

A management framework for preventing the secondary spread of aquatic invasive species

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Abstract: Biological invasions continue to accelerate, and there is a need for closer integration between invasive species research and on-the-ground management. In many regions, aquatic invasive species have established isolated populations, but have not yet spread to many sites that provide suitable habitat. In the Laurentian Great Lakes region, several Great Lakes invaders such as zebra mussel (*Dreissena polymorpha*), rainbow smelt (*Osmerus mordax*), and spiny water flea (*Bythotrephes longimanus*) are currently undergoing secondary spread to the smaller inland lakes and streams. This paper describes recent advances in forecasting the secondary spread of aquatic invasive species and presents a framework for assessing vulnerability of inland waters based on explicit assessment of three distinct aspects of biological invasions: colonization, site suitability, and adverse impact. In many cases, only a fraction of lakes on the landscape are vulnerable to specific invasive species, highlighting the potential application of this type of research for improving invasive species management. Effective application to on-the-ground resource management will require that research aimed at assessing site vulnerability be translated into management tools.

Résumé : Les invasions biologiques continuent à augmenter en nombre, c'est pourquoi il est nécessaire de mieux intégrer la recherche sur les espèces envahissantes et leur gestion sur le terrain. Dans plusieurs régions, les espèces aquatiques envahissantes ont établi des populations isolées, mais ne se sont pas encore propagées dans plusieurs sites qui constituent des habitats appropriés. C'est le cas de la région des Grands Lacs laurentiens où des espèces qui ont envahi les Grands Lacs, telles que les moules zébrées (*Dreissena polymorpha*), l'éperlan arc-en-ciel (*Osmerus mordax*) et la puce d'eau épineuse (*Bythotrephes longimanus*), sont actuellement en train d'étendre secondairement leur répartition aux petits lacs et cours d'eau de l'intérieur des terres. Notre travail fait la synthèse des développements récents dans la prédiction de la dispersion secondaire des espèces aquatiques envahissantes et présente un cadre pour évaluer la vulnérabilité des eaux intérieures d'après une détermination explicite de trois aspects différents des invasions biologiques, soit la colonisation, la convenance des sites et l'impact négatif. Souvent, seule une fraction des lacs dans un paysage sont vulnérables à une espèce envahissante donnée, ce qui démontre l'intérêt potentiel de ce genre de recherche pour l'amélioration de la gestion des espèces envahissantes. Une application efficace à la gestion des ressources sur le terrain requerra cependant que la recherche sur l'évaluation de la vulnérabilité des sites soit incorporée dans des outils de gestion.

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Introduction: the challenge of invasive species management

In this age of globalization, human activities are rapidly dissolving the natural barriers that have historically isolated animal and plant species, providing vast opportunities for species to become biological invaders (Elton 1958). Invasive species are a leading threat to native species and biodiversity (Wilcove et al. 1998; Sala et al. 2000), are an important driver of global ecological and evolutionary change (Myers and Knoll 2001; Olden et al. 2004; Lodge et al. 2006), and have caused significant economic damage (Pimentel et al.

2005). Freshwater ecosystems are especially vulnerable to biological invasions and species extinctions because of their high degree of isolation and endemism (Richter et al. 1997; Ricciardi and Rasmussen 1999; Dudgeon et al. 2006). In response, many governments are developing management strategies for prohibiting new introductions and reducing the impacts of aquatic invasive species. The task is daunting: landscapes to be managed are vast, there are numerous invasive species, and resources available for invasive species management activities are limited.

Because biological invasions are generally irreversible, invasive species prevention is the cornerstone of many man-

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Table 1. Comparison of two invasive species prevention strategies: preventing new species from being introduced in the first place and preventing or slowing the secondary spread of invasive species that have already established regionally.

