion. Using ArcGIS 9 (ESRI 2004), we calculated the distance from each lake to the nearest invaded lake, and based on MDNR invasion records, calculated the length of time since the nearest lake had been invaded.

Environmental variables in the data set included lake area, Secchi depth, total alkalinity, percent of the lake in the littoral zone as defined in Minnesota regulations (water depth ≤ 4.57 m), shoreline development index (ratio of perimeter length to circumference of a circle), maximum depth, and Schupp’s lake class (Schupp 1992). Secchi depth and alkalinity were obtained from the MPCA STORET database. Secchi depths were annual averages from the most recent year data were available. Two-thirds of the data were from 2002, and most of the remaining data were from 2001. Secchi depth was measured 1–64 times per year, with most lakes measured at least 5 times. Alkalinity data were the 10-year average (from 1992–2002) and were measured 1–126 times in 10 years, with more than half of the lakes measured at least 3 times. Physical parameters were obtained from MDNR, and we used the most recent estimate for each lake. Schupp’s lake class (from the MDNR database) is based on lake area, alkalinity, trophic state index, maximum depth, percent littoral, Secchi depth, shoreline development factor, and morphoedaphic index, and was developed to provide an ecological classification for fish lakes. It provides a convenient and biologically meaningful way to classify lakes.

Only lakes with data for all the variables were included in the analysis, and the final data set included 3,446 lakes, 127 of which were invaded as of 2003. Thirty percent of the lakes had public boat accesses (MDNR 2005). Most lakes excluded from the analysis lacked water quality data such as Secchi depth or alkalinity. Only lakes invaded as of 2003 were used in initial model development; an additional 16 of the 20 lakes found to be invaded in 2004 and 2005 (Invasive Species Program 2005, 2006) were considered uninvaded in the model development data set and were used in model validation.

We randomly divided the dataset (both invaded and uninvaded lakes) into thirds, and used two-thirds of the data for model development and one third for validation, a procedure known as third-sample validation (Olden and Jackson 2000). Normalizing transformations were conducted on the data. In addition, there was a Gaussian relationship between milfoil presence and Secchi depth and alkalinity, so a squared component of each of these variables was added to the data set. The data were analyzed with linear discriminant function analysis (DFA) using JMP 5.1 (SAS 2002), and logistic regression analysis (LRA) using Arc (Cook and Weisberg 2004). Linear discriminant function analysis is a technique in which data are placed into groups such that maximal separation between groups is achieved (McCune and Grace 2002). Logistic regression is a specialized linear regression technique that can be used on dichotomous (presence-absence) data (Cook and Weisberg 2004).
Before performing the LRA, we computed an optimal inverse regression (Cook and Ni 2005). Inverse regression predicts \( Y \) values based on \( X \) (in contrast to classical regression, which predicts \( Y \) values based on \( X \)). The LRA was completed on the resulting linear combination. For both DFA and LRA, we used backward elimination to determine which variables would be included in the models, and required a \( P \)-value < 0.05 for inclusion.

The general model for LRA is:

\[
P = \frac{\exp(\alpha + \beta_1 X_1 + \ldots + \beta_n X_n)}{1 + \exp(\alpha + \beta_1 X_1 + \ldots + \beta_n X_n)}
\]

where \( \alpha \) is a constant, \( \beta \) is a coefficient, and \( X \) is a predictor variable. The addition of optimal inverse regression results in an additional coefficient:

\[
P = \frac{\exp(\alpha + \lambda(\beta_1 X_1 + \ldots + \beta_n X_n))}{1 + \exp(\alpha + \lambda(\beta_1 X_1 + \ldots + \beta_n X_n))}
\]

where \( \lambda \) is the additional coefficient and \( \alpha \) is an intercept determined via logistic regression. The linear combination \( (\beta_1 X_1 + \ldots + \beta_n X_n) \) is determined through optimal inverse regression. The result of this model is a probability. Lakes with a probability that is greater than the decision threshold are predicted to be invaded, and those with a probability below the decision threshold are predicted to be uninvaded. Often, the decision threshold is set at 0.5, but we adjusted this threshold in each logistic regression model to maximize sensitivity (i.e., the ability of the model to correctly predict invaded lakes) as described by Olden and Jackson (2002). Because the total probability of misclassification is the sum of the probability of misclassifying an invaded lake (Type I error) and the probability of misclassifying an uninvaded lake (Type II error), this threshold adjustment did not affect the overall error.

