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Forecasting the Vulnerability of Lakes to Aquatic Plant Invasions

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Prevention is an integral component of many management strategies for aquatic invasive species, yet this represents a formidable task when the landscapes to be managed include multiple invasive species, thousands of waterbodies, and limited resources to implement action. Species distributional modeling can facilitate prevention efforts by identifying locations that are most vulnerable to future invasion based on the likelihood of introduction and environmental suitability for establishment. We used a classification tree approach to predict the vulnerability of lakes in Washington State (United States) to three noxious invasive plants: Eurasian watermilfoil (*Myriophyllum spicatum*), Brazilian egeria (*Egeria densa*), and curlyleaf pondweed (*Potamogeton crispus*). Overall, the distribution models predicted that approximately one-fifth (54 out of 319 study lakes) of lakes were at risk of being invaded by at least one aquatic invasive plant, and many of these predicted vulnerable lakes currently support high native plant diversity and endemism. Highly vulnerable lakes are concentrated in western Washington in areas with the highest human population densities, and in eastern Washington along the Columbia Basin Irrigation Project and the Okanogan River Basin that boast hundreds of lakes subject to recreational use. Overall, invasion potential for the three species was highly predictable as a function of lake attributes describing human accessibility (e.g., public boat launch, urban land use) and physical–chemical conditions (e.g., lake area, elevation, productivity, total phosphorous). By identifying highly vulnerable lake ecosystems, our study offers a strategy for prioritizing on-the-ground management action and informing the most efficient allocation of resources to minimize future plant invasions in vast freshwater networks.

Nomenclature: Eurasian watermilfoil, *Myriophyllum spicatum* L. MYPSP; Brazilian egeria, *Egeria densa* Planch. ELDDE; curlyleaf pondweed, *Potamogeton crispus* L. PTMCR.

Key words: Aquarium trade, ecological niche models, exotic plants, nursery plants, prevention.

Invasive species are a significant concern in freshwater lakes and rivers, as they can spread rapidly into new locations via numerous pathways including commercial and recreational boats (ballast water, hull fouling), aquarium and ornamental trades, angling (discharging live bait, trailer boats), schools (release by teachers and students), and introductions associated with intentional stocking (Drake and Mandrak 2010; Keller and Lodge 2007; Larson and Olden 2008; Padilla and Williams 2004; Rothlisberger et al. 2010; Strecker et al. 2011). Severe ecological and economic damages associated with some aquatic invasive species have resulted in government and private entities spending hundreds of millions of dollars annually to prevent, control and eradicate invasions (Lovell et al. 2006; Vilà et al. 2010). Indeed, aquatic invasive plants in the United States alone are estimated to result in billions of dollars annually in economic impacts, and require millions of dollars annually to manage (Pimentel et al. 2005; Rockwell 2003).

Risk assessment frameworks are increasingly used to predict the likelihood that a species will be transported, introduced and establish in a new region (reviewed in Leung et al. 2012). In the freshwater sciences, these approaches have been developed to make them more readily available to resource managers (see Papeş et al. 2011; Vander Zanden and Olden 2008). Furthermore, mounting evidence suggests that the economic benefits of preventing the spread of aquatic invasive species outweigh the costs of controlling them once they become established (Keller et al. 2008). Model simulations of invasive species management indicate that there is a higher risk of invasion and lower social welfare when control strategies are favored over prevention strategies (Finnoff et al. 2007). Models also show that there are benefits to adopting early detection and rapid response strategies (Kaiser and Burnett 2010).

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Management Implications

Preventing introductions of aquatic invasive plants to new ecosystems requires predictive models that can be used to help guide resource allocation and prioritize management activities. The present study identifies those lakes most vulnerable to future invasions of three widespread nonnative plants — Eurasian watermilfoil, Brazilian egeria, and curlyleaf pondweed — with the goal of preventing aquatic plant invasions in Washington State (United States) by focusing on surveillance, control, education, and future research. These are management themes that are relevant to other regions of the United States and elsewhere.

First, surveillance of the 54 lakes identified as having the greatest risk of future plant invasions is paramount to prevent new invasions (see Supplemental Table 1, http://dx.doi.org/10.1614/IPSM-D-13-00036.TS1). Based on habitat suitability, areas within and around human populated areas in western Washington, the Columbia Basin Irrigation Project, and the Okanogan River should be prioritized because they have the greatest number of vulnerable lakes and may be key invasion hubs. Second, there is a need for early detection and rapid response strategies to eradicate and control early infestations that are discovered by lake monitoring. These strategies can reduce the risk of heavy infestation and may even lead to successful eradication. One strategy is to adopt an online early detection network to link existing local, regional, and national databases on invasive species and provide a data portal where new data can be added and shared easily through an interactive website. Third, education is critical in preventing invasions. We recommend that invasive species signage is posted by the boat launches of all 54 vulnerable lakes to provide information on how to stop the spread of aquatic weeds of concern. Notably, this is in contrast to the current management strategy in Washington (and elsewhere) where signage is only posted on lakes already containing populations of invasive species. Fourth, a better understanding of dispersal vectors is needed. Currently, there is limited information about aquarium and nursery plant disposal and inland boater traffic in Washington. These two areas warrant further research as they will help identify invasion hubs and other vulnerable waterbodies.

Preventing new introductions and the secondary spread of existing nonnative species to new ecosystems requires predictive tools that can be used to help guide resource allocation and prioritize management activities. Early detection and rapid response strategies are notoriously difficult to implement in freshwater landscapes that contain complex networks of lakes and rivers with diverse uses and limited management resources (Drury and Rothlisberger 2008; Vander Zanden and Olden 2008). Recent years have witnessed considerable progress in the application of species distributional modeling and graph theoretic approaches to support local-scale vulnerability assessments (e.g., Leung et al. 2006; Muirhead and MacIsaac 2005, Vander Zanden and Olden 2008). Species modeling investigations have sought to estimate lake-specific probability of nonnative species invasions as a function of waterbody attributes describing the likelihood of introduction (e.g., presence of boat launches, shoreline development) and successful establishment (e.g., lake area, depth, productivity). Examples include aquatic plants (e.g. Jacobs and MacIsaac 2009), invertebrates (e.g. Herborg et al. 2007), fish (e.g. Vander Zanden et al. 2004), and pathogens (e.g. Václavík and Meentemeyer 2009). A small, but growing, fraction of studies have also attempted to incorporate the likelihood of ecological impacts based on the presence/absence of sensitive species (e.g., Mercado-Silva et al. 2006; Vander Zanden et al. 2004) or quantitative estimates of extirpation probabilities (Olden et al. 2011). Identification of which lakes are susceptible to specific invasive species is valuable in directing management efforts where they are likely to provide the greatest benefit in preventing invasions (Vander Zanden and Olden 2008; Vander Zanden et al. 2010). In addition, identifying vulnerable lakes decreases the uncertainty about future invasions and increases the likelihood that prevention strategies will be included in local and regional invasive species management plans (Finnoff et al. 2007).

Here, we evaluate the vulnerability of lakes in Washington State, United States (hereafter referred to as Washington) to the invasion risk from three noxious aquatic invasive plants – Eurasian watermilfoil (*Myriophyllum spicatum* L. MYPSP), Brazilian egeria (*Egeria densa* Planch. ELDDE), and curlyleaf pondweed (*Potamogeton crispus* L. PTMCR). Lakes of Washington contain a rich diversity of plants and animals supporting freshwater ecosystems that supply numerous human goods and services. Aquatic invasive plants threaten this native biodiversity and although government and private agencies, First Nations, and citizen groups actively manage aquatic invasive plants in the state, their resources are insufficient to safeguard the large number of waterbodies (ca. 8,000) in Washington. All three invasive plants can substantially reduce recreation by limiting boating, swimming, and fishing. This loss of recreation can be very costly from an economic perspective. A decline of only 1% in recreation values associated with invasion of Eurasian watermilfoil in the Truckee River watershed (California and Nevada) was estimated to cost $500,000 USD annually (Eiswerth et al. 2000). The economic impacts also extend to property values. In northern Wisconsin, the property values of waterfront homes declined by 8% after Eurasian watermilfoil invaded a lake (Horsch and Lewis 2009); similar values are evident for lakes in Washington (J. D. Olden and M. Tamayo, unpublished data). Hence, prevention of new invasions is essential to both reduce ecological impacts and potential economic damages.