	Preventing introduction	Preventing secondary spread
Goal	To keep out potentially invasive species	To prevent or slow the further spread of invasive species in a region
Geographic focus	Borders, point-of-entry, ballast water	Diffuse on landscape, invasion hubs, vulnerable sites
Approach	Legislative: prohibit trade and transport of potential invaders, border inspection	Education and outreach to the general public
Target audience	Shippers, industry, importers	Recreational boaters, vacationers, general public
Taxonomic focus	Many potential species, identity of species often unknown	Small number of species, identity of species known

Note: This comparison is based on the experience in the Laurentian Great Lakes, which currently support a large number of non-native species and also acts as a source habitat for the secondary spread of invasive species to smaller inland waters in the region.

agement strategies (Ruesink et al. 1995; Mack et al. 2000; Simberloff 2003). The term “prevention” generally refers to prohibiting the entry of potentially invasive species into a country or new range, as conventional wisdom dictates that once a new invasive species establishes, it is usually impossible to eradicate or prevent its subsequent spread (Table 1). A number of national regulations and international agreements govern the movement of potentially invasive or harmful species, and protocols have been developed for assessing potential harm or invasiveness of a species being considered for import (Hayes 2003; Orr 2003; Lodge et al. 2006). More recently, quantitative approaches have been used to identify species most likely to become invasive (Ricciardi and Rasmussen 1998; Kolar and Lodge 2002; Marchetti et al. 2004). Although preventing the introduction of new invasive species is a critically important task, this approach represents only one aspect of the broader concept of invasive species prevention. Many potentially harmful invasive species have established populations outside of their native range, yet may be far from achieving their potential geographic distribution. Preventing or slowing the secondary spread of known and established invasive species to uninvaded sites is an additional aspect of invasive species prevention (Table 1) and involves a different set of goals, strategies, and target audiences than efforts to halt the import of new species (Table 1).

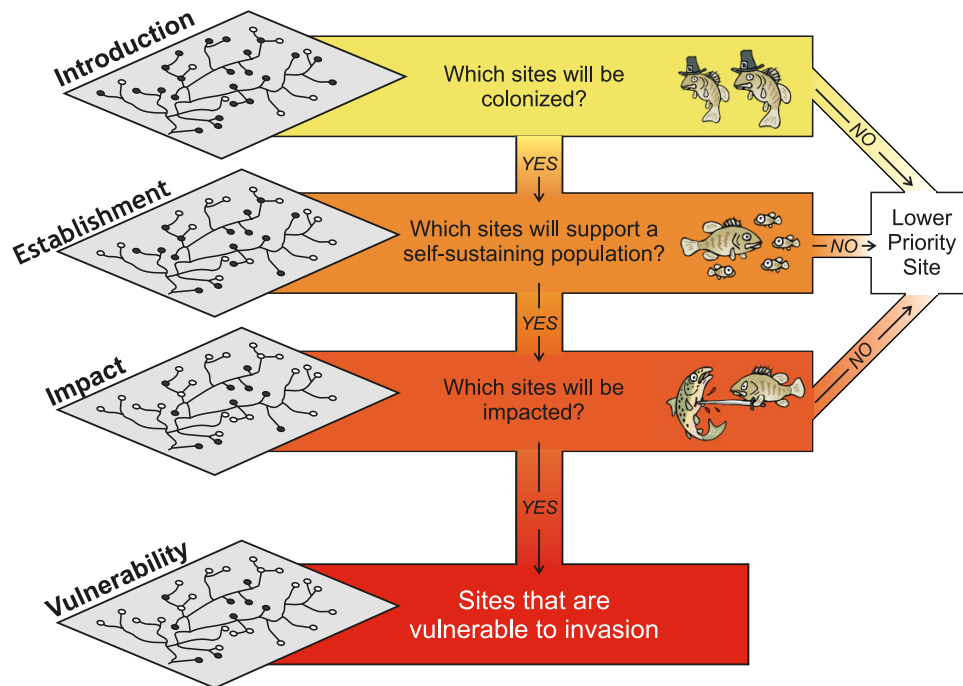
To explore the issue of secondary spread of aquatic invasive species, we draw upon examples in the Laurentian Great Lakes region of North America. The number of non-native species that have invaded the Great Lakes now exceeds 180, and new invaders continue to establish, primarily as the result of ballast water discharge from transoceanic vessels (Holeck et al. 2004; Ricciardi 2006). A subset of these Great Lakes invaders is spreading into the small inland lakes and streams in the surrounding region, often as unintentional hitchhikers on recreational and fishing boats. In effect, the Great Lakes are acting as stepping stones for these invasive species to reach the many thousands of ecologically diverse, smaller inland waters of North America. Inland lakes are relatively discrete ecosystems that are physically separated by land, habitat that is inhospitable to aquatic species. As a result, overland dispersal of these invasive species has been slow, and many suitable ecosystems have remained uninvaded for long periods (Johnson et al. 2006). In addition, inland lakes vary widely with regards to suitability to invasive species, a function of their individuality in physical,