The models were evaluated on the correct classification of lakes in the validation set (1/3 of data) and also on correct classification of new (2004–2005) invasions. The ability of the model to correctly predict invaded lakes (sensitivity) was considered the most important classification criterion. The ability of the model to correctly predict uninvaded lakes (specificity) was also considered, but was not as relevant because these lakes could become invaded. Uninvaded, misclassified lakes were considered susceptible to Eurasian watermilfoil invasion; these lakes had characteristics of invaded lakes, but were not yet recorded or detected as invaded. We also evaluated the model’s ability to correctly predict invasions that occurred in 2004 and 2005. Model predictions are relative to a detectable population, and most of the lakes classified as invaded in our dataset have high, easily detected populations of milfoil. Models with similar classification abilities were evaluated for their simplicity:

other criteria being similar, the most parsimonious model was selected.

These analyses and evaluations were performed on three data subsets: the entire state (\( N = 3,446 \) lakes); the metro area, defined as lakes within 50 km of Lake Minnetonka (\( N = 252 \)); and Greater Minnesota, (the nonmetro area, \( N = 3,194 \)). The data were divided to reflect differences not captured in the variables: the metro area is highly developed and densely populated, with a relatively high rate of invasion (32%), while Greater Minnesota is largely rural and sparsely populated, with a low level of milfoil invasion (1.5%). Furthermore, metro lakes were invaded earlier, and the majority of Greater Minnesota invasions occurred after 1997. In the metro and Greater Minnesota data sets, the Gaussian relationship between milfoil presence and Secchi depth and alkalinity did not exist, so the squared component was not used for these data sets.

**Results**

Compared to uninvaded lakes, those invaded by Eurasian watermilfoil were closer to the nearest invasion, and the nearest invasion had occurred for a longer period of time (Table 1). Invaded lakes also tended to be deeper and larger and had low- to moderate Secchi depths and high- to moderate alkalinity. In the metro area, invaded lakes generally had a deeper Secchi depth than uninvaded lakes, and in Greater Minnesota, invaded lakes generally had a shallower Secchi depth (Table 1). Invaded lakes had significantly more boat accesses than uninvaded lakes (54% vs. 30%; \( \chi^2 \), \( P = 0.01 \)), but this difference was not significant for Greater Minnesota (\( \chi^2 \), \( P = 0.3 \)). In the metro region, there were slightly more boat accesses (45% of invaded vs. 28% of uninvaded; \( \chi^2 \), \( P = 0.04 \))

Schupp’s lake class was evaluated, but because it is a categorical variable with 43 categories it was not a meaningful predictor in any of our analyses. Analyses within lake class were limited by sample size and did not provide meaningful results.

Distance to the nearest invasion was the most significant variable in every analysis, and all the initial best-fit models included distance. After examining maps of predicted invasions, distance seemed to drive some of the models, so to determine the importance of the other variables, we also performed all the analyses without distance.

The percentage of invaded lakes correctly classified was almost always higher than the percentage of uninvaded lakes correctly classified because we set the decision threshold to maximize classification of invasions. Despite this, correct classification of uninvaded lakes remained reasonable: above 60% for most models (Table 2). Percentages of correct clas-
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Table 1.-Means and standard errors of explanatory variables for Minnesota lakes classified either as being invaded or uninvaded by Eurasian watermilfoil by data subset.