Our study aims to facilitate the implementation of prevention and early detection strategies by helping decision makers prioritize management efforts for Eurasian watermilfoil, Brazilian egeria, and curlyleaf pondweed. Our vulnerability assessment also evaluates the risk of future invasion to lakes with perceived ecological importance based on native plant diversity. Beyond the study region and species, our paper presents a quantitative approach and useful framework to guide invasive species management that is readily accessible to various stakeholders through the use of decision trees and mapping of ecosystem vulnerability.

Materials and Methods

Aquatic Invasive Plants. Our study examined Eurasian watermilfoil, Brazilian egeria, and curlyleaf pondweed because they are the focus of significant management effort, are classified as state noxious weeds, and have expanded their distribution in Washington (and across many parts of the United States) since the 1990s (WADOE 2012a). These submersed perennials are canopy-forming plants and create dense monospecific stands with dramatic ecological and economic impacts. For example, they have been shown to reduce native plant diversity, alter water quality and circulation, increase sedimentation, and create unsuitable habitats for wildlife (Frodge et al. 1990; Madsen et al. 1991; Santos et al. 2011; Smith and Barko 1990; WADOE 2012b). In addition, these aquatic weeds hinder recreational activities and power generation, and can have a negative effect on waterfront property values (Eiswerth et al. 2000; Horsch and Lewis 2009).

Eurasian watermilfoil is native to Europe, Asia, and northern Africa (Couch and Nelson 1985) and is now found on all continents except Australia and Antarctica. It was first introduced into North America in the 1940s and is now present in almost all states and provinces of the United States and Canada. This plant spreads primarily through vegetative fragments via the mass flow of water and by accidental introduction from boat trailers (Kimbel 1982; Madsen and Smith 1997). Eurasian watermilfoil was first recorded in Washington State in 1965 (WADOE 2012c) and is now widespread occurring in $>$ 170 waterbodies primarily along the Okanogan and Columbia Rivers and in close proximity to major roadways (Parsons 1997; WADOE 2012a).

Brazilian egeria is native to central Brazil and coastal areas of Argentina and Uruguay. Because of its popularity as an aquarium plant, this species has spread to New Zealand, Australia, Hawaii, Denmark, Germany, France, Japan, and Chile. In the United States, Brazilian egeria has been documented from west to east coasts and was first found in Washington in the early 1970s (WADOE 2012b). Currently, only male plants of Brazilian egeria have been found in the United States, and therefore the plant reproduces and spreads through vegetative fragments (WADOE 2012b). To date, Brazilian egeria has been found in $>$ 25 waterbodies scattered over a wide geographic area in western Washington (WADOE 2012a).

Curlyleaf pondweed is a popular aquarium and nursery plant native to Europe, Asia, Africa, and Australia and has spread across continental United States except for Maine and South Carolina since its initial introduction in the mid 1800s (Keller and Lodge 2007). The most likely mode of introduction of curlyleaf pondweed into a body of water is through the transport of plant fragments on aquatic equipment such as boats and trailers. These fragments can root and create a new infestation (Stuckey 1979). Curlyleaf pondweed was first reported in Washington in the late 1940s and is now present in $>$ 120 waterbodies where it currently occurs at low infestation levels. This invasive plant, however, is very problematic in many lakes in the midwestern United States, and research indicates that the life history of curlyleaf pondweed in Washington is similar to these invasions (WADOE 2012a). The distribution of curlyleaf pondweed is expanding in Washington and the plant is being monitored for changes in nuisance level (WADOE 2012a).

Data Collection and Study Sites. We collated data on aquatic plant communities, lake attributes, and land use for 319 lakes throughout Washington (184,827 km^2 [45,467 ac] total area, Figure 1). Plant data was obtained from the Washington Department of Ecology's Aquatic Plant Survey Database with records from 1990 to 2008 (Environmental Assessment Program) and included the presence–absence of our three target species and other aquatic plants. Of the 319 lakes, Eurasian watermilfoil was present in 78 lakes, Brazilian egeria in 13 lakes, and curlyleaf pondweed in 44 lakes (70% of records collected post-2000). In addition, we calculated native plant species richness to evaluate the forecasted distribution of our target invasive plants relative to their potential consequences.

Lake attributes included variables describing physical characteristics (e.g., lake surface area, maximum depth, elevation), water quality and chemistry (e.g., water clarity, total phosphorus, water temperature, surrounding land use), and accessibility (i.e., presence of a public boat launch) (Table 1). Water quality and chemistry data were averages of surface or epilimnetic measurements made during the macrophyte-growing season (April to September) from 1972 to 2010, though the majority of records (60%) were from 1996 to 2008. The lake data were collated from government and private entities, First Nations, academia, and lake books. Land use data (Table 1) were obtained from the Landscape Ecology and Conservation Laboratory at the University of Washington (Seattle, USA) and represented the proportion of three distinct land use variables (urban, farm land, forested) in a 10 km radius around each lake referenced to 2000. Lake accessibility via the presence of a boat launch helped to quantify lake use by people, thus providing a surrogate of propagule pressure (Johnson et al. 2008; Leung et al. 2006). All lake attributes were calculated for years prior to the plant survey, with the exception of land use where 70% of the lake records represented survey dates occurring after the land use characterization. Note that land