chemical, and biological attributes. Though the invasion of a single, small, inland lake is a relatively minor event, the potential impact of Great Lakes invasive species on small inland water bodies may be vast for several reasons. First, the Laurentian Great Lakes region contains at least several hundred thousand small lakes, along with hundreds of thousands of kilometres of rivers and streams on both sides of the Canada–US border. These inland waters provide a suite of valuable ecological services and have high recreational and ecological value (Wilson and Carpenter 1999). Many are heavily used by humans and are preferred sites for recreation and residential development (Schnaiberg et al. 2002). Current and potential economic and ecological impacts of Great Lakes invasive species on these inland water bodies are poorly characterized, though the cumulative magnitude of these impacts may be tremendous.

The sheer number of inland water bodies in the Laurentian Great Lakes region, as well as many regions of the world, presents an enormous invasive species management challenge. In light of limited management resources, knowledge of which sites are vulnerable to specific invasive species is valuable because it can help direct management efforts to where they are likely to provide the greatest benefit with respect to minimizing undesired impacts of introduced species. Some of the earlier invasive species studies considered invasibility as a general attribute of a site, posing questions such as whether altered disturbance regimes and anthropogenic nutrient enrichment rendered sites more invulnerable (Oriani 1986; Moyle and Marchetti 2006). More recent research recognizes the importance of multiple interacting factors in determining the outcome of invasions: propagule pressure, the match between site attributes and species requirements, and biotic interactions with native taxa (Kolar and Lodge 2002; Vander Zanden et al. 2004a).

This paper examines the interface of research and resource management aimed at preventing or slowing the secondary spread of freshwater invasive species. There has been a great deal of progress in recent years in understanding and modeling aquatic invasive species on landscapes, specifically with regards to propagule introduction, site suitability, and impact. Each of these three factors represents a critical component of the biological invasion process, and each can contribute to assessment of site vulnerability. Identifying the specific sites on a landscape that are vulnerable to invasive species has the potential to help guide invasive species prevention programs to the locations where manage-

Fig. 1. A conceptual framework for assessing site vulnerability on a landscape comprised of multiple lakes. The approach separately assesses potential for introduction, establishment, and adverse impact of a specific invasive species for each of a suite of lakes. Assessment of vulnerability for individual lakes can help guide the targeting of invasive species prevention and management efforts.



ment and prevention are expected to produce the greatest benefit. We refer to the application of this research to on-the-ground management as “smart prevention” of invasive species.

Modeling site vulnerability to freshwater invasive species

Our approach to assessing site vulnerability explicitly considers each of three discrete stages or filters that need to be overcome for an invasion to occur and be of management concern (Fig. 1). The first stage is whether viable propagules or colonists will reach a site of interest (arrival). The second is whether colonists will establish a self-sustaining population by surviving environmental conditions and interactions with residents of the community and successfully reproduce (establishment). The third is whether the species will have adverse ecological or economic impacts (impact). This conceptual approach for assessing vulnerability to a hypothetical invasive species on a landscape comprised of multiple lakes is illustrated (Fig. 1). The framework provides a basis for classifying sites according to vulnerability, which reflects the risk of invasion and impact from a specific invasive species. Geographic information systems (GIS) provide a tool for mapping and visualizing ecosystem vulnerability on the landscape. In the following sections, we highlight advances in modeling each of these three stages using examples from the Laurentian Great Lakes region.

Introduction: can colonists get there?

Several authors have identified propagule pressure as a central predictor of invasions (Williamson 1996; Colautti et al. 2006), though the predictive importance of propagule

pressure itself varies depending on the situation (Buchan and Padilla 2000). We view the arrival of viable propagules or colonists at an uninvaded site as a critical step of the invasion process and the first of three filters of our framework (Fig. 1). Progress in predicting arrival and propagule pressure on landscapes begins with knowledge of the vectors responsible for the movement of individuals of a species among sites. For example, Johnson and Carlton (1996) reported that aquatic birds play a minor role relative to recreational boaters in the transport of zebra mussels. Further work on recreational boat pathways has found that mussels are most likely to be transported in the adult stage on macrophytes that are entangled on boat trailers (Johnson et al. 2001). For some invasive fishes, bait bucket transport represents the major vector of spread among inland water bodies (Litvak and Mandrak 1993; Ludwig and Leitch 1996), in contrast with natural dispersal through connected waterways. It is clear that knowledge of the vector provides an important starting point for further efforts to characterize the likelihood of species transport to a given site.