<table>
<thead>
<tr>
<th>Region</th>
<th>Method</th>
<th>Predictors</th>
<th>Invaded</th>
<th>Uninvaded</th>
<th>Total</th>
<th>Invaded</th>
<th>Uninvaded</th>
<th>Total</th>
<th>Invaded Threshold</th>
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<tbody>
<tr>
<td>Entire</td>
<td>DFA - D</td>
<td>D,A,L</td>
<td>96</td>
<td>96</td>
<td>192</td>
<td>85</td>
<td>85</td>
<td>170</td>
<td>63</td>
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<tr>
<td>State</td>
<td>DFA - ND</td>
<td>L,S,M,T</td>
<td>81</td>
<td>81</td>
<td>162</td>
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<td>81</td>
<td>162</td>
<td>44</td>
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<tr>
<td>Metro</td>
<td>DFA - D</td>
<td>D,A,L</td>
<td>87</td>
<td>87</td>
<td>174</td>
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<td>67</td>
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<tr>
<td>Greater</td>
<td>DFA - ND</td>
<td>A,L,M</td>
<td>77</td>
<td>77</td>
<td>154</td>
<td>77</td>
<td>77</td>
<td>154</td>
<td>0</td>
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<tr>
<td>Minnesota</td>
<td>LRA - D</td>
<td>D,A,L</td>
<td>83</td>
<td>83</td>
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<td>83</td>
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Table 2.-Percentages of lakes invaded by Eurasian watermilfoil, uninvaded by Eurasian watermilfoil, and the total (invaded and uninvaded) correctly classified in the best, most parsimonious, models with significant (P < 0.05) predictors. The training set (2/3 of data) was used to develop the models and the validation set (1/3 of data) tested these predictions. The percentage of new (2004–2005) invasions correctly predicted indicates model applicability. Logistic regression analysis models used an adjusted threshold to maximize correct prediction of invaded lakes.

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Entire state

The best model, as determined by DFA, included distance to the nearest invasion, duration of nearest invasion, and lake area (Table 2). This model correctly classified 96% of invaded lakes in the validation set and 63% of new invasions (Table...
The best model, as determined by LRA, included distance, duration of invasion, and Secchi depth (Table 3). This model correctly classified 100% of invaded lakes in the validation set and 81% of new invasions; LRA was thus better than DFA at predicting new invasions, although it had lower specificity than DFA. Maximum depth was also a statistically significant variable, but it was not included in the best models. When applied to the entire data set, DFA predicted 621 lakes are susceptible to invasion and LRA predicted that 1,347 of the 3,446 lakes in the data set (including 126 of the current 127 invasions) are susceptible.

Without distance, the best DFA model included duration of nearest invasion, area, and maximum depth. It correctly classified 74% of invaded lakes in the validation set, but the model did not correctly classify any of the new invasions. DFA predicted 102 lakes would become invaded. In the absence of distance, a satisfactory model could not be achieved with LRA. Despite the relatively short distance between metro lakes (Table 1), distance was an important variable for metro models.

**Metro area**

The best models obtained from both DFA and LRA included distance, duration of invasion, and area (Table 2). Secchi depth was also significant in some models but was not included in the best models. Classification of invaded lakes in the validation set was 100% for both analyses, but LRA was slightly better than DFA at classifying the 16 new invasions: 77% versus 69%, respectively; LRA was thus considered the better model. It predicted that 593 of the 3,194 lakes (including all of the current 26 invasions) are susceptible to invasion (Fig. 3A), while DFA predicted 567 invasions.

**Greater Minnesota**

The best models for Greater Minnesota for both DFA and LRA included distance, duration of invasion, and area (Table 2). Secchi depth was also significant in some models but was not included in the best models. Classification of invaded lakes in the validation set was 100% for both analyses, but LRA was slightly better than DFA at classifying the 16 new invasions: 77% versus 69%, respectively; LRA was thus considered the better model. It predicted that 593 of the 3,194 lakes (including all of the current 26 invasions) are susceptible to invasion (Fig. 3A), while DFA predicted 567 invasions.
In the absence of distance, the best model from both DFA analysis and LRA included duration of nearest invasion, area, and total alkalinity (Table 2). DFA correctly classified 86% of invaded lakes in the validation set, and 42% of new invasions. LRA correctly classified 100% of invaded lakes in the validation set, and 92% of new invasions. DFA predicted 674 lakes would become invaded (Fig. 3B), and LRA predicted 1,460 lakes.

Our models predict that 18–39% of the lakes in the dataset are susceptible to invasion. Extrapolating to the more than 12,000 lakes in Minnesota, approximately 2,100–4,700 lakes are susceptible to invasion.