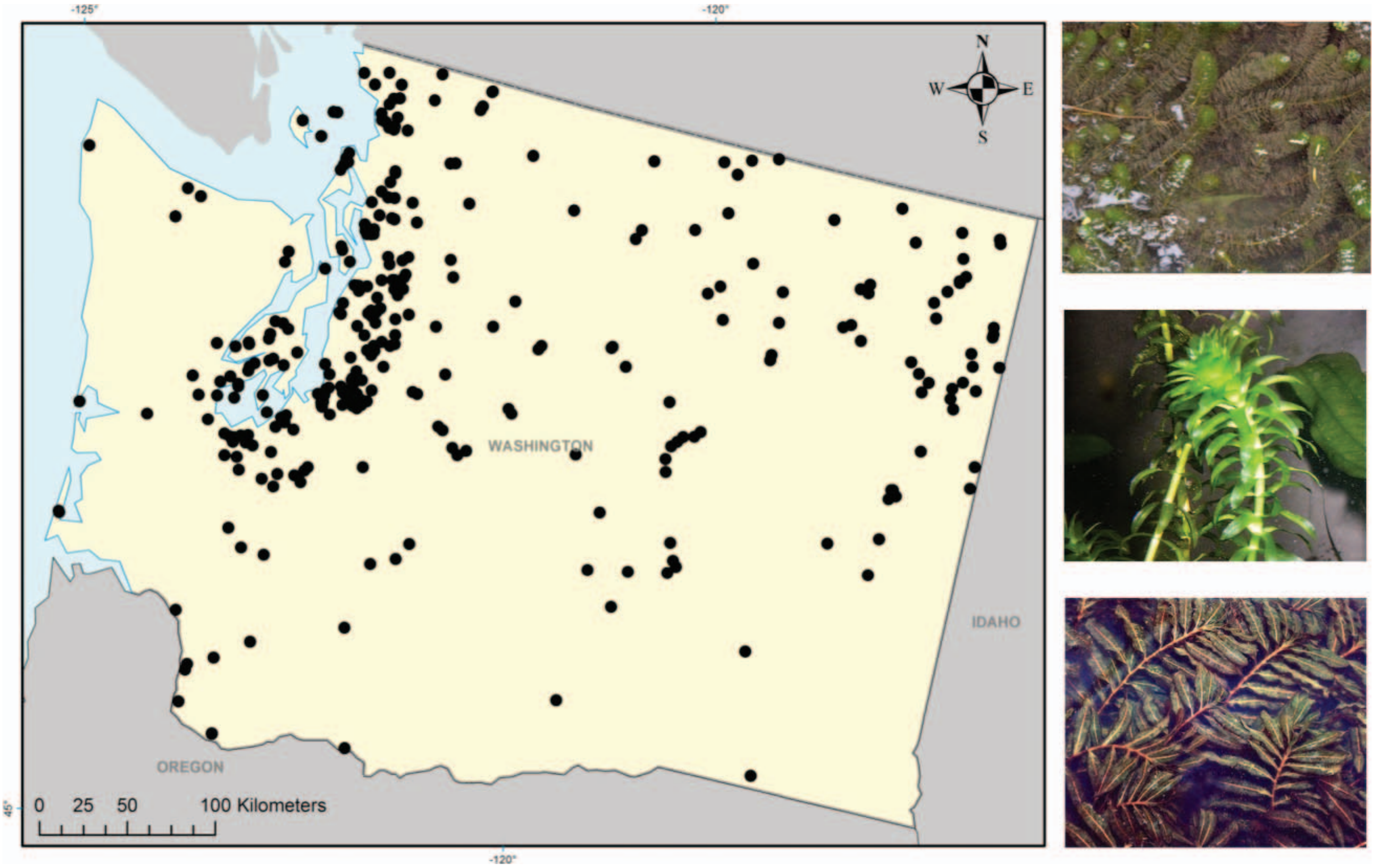

Figure 1. Location of the 319 study lakes in Washington State where invasion patterns of Eurasian watermilfoil (upper right), Brazilian egeria (middle right), and curlyleaf pondweed (lower right) were modeled. All photos are public domain. (Color for this figure is available in the online version of this paper.)

use has changed relatively little since 1990 when plant survey data commenced.

Species Distribution Models. We used classification and regression trees (CART; Breiman et al. 1984) to model presence–absence of Eurasian watermilfoil, Brazilian egeria, and curlyleaf pondweed as a function of 11 lake attributes related to the potential for species introduction and establishment in Washington lakes (Table 1). CART is particularly powerful for ecological analyses because it allows the modeling of nonlinear, nonadditive relationships among mixed variable types; it is invariant to monotonic transformations of the data that are often required prior to using traditional methods, and facilitates the examination of intercorrelated variables in the final model (De'ath and Fabricius 2000; Olden et al. 2008). CART uses a recursive partitioning algorithm to split data into a nested series of mutually exclusive groups with the goal of maximizing homogeneity of the response variable. We used the Gini impurity criterion to determine the optimal variable splits (minimum parent node size: $n = 8$; minimal terminal node size: $n = 5$), and determined the optimal size of the decision tree by constructing a series of cross-validated trees and selecting the smallest tree based on the one-standard-error rule (Olden et al. 2008). Variable importance was determined by calculating for each variable at each node the change in Gini impurity attributed to the best surrogate split on that variable. The values of these deltas are summed over each node and scaled relative to the best-performing variable so that they are expressed as relative importance on a scale of 0 to 100 (Breiman et al. 1984). All analyses were performed in R (R Development Core Team 2008).

Model Validation and Performance. Ten-fold cross validation was used to generate model predictions and evaluate performance of the classification trees for each species. This validation method excludes 10% of the lakes, constructs the model with the remaining 90% of lakes, predicts the response of the excluded lakes using this model, and repeats the procedure 10 times until all lakes are excluded from model construction. Cross validation has been shown to produce unbiased estimates of predictive performance for species distribution models (Olden et al.

Table 1. Lake attributes describing lake accessibility and physical-chemical conditions, which were used to predict the presence-absence of the aquatic invasive plant species. Means and standard errors (SE) are included for each variable.

Lake attribute	Mean	SE
Physical		
Lake surface area (km^2)	2.8	0.7
Maximum depth (m)	19.2	2.0
Elevation (m)	334.8	21.4
Presence of boat launch[b]	0.63	0.03
Water chemistry[a]		
Secchi depth – water clarity of a lake (m)	9.3	0.5
Surface water temperature (°C)	18.4	0.2
Total phosphorus (μg L^{-1})	56.8	14.3
Chlorophyll-*a* (μg L^{-1})	12.2	2.5
Land use[b]		
Urban	0.19	0.01
Farming	0.08	0.01
Forested	0.43	0.01

[a] Water chemistry data are averages of surface or epilimnetic measurements made during the macrophyte-growing season (April to September).

[b] Proportion of lakes containing a boat launch or proportion of land use type based on a 10-km radius around the lake.

2002). Model performance for species' presence–absence was assessed according to three metrics: (1) overall correct classification or the percentage of sites where the model correctly predicts species' presence–absence; (2) sensitivity or the percentage of the sites where species' presence was correctly predicted; and (3) specificity or the percentage of the sites where species' absence was correctly predicted (see Fielding and Bell 1997). The decision threshold (i.e., a threshold probability value that when exceeded the species is predicted to be present) for each species was set to their prevalence (frequency) in the study lakes—Eurasian watermilfoil (0.245), Brazilian egeria (0.041), and curlyleaf pondweed (0.138). This approach produces models that optimally maximize prediction sensitivity and specificity (Olden et al. 2002). Lakes in which a plant species was predicted to be present based on favorable lake attributes, but was not currently observed are considered candidates for future establishment. We used Cohen's Kappa (Fielding and Bell 1997) to evaluate whether the agreement between predicted and observed presences and absences departed significantly from expectations based on chance alone. Kappa values of 1 represent perfect agreement and a value of 0 implies complete disagreement between model predictions and actual species occurrences.

We assessed the statistical significance of species' predictions using a Monte Carlo approach following the protocols of Olden et al. (2002). Null distributions of

Table 2. Performance of the classification trees for predicting plant species' presence-absence in the 319 study lakes. Values are based on 10-fold cross validation. P-value of statistical significance is based on the rate of correct classification.

	Eurasian watermilfoil	Brazilian egeria	Curlyleaf pondweed
Correct classification (%)	81	97	91
Sensitivity (%)	74	46	61
Specificity (%)	83	99	96
Cohen's Kappa	0.52	0.56	0.61
P-value	0.001	0.006	0.002

correct classification rates (CCRs) for each species' presence–absence were generated by randomly permuting the original observations among the lakes, constructing a classification tree using the randomized data and the original predictor variables, and calculating the CCR (based on 10-fold validation). This procedure was then repeated 9,999 times and the significance level of the predictive model was calculated as the proportion of random CCRs (including the observed CCR) that were larger than or equal to the observed CCR.

Model performance measures assume that errors associated with false presences and false absences are equivalent. However, there are situations where this assumption is questionable. For example, if a model is used to predict the occurrence of an invasive species, failure to correctly predict presence locations will be more 'costly' (both ecologically and economically) than would the prediction of false presences. In other words, the false negative cost (FNC) is greater than the false presence cost (FPC). Although these inequalities can be compensated for partly by the choice of error measure and threshold, it is possible to develop a cost matrix that weights errors prior to the calculation of model accuracy (Fielding and Bell 1997). In the absence of clear ecological/economic gains and losses, the allocation of costs is subjective. Here, we assigned the false negative cost to be twice that of the false presence cost (i.e., 2 : 1 ratio of FNC to FPC) to account for the fact that misclassifying a lake as unlikely to support a population of an invasive plant is more problematic. Preliminary analysis using different costs did not substantially change the results.

Results

Species occurrence of Eurasian watermilfoil, Brazilian egeria, and curlyleaf pondweed in Washington lakes was highly predictable as a function of the 11 lake attributes (correct classification = 81 to 97%, Cohen's Kappa = 0.52 to 0.61, P = 0.001 to 0.006, Table 2). Eurasian watermilfoil had the highest percentage of correct predictions of species' presence, while Brazilian egeria

Table 3. Relative importance (0–100) of the lake attributes in the classification trees for predicting plant species' presence-absence. Attributes are ranked from most important to least important based on mean relative importance across all species.