Where boating and other human activities are responsible for invasive species transport, simple variables that reflect intensity of human use of lakes such as degree of residential development and the presence of roads and boat launches are easy to collect and have been used as indicators of potential propagule pressure in studies of invasions (Johnson et al. 2009). For example, lakeshore residential development and geographic isolation were significant predictors of invasive rusty crayfish (*Orconectes rusticus*) occurrence in northern Wisconsin lakes (Capelli and Magnuson 1983).

Recent studies have taken a more dynamic approach to modeling invasive species on landscapes (Schneider et al. 1998). Though the spread of invasive species has tradition-

Table 2. Summary of studies that have used an ecological niche modeling approach to identify locations that are suitable habitat for freshwater invasive species in the Laurentian Great Lakes region.

Studies	Region	No. of lakes	Modeling approach	Comments
Zebra mussel (<i>Dreissena polymorpha</i>)				
Koutnik and Padilla 1994	Wisconsin	194	DFA	Examined relationship between predicted occurrence and environmental variables; did not list suitable sites
Drake and Bossenbroek 2004	United States	—	GARP	Broad-scale predictions from climate and terrestrial variables; no lake-specific predictions
Neary and Leach 1992	Ontario	6000	Environmental thresholds	Based on estimated pH and Ca; generates regional predictions of presence or absence
Strayer 1991	North America	—	Climate match	Regional predictions based on climate; no predictions for specific sites
Spiny water flea (<i>Bythotrephes longimanus</i>)				
MacIsaac et al. 2000	North American lakes	49	DFA	Model developed with European database applied to North America
Branstrator et al. 2006	Minnesota	179	DFA	Application of the MacIsaac et al. (2000) model to assess vulnerability of Minnesota lakes
Rainbow smelt (<i>Osmerus mordax</i>)				
Mercado-Silva et al. 2006	Wisconsin, Ontario, Maine	5000	CART	Model developed in native range, applied to invaded range; combined with assessment of potential impact
Drake and Lodge 2006	North America	—	GARP	Broad-scale predictions from climate and terrestrial variables; no lake-specific predictions
Smallmouth bass (<i>Micropterus dolomieu</i>)				
Vander Zanden et al. 2004a	Ontario	3046	ANN	Combined with assessment of road access and potential impact based on food-web structure

Note: DFA, discriminant function analysis; GARP, genetic algorithm; CART, classification and regression tree; ANN, artificial neural network.

ally been modeled as a diffusion process, a more appropriate approach for aquatic invasive species has been to consider the movement of recreational boaters, which comprise the major vector of secondary spread of many aquatic invasive species in the Great Lakes region. Buchan and Padilla (1999) compared a standard diffusion model with patterns of recreational boater activities and found that boater behavior provided better descriptions of the observed pattern of zebra mussel invasions in Wisconsin. The diffusion model underestimated the rate and geographic extent of the invasions because it was unable to incorporate long-distance movements of boaters across unsuitable habitat.

Though detailed boater movement data is often not available, gravity models have been used to estimate the probability of boater movements among sites as a function of boat usage at individual sites and the distance among sites (Schneider et al. 1998). Such models become particularly useful for modeling invasive species spread when they incorporate invasive species life history and dispersal information, as well as the relative positioning of invaded and suitable sites on the landscape. The latter incorporates a critical aspect of invasion dynamics. As new sites are invaded, they themselves can become source populations for further invasions on the landscape (Schneider et al. 1998; MacIsaac et al. 2004; Muirhead and MacIsaac 2005). Thus, propagule pressure at a given site is dependent on the occurrence of the invasive species on the surrounding landscape and would

change (presumably increase) over time as the invasion proceeds. Gravity models have proven useful for modeling propagule transport and the risk of species introduction to lakes (Bossenbroek et al. 2001; Leung et al. 2006) and will likely increase in importance as a tool for modeling propagule pressure and the likelihood of aquatic invasive species introductions to new sites on landscapes.

Establishment: can the site support a self-sustaining population?