**Lake class**

Despite its lack of utility in the models, lake classes described by Schupp (1992) were useful in interpretation. None of the 1,165 lakes in classes 1–19, which are primarily soft-water lakes in northeastern Minnesota, are invaded, and the models predicted that few of these lakes would become invaded (generally < 2%). Invaded lakes were concentrated in classes 24, 30, and 38 (Fig. 4), which were invaded at significantly higher rates than other classes ($\chi^2$, all $P < 0.0001$). Lakes in class 30 are mostly located in the metro area, however, and are not invaded at a higher rate than other metro-area lakes. Lakes in class 24 are also primarily located in the metro and are invaded at a higher rate than other lakes in the metro ($\chi^2$, $P < 0.0001$). Lakes in class 38 are primarily located in Greater Minnesota and were invaded at a significantly higher rate than other lakes in Greater Minnesota ($P < 0.0001$).

**Alkalinity**

Soft water lakes (alkalinity < 100 mg/L; Valley et al. 2004) were invaded at very low rates (<1%). Additional invasions in soft water lakes were predicted, but nearly all models predicted hard water lakes to account for a significantly larger number of invasions. Both soft water and hard water lakes are predicted to have some invasions, but models predict soft water lakes to be invaded at a lower rate than hard water lakes in the Greater Minnesota and entire state data sets ($\chi^2$,
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Discussion

Milfoil invasions can be predicted by transport and physicochemical variables (i.e., both exposure and establishment). Specifically, distance to nearest invasion, duration of nearest invasion, lake area, Secchi depth, alkalinity, and maximum depth were significant predictors in some models.

Distance to the nearest invaded lake was the most important predictor of milfoil invasions. Without it, the models correctly classified fewer lakes, but most still correctly classified more than 60% of invaded lakes. Duration of nearest invasion was also included in all of the best models, and area was included in most. Distance and duration of nearest invasion address the likelihood of milfoil to be introduced: lakes close to an invaded lake are more likely to be visited by boats or birds that have been on the invaded lake, and lakes that are connected by a stream may be invaded by milfoil fragments on boat traffic or floating downstream. The longer the nearest invasion has been present, the more opportunities for introductions to occur in a nearby lake.

One problem with including distance to nearest invasion and duration of nearest invasion is the update of predictions as more lakes become invaded. This could result in further increases in the number of lakes predicted to become invaded. Models that did not include distance all predicted more invasions than models that did include distance; in some cases, they predicted more than twice as many invasions. This suggests that models without distance may not predict current invasions as accurately as do models with distance. However, predictions of the total number of susceptible lakes based on lake attributes, rather than distance, may better represent the number of lakes potentially invaded.

In the metro, the geographic distribution of invaded lakes was similar between models with and without distance. In Greater Minnesota, models with distance predict invasions to cluster around current invasions, whereas models without distance predict a broader, more scattered distribution of invaded lakes (Fig 3).

When distance was removed from the analysis, Secchi depth, alkalinity, area, and maximum depth were included in some models. Previous studies have shown that Secchi depth is often higher in uninvaded lakes (Buchan and Padilla 2000) and that milfoil grows best at intermediate turbidity (Van den Berg et al. 2003). At very low Secchi depths (< 0.5 m), milfoil is probably inhibited by light, and at high Secchi depths, it may be limited by nutrients (Smith and Barko 1990).

We found low rates of invasion, both observed and predicted, in soft water lakes (alkalinity < 100 mg/L), even in the highly invaded metro area. This suggests that even where exposure is high (i.e., there are many invaded lakes and high boat traffic in the area), invasion in soft water lakes still occurs at a much lower rate than in hard water lakes. These results are consistent with previous studies, which showed that although milfoil is capable of growing in a wide range of alkalinites, it tends to occur more frequently and grow more profusely in hard water lakes (Nichols 1994, Madsen 1998, Buchan and Padilla 2000), probably because these systems are not carbon-limited (Smith and Barko 1990). In addition, an invasion is often not discovered until it reaches nuisance level, which means that lakes supporting low levels of milfoil (e.g., low alkalinity lakes) may not be detected (Invasive Species Program 2006).

These results could also be a reflection of trophic state: Secchi depth typically decreases and alkalinity increases with lake fertility (Moyle 1946, Schupp 1992). Milfoil tends to occur in meso- to moderately eutrophic lakes, which would have moderate-to-low Secchi and moderate-to-high alkalinity (Smith and Barko 1990, Madsen 1998).