Predictor variables	Eurasian watermilfoil	Brazilian egeria	Curlyleaf pondweed
Urban land use	61	100	59
Elevation	79	16	79
Lake area	66	5	100
Farming land use	44	75	27
Maximum depth	100	0	15
Total phosphorus	21	0	72
Secchi disk depth	0	0	86
Chlorophyll-*a*	19	1	57
Forested land use	37	0	38
Water temperature	42	4	14
Public boat launch	43	0	0

had the lowest. Classification trees demonstrated greater specificity (accurately predicting species' absence) compared to sensitivity (accurately predicting species' presence), reflecting the generally low prevalence of these invasive plants in the study lakes (Table 2).

The explanatory power of the lake attributes in the classification trees varied among species (Table 3). Lake size and elevation, land use, and lake accessibility were identified as key determinants of Eurasian watermilfoil occurrence (Figure 2; Table 3). The presence of a public boat launch was among the top predictors of Eurasian watermilfoil; this plant species was absent in 95% of the study lakes lacking a public boat launch (n = 113 lakes, node A in Figure 2). Eurasian watermilfoil was predicted to occur in relatively small lakes (< 0.5 km^2) surrounded by heavily-altered landscape ($> 16\%$ farming (node C) or $> 50\%$ urban development (node D)). In relatively larger lakes (but still < 20 km^2), Eurasian watermilfoil was more prevalent in low (< 38 m) and high (> 626 m) elevation regions (all elevations reported above sea level), and in

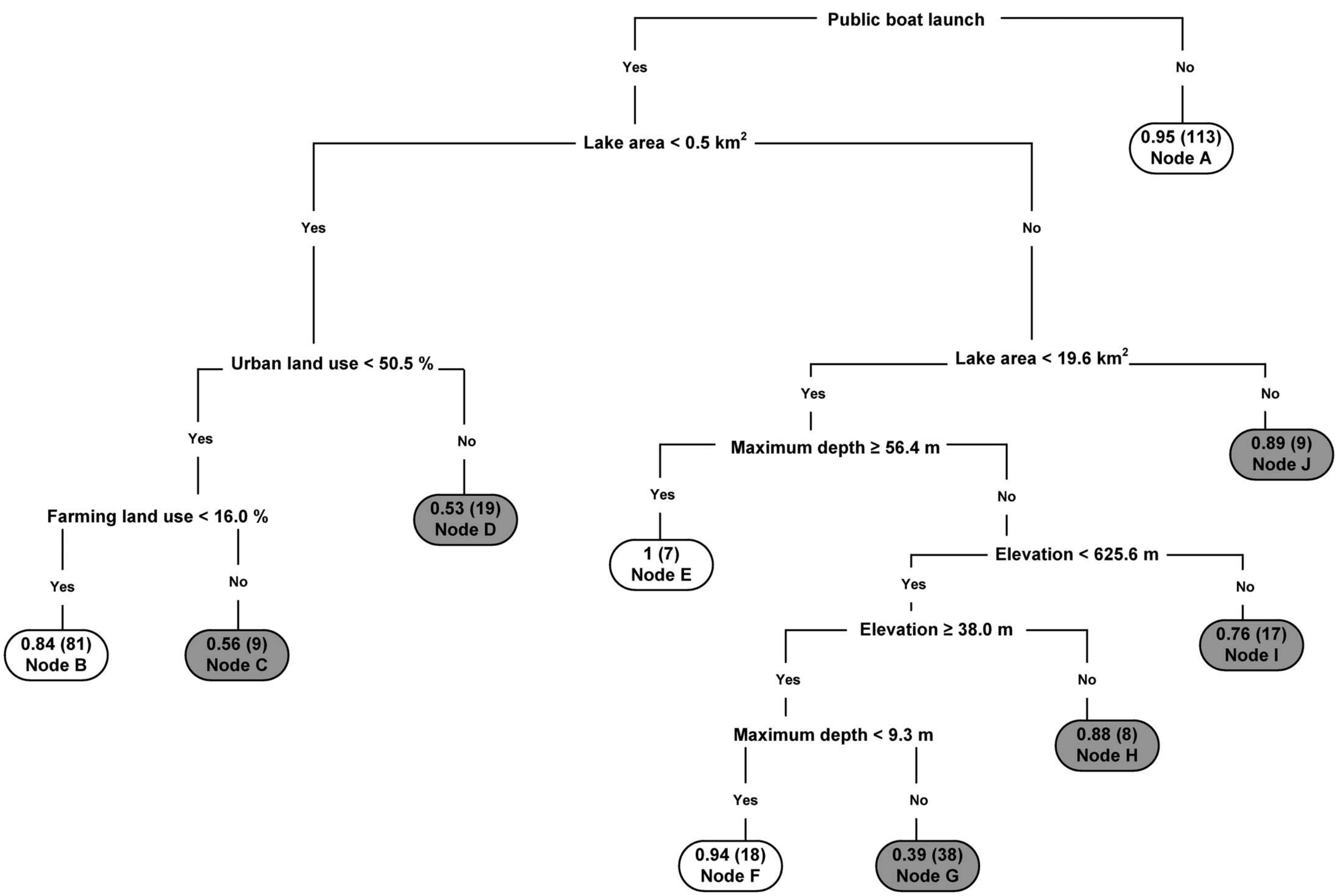

Figure 2. Classification tree for Eurasian watermilfoil, where each split in the tree shows the lake attribute and its value (condition) determining the split. Terminal nodes represent the predicted presence (gray ovals) or absence (white ovals) of Eurasian watermilfoil. Each terminal node contains the proportion of lakes that were classified correctly, the total number of lakes in the node (in parentheses) and node number (labeled A–J).