The second stage considers whether an invasive species, if introduced, would be able to survive and establish a self-sustaining population at a site. Even high levels of propagule pressure of an invasive species at an unsuitable site would fail to result in establishment of a population. Ecological niche modeling has emerged as an approach for modeling suitability of specific sites to biological invaders (Peterson and Vieglais 2001). This approach is based on the concept of the ecological niche as constraining the distribution of a species and is a logical extension of the classical niche concept — that species can occur only in areas that match the ecological conditions to which they are limited. Results of ecological niche modeling can then be projected onto landscapes using a GIS to identify sites inside and outside of the species' niche, thus identifying suitable habitat to a potentially invasive species.

A number of studies have used environmental data to

identify which inland lakes in the Laurentian Great Lakes region of North America are ecologically suitable for specific aquatic invasive species (Table 2). The simplest approach is to simply consider whether sites have the environmental conditions required for species survival. For example, the zebra mussel requires dissolved Ca concentrations greater than $15 \text{ mg}\cdot\text{L}^{-1}$ (Sprung 1987; Ramcharan et al. 1992; Mellina and Rasmussen 1994). Provided that dissolved calcium data are available, lakes can be classified as suitable or not suitable based on this threshold value (Vander Zanden et al. 2004b). Most studies have used more sophisticated modeling approaches to relate species occurrence to environmental variables. Approaches employed include discriminant analysis, logistic regression, classification and regression tree (CART), artificial neural networks, and genetic algorithm for rule-set production (GARP). GARP is gaining widespread application in forecasting the spread of aquatic invasive species (Drake and Bossenbroek 2004; Iguchi et al. 2004; Chen et al. 2007). The attraction is that predictions can be generated from readily available climate and geology GIS data layers. Applications of GARP to forecasting aquatic invasive species spread to date have not employed site-specific environmental variables (such as pH and dissolved calcium) known to physiologically constrain the distribution of invasive species. Though this approach is useful for scoping the potential distribution of aquatic invasive species at broad spatial scales, it has not yet proven applicable for assessing suitability of specific sites (Drake and Bossenbroek 2004).

Impact: will there be undesired consequences?

The third stage is whether the establishment of an invasive species is predicted to have adverse impacts on the native ecosystem or biota. Impact is the most challenging step of biological invasions to understand and predict (Parker et al. 1999). Invasive species can have a variety of economic or ecological impacts, including declines in native species, habitats, fisheries, and ecosystem goods and services (Parker et al. 1999). Individual invasive species differ widely with regards to their impacts. Many non-native species have established one or more populations but have failed to either spread rapidly or produce measurable adverse impacts (Lodge et al. 1998). Considering that stated management goals are often to minimize the undesired consequences of invasive species (as opposed to simply stopping invasions), these low-impact species should be of lower priority in invasive species management efforts. On the other hand, many invasive species exhibit long time lags in their spread and impact (Crooks 2005), making it difficult to know whether a species has the potential to become problematic in the future.

Although some species appear not to have major adverse impacts, others species are generally considered to have impacts wherever they occur. This is the common assumption for several of the high profile freshwater invasive species of the Great Lakes region, such as rusty crayfish and zebra mussel. Studies of rusty crayfish in the North Temperate Lakes Long-Term Ecological Research (NTL-LTER) lakes in northern Wisconsin found that rusty crayfish reached exceptionally high abundances ($20 \text{ crayfish}\cdot\text{trap}^{-1}\cdot\text{day}^{-1}$ in Sparkling Lake and $55 \text{ crayfish}\cdot\text{trap}^{-1}\cdot\text{day}^{-1}$ in Trout Lake),

producing dramatic adverse impacts on native aquatic plants, invertebrates, and certain fishes. Wilson (2002) reported adverse impacts on aquatic plants in lakes with catch rates greater than $5 \text{ crayfish}\cdot\text{trap}^{-1}\cdot\text{day}^{-1}$. Interestingly, a recent survey of 58 lakes in the region found that of the 18 lakes that contained rusty crayfish, only seven (38% of rusty crayfish lakes) had average catch rates that exceeded $5 \text{ crayfish}\cdot\text{trap}^{-1}\cdot\text{day}^{-1}$, and only one lake had catch rates exceeding $15 \text{ crayfish}\cdot\text{trap}^{-1}\cdot\text{day}^{-1}$ (M.J. Vander Zanden, unpublished data). Thus, the abundance (and, presumably, the impact) of this invader appears to be highly variable among lakes, certainly more heterogeneous than indicated from long-term studies on Sparkling Lake and Trout Lake.