The influences of geography and chemistry are difficult to separate in Minnesota. Lakes that are remote and far from population centers, especially in northeastern Minnesota, also tend to have low alkalinity and high Secchi depth. Furthermore, the remote northeastern lakes (classes 1–19) have rocky substrate and generally support low densities of aquatic plants (Moyle 1945) and thus may be less likely to support invasions of milfoil (Nichols and Shaw 1986). Lakes that are generally more accessible and closer to invaded lakes tend to have high alkalinity and low Secchi depth.

Lake area and depth were included in several models and may influence introduction and establishment. Large and deeper lakes may have more boat accesses, and thus more boat traffic and potential for introductions. Invasions may also be more likely to be detected in larger lakes due to greater surveillance by the public and agency staff. In addition, clearer water, generally associated with the deeper lakes, may result in more suitable habitat for milfoil establishment and growth. Area may also influence milfoil establishment: large lakes could have more suitable littoral zone or a diversity of habitats for milfoil establishment (Rorslett 1991, Makela et al. 2004). However, percent littoral and shoreline development index were not significant variables in any model. The distribution of invaded and uninvaded lakes was virtually identical for both of these variables, which is consistent with previous studies (Buchan and Padilla 2000).
Lakes in classes 24 and 38 are particularly susceptible to invasion; both were invaded at significantly higher rates than other lakes. It is impossible to determine exactly what makes these classes susceptible, but their alkalinity (relatively high) and clarity (intermediate) (Table 1; Schupp 1992) are consistent with characteristics identified by previous studies (Smith and Barko 1990, Nichols 1994, Madsen 1998, Buchan and Padilla 2000). Furthermore, lakes in these classes were invaded without regard to geography, indicating the importance of environmental factors for establishment.

Because there is no systematic monitoring process, and because milfoil populations can exist at low, undetectable levels, our list of invaded lakes is likely incomplete. Lakes predicted to be invaded may exclude those that will support small, undetectable populations of milfoil. In addition, invasions are not recorded at the moment of establishment, so the actual durations of invasion are likely longer than recorded. This error is present in all lakes, although not necessarily at the same level; we suspect the lag time between establishment and discovery is not consistent. Even so, duration of nearest infestation was a significant predictor in all models.

Buchan and Padilla (2000) found that in Wisconsin, water quality factors were more important than milfoil exposure, but our results indicate that exposure is more important. However, their study was located in a highly invaded area and designed to minimize the effects of transport to understand where milfoil could not grow. We used coarser variables to predict the number of lakes that might become invaded over a large geographic area. As more Minnesota lakes become invaded, transport is likely to become less limiting and physicochemical factors, such as alkalinity and clarity, will likely become more important. In addition, boat access and distance to highway (variables used by Buchan and Padilla 2000) may not be good predictors of propagule pressure. Although proportionally more lakes in Minnesota with public boat accesses are invaded (54%) than lakes without access (34%), there was no difference in percentages of invaded lakes between those with and without public boat accesses in Greater Minnesota, and the difference in the metro area was small. Access may be much less important than distance to nearest invasion and the duration of opportunities for introduction. Our results also suggest that vectors other than boats and trailers may be important.

In the metro area, nearly all susceptible lakes appear to have been invaded by milfoil. Our model predictions suggest that the metro lakes are approaching saturation; only 13–21 new invasions were predicted in the metro area, or an additional 5–8% of available metro lakes. Conversely, 567–1460 of the 3,194 Greater Minnesota lakes analyzed were predicted to become invaded, or an additional 16–44% of available Greater Minnesota lakes. These predictions are consistent with the chronology of invasions in the state: the cumulative number of invasions in the metro area has plateaued, while the number of Greater Minnesota invasions is accelerating (Fig. 5).

The relative importance of exposure and establishment is unclear: while exposure may be the main limiting factor for invasion, physicochemical conditions do influence establishment and are likely to become more important as milfoil becomes more widespread in the state. Other variables, such as diversity of the native plant community, may also be important to the probability of milfoil establishment. The use of more sophisticated modeling techniques, such as gravity modeling and artificial neural networks, may clarify lake susceptibility, although they require additional data (Lodge 1993, Nichols and Buchan 1997). Many Minnesota lakes are susceptible to invasion; our models predict that 18–39% additional lakes, or 2,100–4,700 total lakes may be invaded by milfoil. Furthermore, most future invasions likely will occur in Greater Minnesota. Continued diligence in monitoring and prevention are thus important, especially in susceptible lakes.

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