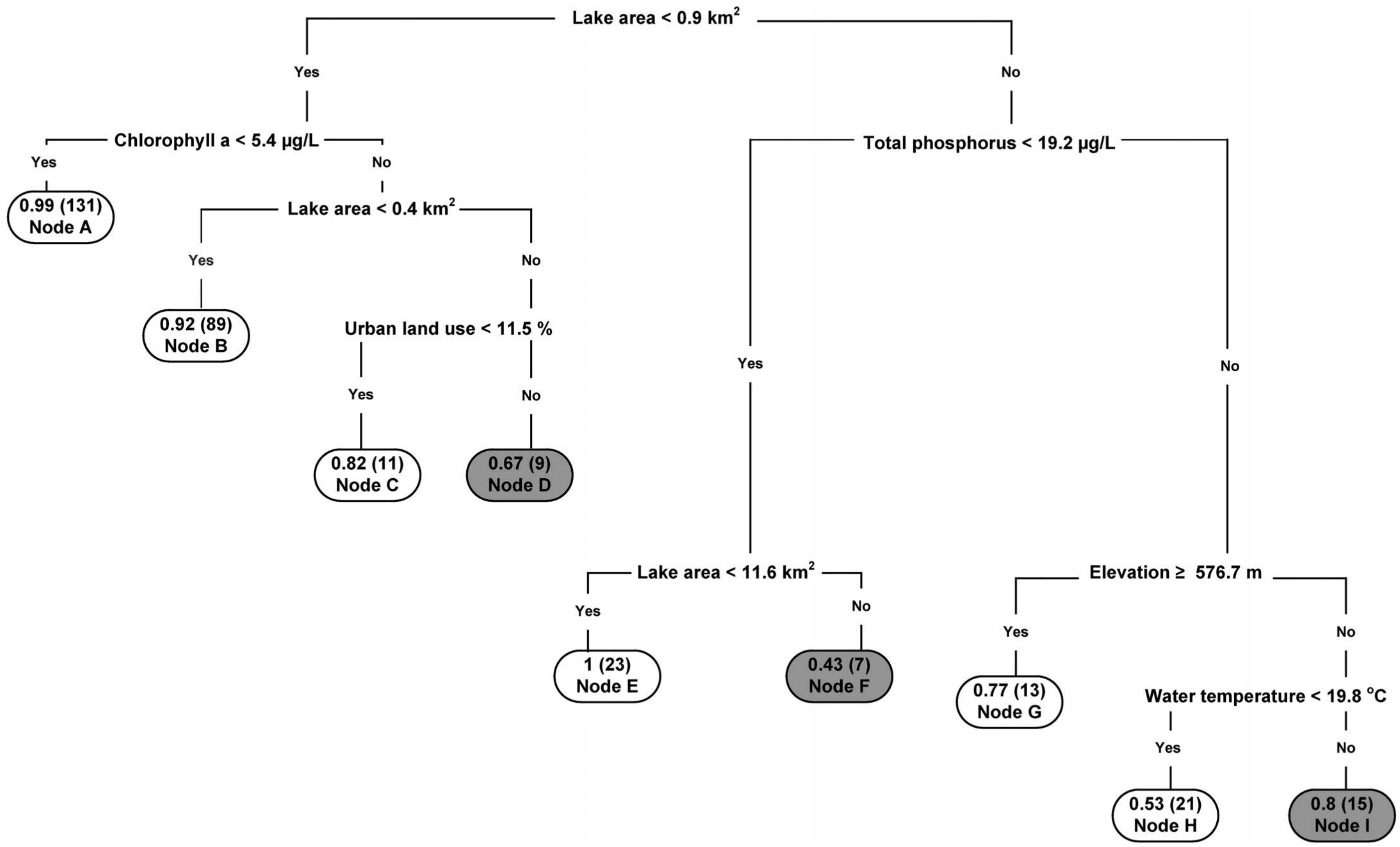

Figure 3. Classification tree for curlyleaf pondweed, where each split in the tree shows the lake attribute and its value (condition) determining the split. Terminal nodes represent the predicted presence (gray ovals) or absence (white ovals) of curlyleaf pondweed. Each terminal node contains the proportion of lakes that were classified correctly, the total number of lakes in the node (in parentheses) and node number (labeled A–I).

relatively deeper lakes (> 9 m) (Figure 2). In summary, Eurasian watermilfoil was predicted to occur primarily in lakes with public boat launches that were either large lowland lakes or small upland lakes surrounded by human land uses (Table 3).

Three distinct combinations of lake conditions led to a higher probability of occurrence for curlyleaf pondweed. First, curlyleaf pondweed was predicted in relatively smaller (0.4 to 0.9 km^2) and more productive lakes (chlorophyll-*a* concentration > 5 µg L^{-1}) surrounded by moderate to high urban land use (> 12%) (node D in Figure 3). Second, very large (> 12 km^2) and relatively nutrient-poor lakes (phosphorus concentration < 19 µg L^{-1}) were more likely to support curlyleaf pondweed (node F). Third, moderate elevation lakes (< 577 m) characterized by greater nutrient enrichment (phosphorus concentration > 19 µg L^{-1}) and warmer water temperatures during the growing season (> 20 C) were predicted to support curlyleaf pondweed populations (node I). Overall, four variables—lake area, elevation, urban land use and productivity—were key predictors of the distribution of curlyleaf pondweed (Table 3).

Patterns of Brazilian egeria occurrence were driven predominately by urban and farming land use and lake elevation (Figure 4; Table 3). The classification tree predicted that Brazilian egeria primarily occurred in low elevation lakes (< 37 m), with minimal farming land use (< 3%) but more than 5% urban development. Overall, Brazilian egeria was forecasted to occur in lowland lakes surrounded by urban development.

In 54 of the 319 study lakes (or 17%), Eurasian watermilfoil, Brazilian egeria, and/or curlyleaf pondweed were predicted, but not currently observed (i.e., false presence) (Figure 5; Supplemental Table 1, http://dx.doi.org/10.1614/IPSM-D-13-00036.TS1). These lakes are considered likely candidates for aquatic plant invasion because they are susceptible to introduction and have the appropriate environmental conditions for establishment, but do not presently support a population. The vulnerable lakes had a probability of invasion ranging from 0.40 to 0.89 (Supplemental Table 1, http://dx.doi.org/10.1614/IPSM-D-13-00036.TS1). The lakes were primarily vulnerable to one of the three invasive plants (53 out of 54 lakes), in particular to Eurasian watermilfoil (41 lakes)

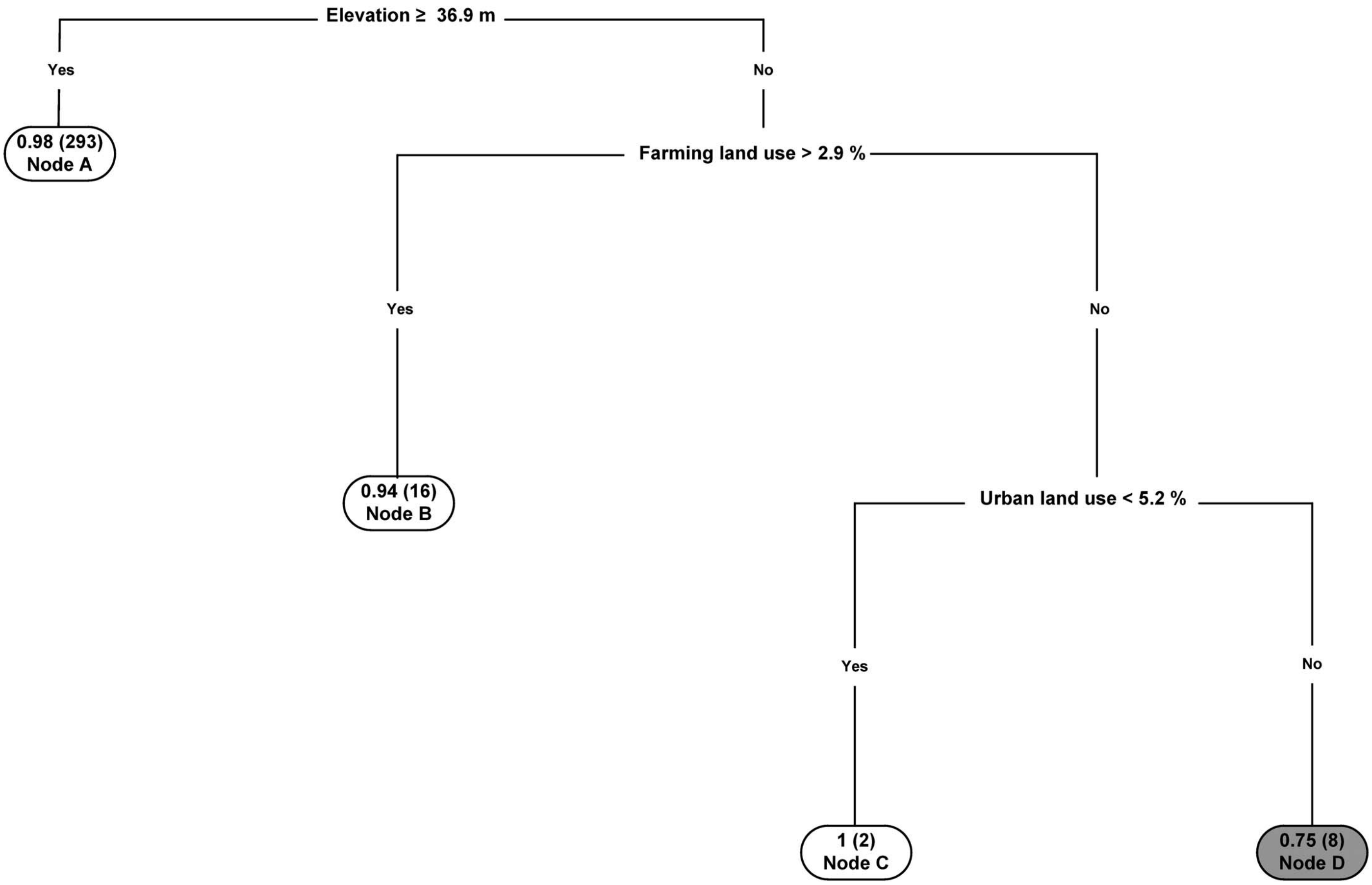

Figure 4. Classification tree for Brazilian egeria, where each split in the tree shows the lake attribute and its value (condition) determining the split. Terminal nodes represent the predicted presence (gray ovals) or absence (white ovals) of Brazilian egeria. Each terminal node contains the proportion of lakes that were classified correctly, the total number of lakes in the node (in parentheses) and node number (labeled A–D).