Zebra mussel are another species that are commonly assumed to have major impacts wherever they occur, and only recently has there been explicit consideration of the among-site variation in impact (Ricciardi 2003). In fact, zebra mussel abundance (population density) varies widely among systems (Mellina and Rasmussen 1994; Ramcharan et al. 1992; Strayer 1991). Several measures of ecological impact were found to increase with increasing zebra mussel population density (Ricciardi 2003) such that population density can reasonably be considered a measure of impact. Ramcharan et al. (1992) developed models predicting zebra mussel population density and found that zebra mussel density increased as a function of dissolved calcium concentration and lake trophic status. These findings suggest that using environmental data to classify sites according to potential for adverse impact may be a viable approach (Ricciardi 2003), though it has not yet been widely adopted. Forecasting and habitat suitability studies have generally modeled potential distribution (species presence or absence). The fact that invasive species abundance and impact can vary widely highlights the need to develop a predictive understanding of site attributes that favor high species density and undesired impacts (Byers et al. 2002; Parker et al. 1999; Vander Zanden et al. 2004a).

Impact of invasive species can also vary as a function of food-web structure. Vander Zanden et al. (2004a) found that the introduction of non-native smallmouth bass (*Micropterus dolomieu*) into Ontario lakes containing pelagic prey fish (such as *Coregonus* spp.) did not affect the forage base of the native top predator, lake trout (*Salvelinus namaycush*). On the other hand, in lakes lacking pelagic prey fish, littoral prey fish are the predominant prey of lake trout. Smallmouth bass introduction dramatically decreases littoral-zone prey fish availability, with negative consequences for lake trout. Thus, the simple presence or absence of pelagic prey fish mediates the impact of smallmouth bass introduction on native lake trout.

Another approach is to consider the value or amenities that the receiving ecosystem provides to humans. Sites or ecosystems that support valuable fisheries and rare and endangered species or are of high recreational value are assumed to experience greater impact if invaded. For example, a study aimed at identifying lakes vulnerable to rainbow smelt invasion considered whether lakes contained fish species previously shown to be negatively impacted by rainbow smelt (Mercado-Silva et al. 2006). Similarly, Schneider et al. (1998) used mussel diversity and the occurrence of threat-

ened or endangered mussel species as a measure of potential zebra mussel impact on native biota.

Integrating the three stages of species invasion

The conceptual framework presented here (Fig. 1) represents the “scaling-up” of our understanding of biological invasions to the landscape level by viewing a landscape as comprised of many sites that are heterogeneous in terms of their potential for invasive species arrival, establishment, and impact. Though progress has been made in modeling each of the three stages individually (see examples in above section), the power of the approach emerges when assessments at each of the three stages are combined to produce a composite measure of ecosystem vulnerability to an invasive species (Fig. 1). “Vulnerable” ecosystems are those that are most susceptible based on a synthetic and dynamic consideration of propagule introduction, potential for species establishment, and adverse impact (Fig. 1). Studies are now beginning to assess site vulnerability as described here (see below). Notably, these studies tend to find that vulnerable sites comprised a relatively small proportion of all sites on the landscape.

Rainbow smelt in Wisconsin

Rainbow smelt were introduced to Lake Michigan, spread through the Great Lakes, and subsequently spread to inland lakes of the regions, with negative consequences for native species and communities (Evans and Loftus 1987; Hrabik et al. 1998). Mercado-Silva et al. (2006) assessed the vulnerability of lakes in Wisconsin, Ontario, and Maine using this approach. Here, we highlight the three filters of vulnerability for Wisconsin using a lake data set comprised of >5000 Wisconsin lakes (Fig. 2). We assume that the potential for rainbow smelt arrival is based on the presence and number of boat landings at each lake, and that lakes with more than one boat landing are the greatest candidates for introduction. Doing so reduces the number of lakes under consideration from 5000 to 1350 lakes. Environmental suitability (establishment potential) is based on an environmental niche modeling study (Mercado-Silva et al. 2006). CART was used to model rainbow smelt presence or absence using data from their native range in Maine. Application of this model to Wisconsin lakes identified 553 lakes with suitable physical and chemical conditions for rainbow smelt. Finally, potential impacts were assessed based on the presence of five fish species (including species of economic importance) known to be negatively impacted by smelt invasion. Lakes containing one or more species sensitive to smelt introduction were considered candidates for adverse impact ($n = 1255$ lakes). “Lake vulnerability” is a composite of the three stages of invasion: arrival, establishment, and impact. Of the >5000 Wisconsin lakes considered here, 269 lakes were classified as highly vulnerable to smelt invasion, representing ~5% of the lakes included in the analysis (Mercado-Silva et al. 2006).