followed by curlyleaf pondweed (10 lakes). Forbes Lake (Mason County) and Island Lake (Pacific County) were the only study lakes at risk of being invaded by Brazilian egeria, and Wannacut Lake (Okanogan County) was susceptibility to both watermilfoil and pondweed. Data on native plant diversity were available for 40 of the 54 vulnerable lakes and these waterbodies supported an average of 18 $\pm$ 2 native plant species (compared to 16 $\pm$ 4 native plant species for nonvulnerable lakes). The most frequently occurring native species in vulnerable lakes included: common elodea (*Elodea canadensis* Michx), northern watermilfoil (*Myriophyllum sibiricum* Kom), slender naiad (*Najas flexilis* Rostk & Schmidt), yellow pondlily [*Nuphar lutea* (L.) Sm. ssp. *polysepala* (Engelm.) E.O. Beal], and sago pondweed [*Stuckenia pectinata* (L.) Börner]. Rare aquatic plants occurred in seven lakes, five of which were in western Washington (Figure 6). Among the vulnerable lakes, Spencer Lake (Mason County) had the highest plant richness (43 native taxa) including the state threatened Dortmann's cardinalflower (*Lobelia dortmanna* L.).

Discussion

Enhancing our predictive understanding of invasive species and their impacts on native species and ecosystems remains a central goal in invasion biology (Lodge et al. 2006). In freshwater ecosystems, the efficient allocation of prevention efforts for nonnative species depends on the ability of managers to accurately identify areas and specific waterbodies that are vulnerable to invasion (Vander Zanden and Olden 2008). In lake-rich regions such as our study area, invasion-prone systems could become the target of focused management efforts for preventing future introductions of aquatic plants or limiting the negative effects of invasive plants if they are already established.

Our results show that three invasive plants species of concern—Eurasian watermilfoil, curlyleaf pondweed, and Brazilian egeria – are highly predictable as a function of lake attributes describing human accessibility (influencing likelihood of introduction) and physical–chemical conditions (influencing likelihood of establishment). Overall, the

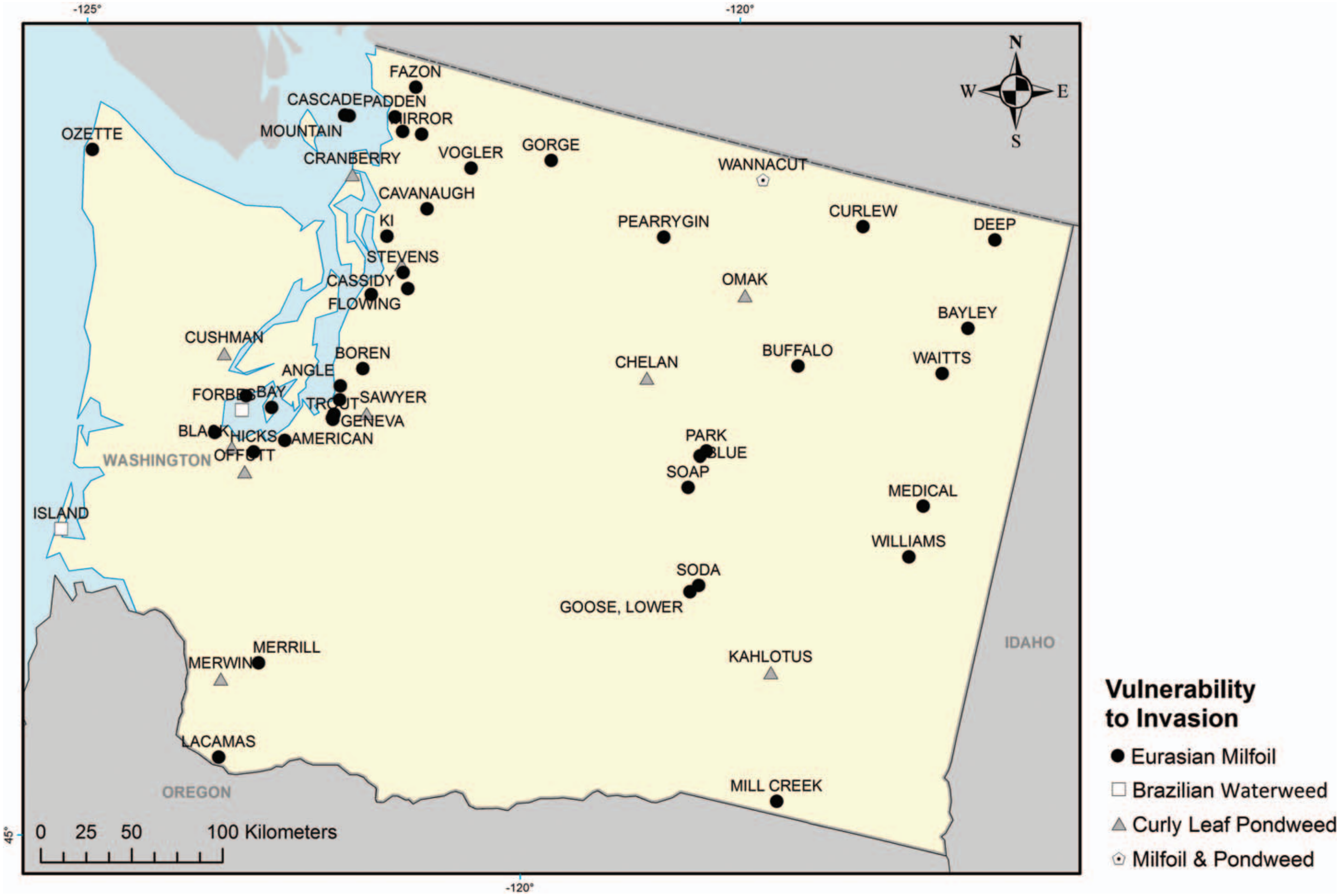

Figure 5. Location of the 54 study lakes that exhibit conditions suitable for establishment of Eurasian watermilfoil, Brazilian egeria and/or curlyleaf pondweed according to the classification trees (Figures 2–4). (Color for this figure is available in the online version of this paper.)

classification trees provided a versatile approach to visualize a complex model that assesses the risk of invasion in lakes across a vast landscape, thus helping to identify high priority areas to target prevention and early detection strategies. Our modeling effort also joins a small number of previous studies that use predictions from species distributional modeling to also identify locations of sensitive native communities that are vulnerable to future impacts (e.g., Mercado-Silva et al. 2006; Vander Zanden et al. 2004).

Lakes Vulnerable to Future Invasion. We identified 54 lakes (17% of the study lakes) that exhibit conditions suitable for establishment of Eurasian watermilfoil, curly-leaf pondweed and/or Brazilian egeria. Three-quarter of these lakes are vulnerable to Eurasian watermilfoil, which was expected given that this plant is considerably more widespread in Washington (and many other regions of the United States: Smith and Barko 1990) than the other two aquatic invasive plants. Most of the lakes vulnerable to invasion are concentrated in western Washington in areas with the highest human population densities (e.g., cities of Bellingham, Seattle, Olympia, and Vancouver).

The second most vulnerable region is in eastern Washington along the Columbia Basin Irrigation Project and the Okanogan River Basin, especially in Grant and Okanogan counties. Both of these areas are popular with recreational boaters and boast hundreds of lakes subject to recreational fishing. The Columbia Basin Irrigation Project is the largest reclamation project in the United States and supports vast agricultural lands in eastern Washington (Bloodworth and White 2008). Resource managers actively control Eurasian watermilfoil and other aquatic plants to maintain flow in the project's irrigation canals and reservoirs. If the lakes that are vulnerable to Eurasian watermilfoil in this region become invaded, they will not only increase the costs of control but also magnify the risk of re-infestation within the irrigation project.

Two of the largest natural lakes in Washington, Lake Chelan and Lake Ozette, are vulnerable to either Eurasian watermilfoil or curlyleaf pondweed. Their size, location, and fishing opportunities make these lakes attractive among

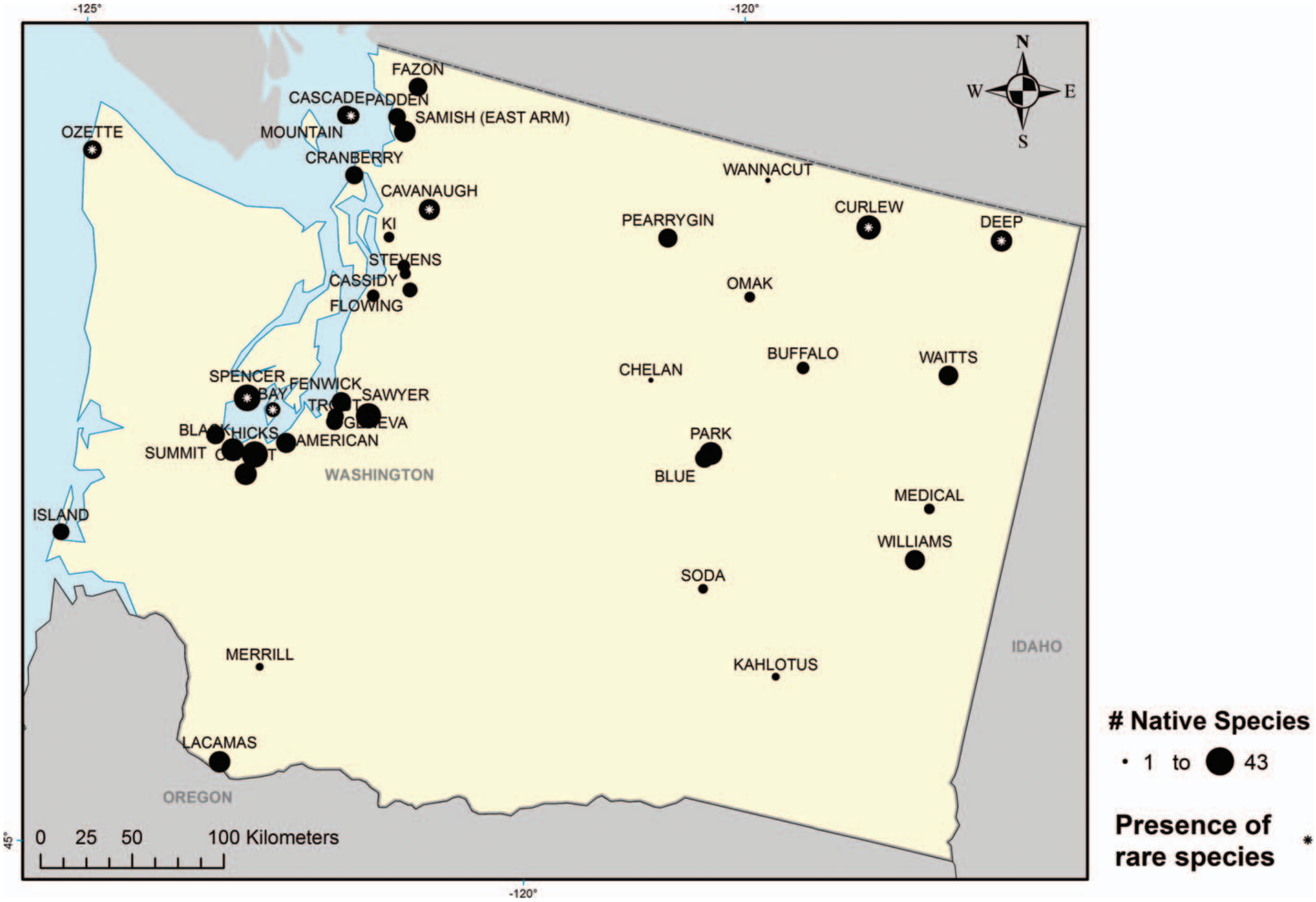

Figure 6. Native plant richness (symbol size) and presence of rare plant species (*) for the 54 lakes vulnerable to plant invasion. Rare plants represented species that were state (Washington) or federally (United States) listed as threatened, sensitive or endangered.

boaters. Lake Chelan has a thriving coldwater fishery that is open year-round (WDFW 2012). Eurasian watermilfoil is present in Lake Chelan and our model shows that curlyleaf pondweed has a 43% chance of also invading the lake. Lake Ozette is located in the Olympic National Park and supports relatively high aquatic plant richness (21 native taxa), including two rare plants. This is a concern given the ability of Eurasian watermilfoil to replace native aquatic plant communities (e.g., Boylen et al. 1999). The lake also supports sockeye salmon (*Oncorhynchus nerka* Walbaum) that are listed as threatened under the Endangered Species Act (NOAA 2009). Our model indicates Lake Ozette is very vulnerable to Eurasian watermilfoil, with an 89% chance of invasion. This is of great concern because Eurasian watermilfoil can reduce shoreline rearing habitat for salmon (Tabor et al. 2006).

With respect to Brazilian egeria, we found that Forbes Lake and Island Lake on the Olympic Peninsula both exhibit a 75% probability of occurrence based on suitable habitat. Forbes Lake is within 20 km of Limerick Lake (Mason County), a lake infested with Brazilian egeria and thus a likely source of propagules. Similarly, Island Lake (Pacific County) is <1 km to Loomis Lake that supports Brazilian egeria and Eurasian watermilfoil. An herbicide treatment in 2002 greatly reduced the biomass of both invasive plants in Loomis Lake (Parsons et al. 2009); however, by 2007 Brazilian egeria had regained dominance (WADOE 2012a).

Environmental and Human Drivers of Plant Species Distributions. The presence of a public boat launch was a key predictor of Eurasian watermilfoil occurrence, thus supporting the evidence of recreational and trailered boats as an important driver of secondary spread in lakes across Washington. Public boat launches facilitate human access and lake use and they may increase boater traffic and trailering, both of which are known vectors of Eurasian watermilfoil and other invasive species (Johnson et al. 2008; Leung et al. 2006; Rothlisberger et al. 2010). Johnson et al. (2008) found a positive correlation between the number of boat launches and human visitation in Wisconsin. When they used the number of boat launches as a surrogate for invader propagule pressure, it proved to be a strong predictor of presence of Eurasian watermilfoil. Buchan and Padilla (2000), however, observed that having a public boat launch was less significant in forecasting the distribution of Eurasian watermilfoil in lakes in Wisconsin compared to the degree of forest cover, dissolved inorganic carbon and alkalinity. Their results illustrate that the relevance of boat launches to predict invasions can vary (Vander Zanden and Olden 2008), and may require in some situations using more refined predictors or considering other variables that capture human lake use (Buchan and Padilla 2000).