Smallmouth bass in Ontario

A second example of this approach is the spread of smallmouth bass in Ontario (Vander Zanden et al. 2004a). Smallmouth bass were historically confined to portions of Mississippi and Great Lakes drainages but have gradually been introduced and spread across much of Canada and the

US (Rahel 2000). In particular, they have rapidly spread at the northern portion of their native range due to a combination of consistently warm summers during the past two decades, unauthorized introduction by anglers, and accidental bait-bucket transfers (Jackson 2002; Jackson and Mandrak 2002).

Adult smallmouth bass are efficient piscivores and can have substantial predatory impacts on littoral prey fish communities in north-temperate lakes (Vander Zanden et al. 1999). In a study of nine Ontario lake trout lakes, bass invasion was associated with a sharp reduction in fish species richness and abundance in littoral zone habitats. Food-web studies revealed that native lake trout shifted from a diet of littoral fish to one consisting primarily of plankton following bass invasion (Vander Zanden et al. 1999). This food-web change has adversely affected lake trout growth rates, biomass, and productivity.

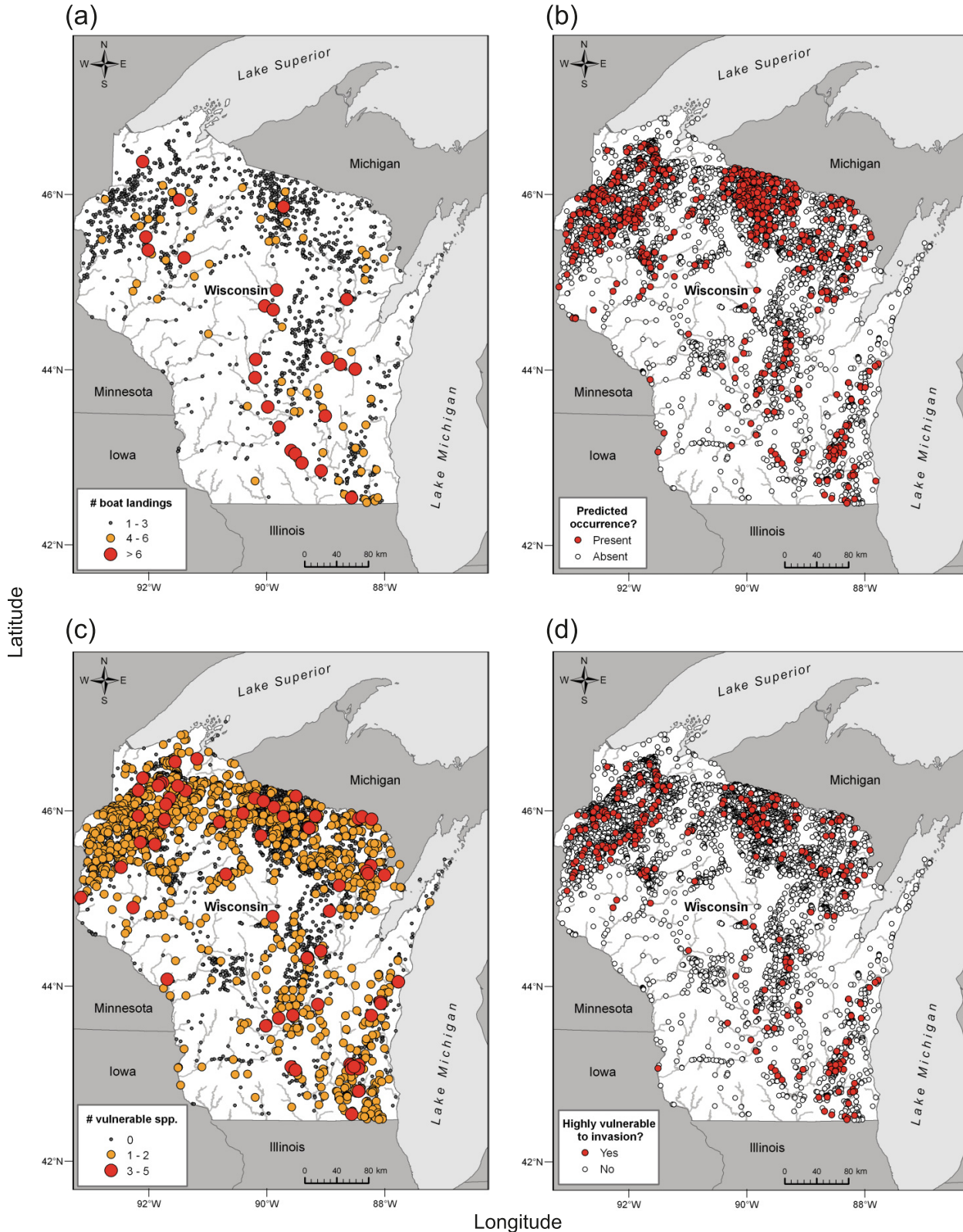
Considering the tremendous number of lakes in Ontario (>250 000), minimizing the adverse impacts of bass introductions is a daunting task. Vander Zanden et al. (2004a) identified a subset of lakes considered vulnerable to bass invasion. The study assessed (i) which lakes are likely to receive bass colonists, (ii) which lakes are likely to be able to support a viable bass population, and (iii) which lakes are likely to be adversely impacted if bass were to establish a population. From this analysis, 30 lakes out of ~800 initial study lakes (<5% of the study lakes) were classified as vulnerable to smallmouth bass invasion. This manageable number of vulnerable lakes would be the obvious focus of management efforts to prevent or slow the further spread of smallmouth bass.