Lake morphology also played an important role in forecasting the distribution of Eurasian watermilfoil and curlyleaf pondweed. Maximum depth was a good predictor of Eurasian watermilfoil presence in Washington; this was also the case for lakes in Minnesota (Roley and Newman 2008). However, lakes predicted to harbor Eurasian watermilfoil in Washington tended to be deeper (maximum depth = 24 ± 5 m) and larger (lake area = 8 ± 24 km^2) than those in Minnesota (13 ± 2 m and 7 ± 4 km^2, respectively). The vulnerability of large lakes to aquatic invasive plants is likely related to greater boater use and the increased complexity and availability of littoral zone habitat. Researchers have seen a strong positive correlation between the number of boats and lake area, indicating that recreational boaters are more attracted to larger lakes (Reed-Andersen et al. 2000). They have also observed a significant relationship between lake use by boaters and the landscape position of a lake (i.e., lake order — headwater lakes versus drainage lakes), the availability of recreational facilities (e.g., number of campgrounds), and the perception of fishing quality (Reed-Andersen et al. 2000).

For all species we found that invasion vulnerability increased with greater urban land use surrounding the lake. Our models identified three thresholds in urban land use above which the risk of invasion was elevated: Brazilian egeria (> 5%), curlyleaf pond weed (> 12%), and Eurasian watermilfoil (> 50%). The specific mechanism responsible for this relationship is likely associated with greater propagule pressure and increased nutrient runoff and sedimentation in more urbanized landscapes (Alexander et al. 2008). These changes can create environmental conditions such as high turbidity and low water clarity that are less favorable to native plants, but that Eurasian watermilfoil and curlyleaf pondweed are able to exploit (Engel and Nichols 1994; Smith and Barko 1990). Similarity, Carillo et al. (2006) observed that Brazilian egeria achieved high biomass near the stream mouths of a reservoir where nutrient, sediment and stream water inputs were concentrated.

Water quality and chemistry variables were particularly important for predicting the presence of curlyleaf pondweed. Curlyleaf pondweed grows well in nutrient-rich waterbodies and may be a bioindicator of eutrophication, but it can also grow in mesotrophic conditions (Nichols 1999; Nichols and Shaw 1986). Our model captured this affinity to nutrient-rich conditions, where higher chlorophyll-*a* (> 5 µg L^{-1}) and total phosphorus levels (> 19 µg L^{-1}) were associated with curlyleaf pondweed presence (but with some notable exceptions). Water temperature was also an important predictor. The model showed that curlyleaf pondweed is more commonly found where annual summer water temperatures exceed 20 C, despite its ability to survive and grow in low water temperatures (1 to 4 C [34 to 39 F] and 10 to 15 C, respectively), and produce turions at < 11 C (Woolf and Madsen 2003). We hypothesize that water temperatures in Washington may be limiting plant growth and turion production, keeping curlyleaf pondweed at low infestation levels. However, curlyleaf pondweed may become problematic in the future, if water temperatures in lakes and streams in Washington continue to rise because of climate change (Mantua et al. 2010).

Improving Predictive Models of Plant Species Invasion. Overall model performance for predicting species occurrence was strong, however the sensitivity of our models may be improved by including variables describing the potential for introduction, such as the degree of hydrologic connectivity among lakes, the likelihood (or surrogate) of aquarium and nursery plant disposal into local lakes, and/or the travel distance to the closest invaded lake. Our models for curlyleaf pondweed and Brazilian egeria showed that having a public boat launch in a lake was not an important predictor, even though public boat launches occurred in > 75% of lakes supporting either species. This suggests that additional pathways may be more important in dispersing these aquatic invasive plants in Washington, or alternatively, this measure of propagule pressure lacked the resolution to accurately reflect the likelihood of introduction. For example, given that both of these species occupy only a small number of lakes, we suspect that vectors of initial introduction associated with aquarium and nursery plant trade (perhaps related to urban land use surrounding a lake or presence of a park) would better represent introduction likelihood compared to the presence of a boat launch that dictate secondary spread via entrainment on boats and trailers. Downstream transportation can also be considered through hydrologic connectivity and flow direction between invaded and uninvaded waterbodies. These variables were useful in predicting the potential spread of the invasive fanwort (*Cabomba caroliniana* A. Gray) in lakes across Ontario, Canada (Jacobs and MacIsaac 2009), and we expect would be important given the downstream transport of plant fragments of curlyleaf pondweed that root and create new infestations (Stuckey 1979).

The horticulture, aquarium, and ornamental trades are also major sources of aquatic invasive species (Keller and Lodge 2007; Padilla and Williams 2004), yet we are just beginning to understand these pathways in Washington (Hamel and Parsons 2001; Strecker et al. 2011). The interest in water gardening and aquarium hobbies has increased the sale of aquatic plants among these trades in the United States (Bradley et al. 2012). In Minnesota for example, researchers were able to buy federally listed and state prohibited aquatic invasive plants, including curlyleaf pondweed and purple loosestrife (*Lythrum salicaria* L.) (Maki and Galatowitsch 2004). Brazilian egeria is a popular aquarium plant, and although illegal to sell in Washington, the plant is available for purchase on the internet (WISC 2012). The disposal of unwanted aquarium organisms into local waterbodies may be an important dispersal pathway for Brazilian egeria.

Management Recommendations. Our study provides an illustrative case example of identifying lake ecosystems most vulnerable to future plant invasions with the goal of informing management. Although the focus is on the Pacific Northwest region of the United States, its applicability is geographically broader. Below we discuss how the results from this study inform management strategies that focus on four broad areas: surveillance, control, education, and future research. These are management themes that are relevant to the many other regions in the United States and the world (Gassmann et al. 2006).

First, surveillance of the 54 lakes at risk is paramount to prevent new invasions. Based on habitat suitability, areas within and around human populated areas in western Washington, the Columbia Basin Irrigation Project, and the Okanogan River should be prioritized because they have the greatest number of vulnerable lakes and may be key invasion hubs (i.e., centers of invasion and spread; Muirhead and MacIsaac 2005). Moreover, vulnerable lakes that have rare aquatic plants, threatened fishes, or high aquatic plant diversity should be prioritized as well (e.g., Lake Ozette) given that the focal invasive species often dominate invaded communities (e.g., Boylen et al. 1999). To compliment surveillance efforts, we recommend boat inspections in large lakes (e.g., Lake Chelan) that tend to be popular with boaters.

Second, there is a need for early detection and rapid response strategies to eradicate and control early infestations that are discovered by lake monitoring. These strategies can reduce the risk of heavy infestation and may even lead to successful eradication. One strategy is to adopt an online early detection network as described for the Laurentian Great Lakes (Crall et al. 2012). This framework aims to link existing local, regional, and national databases on invasive species and provide a data portal where new data can be added and shared easily through an interactive website. The Washington State Department of Ecology Aquatic Plant Monitoring Program would provide a logical starting point for such an effort.

Third, education is critical in preventing invasions. We recommend that invasive species signage is posted by the boat launches of all 54 vulnerable lakes. The signs would include information on how to stop the spread of invasive species and the aquatic weeds of concern. Notably, this is opposite to the current management strategy in Washington (and elsewhere) where signage is only posted on lakes already containing populations of invasive species. Also, increasing the signage at invaded lakes that are close to vulnerable lakes would help raise awareness and promote the cleaning of boats that might contain propagules. Furthermore, it is beneficial to work with schools, pet shops, and bait and tackle shops to develop and disseminate educational materials that encourage lake stewardship. Organizing informal talks to discuss aquatic invasive species with lake associations, fishing groups, social clubs, and local nurseries would encourage public involvement in prevention efforts.

Fourth, a better understanding of dispersal vectors is needed. Currently, there is limited information about aquarium disposal and inland boater traffic in Washington (Strecker et al. 2011). These two vectors warrant further research as they will help identify invasion hubs and other vulnerable waterbodies. Aquarium disposal is potentially important in dispersing Brazilian egeria in western Washington. The likelihood that an aquarium will be emptied into a lake can be evaluated by surveying lake users and residents. Finally, we need a better understanding of boater behavior to determine lake use and dispersal rates of invasive species via boaters. In Wisconsin it was estimated that boaters travelled on average < 50 km to visit a lake, whereas in Michigan it was 76 km (Buchan and Padilla 1999; Leung et al. 2006). We may find that in Washington boater visitation and distance travelled varies among regions.

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