Application to management

Freshwater invasive species are an issue of growing management concern, as local and national government bodies are currently grappling with developing strategies for their prevention, control, and eradication. For example, many US states have recently created invasive species advisory councils that bring together regulators, researchers, and other stakeholders to address research, policy, and management needs (Lodge et al. 2006). Many local and state or provincial governments are currently passing legislation to address the problem of aquatic invasive species and are providing grants for local invasive species control and management efforts. These local granting programs involve selection of invasive species projects for funding, and site vulnerability could be used as a criterion in deciding among invasive species prevention projects. Other strategies for preventing the introduction of invasive species include hiring of watercraft inspectors and (or) educators at boat launches, requiring boats to be cleaned upon entry and exit at boat launches, and even quarantine whereby boats are denied access to certain locations. Such efforts can be costly and even politically controversial and should therefore be directed to the most important locations. In summary, assessment of site vulnerability has the potential to aid in the many aspects of invasive species management currently being implemented at local and regional levels.

In the two examples described above, it was possible to combine the three filters of the invasion processes (Fig. 1)

Fig. 2. Assessing lake vulnerability to rainbow smelt invasion for Wisconsin based on consideration of the three filters of a biological invasion: (a) introduction potential is based on the number of boat landings; lakes with more than one landing are considered candidates for introduction ($n = 1350$ lakes); (b) establishment potential is derived from environmental niche modeling aimed at identifying lakes with suitable environmental conditions to support rainbow smelt ($n = 553$ lakes); (c) impact potential is based on the occurrence of fish species known to be adversely impacted by rainbow smelt; lakes containing one or more species sensitive to smelt introduction are candidates for impact ($n = 1255$ lakes); (d) vulnerable lakes are those that are susceptible to arrival, establishment, and unwanted impact and comprise only 269 lakes (Mercado-Silva et al. 2006).



to assess which lakes on the landscape are most vulnerable to invasion. Notably, a relatively small number of sites were identified as vulnerable to invasion. This makes the approach particularly useful to resource managers because it can help direct interest and concern to a manageable number of sites on the landscape. Yet simply generating lists of vulnerable sites is not sufficient, and the results need to be effectively communicated and made available to end users. Indeed, the concept of “smart prevention” is that knowledge of site vulnerability be used to prioritize and guide invasive species management efforts. For this to occur, it is essential that findings are effectively communicated to resource managers. This will undoubtedly involve developing collaborative relationships between researchers and resource managers. Implementation of this approach can play an important role in bridging the gap between invasive species researchers, resource management agencies, and policy makers (Lodge et al. 2006; McPherson 2004).

One of the important barriers to effective invasive species management programs is that funding for invasive species management and prevention is grossly inadequate. The problem is further confounded by the ineffective allocation of these limited funds. For example, government grants are often made available for invasive species control projects when local citizens become concerned about an invasive species and clamor for action to address the problem. Although invasive species control projects are politically popular, it is generally recognized as a poor use of limited invasive species management resources (Leung et al. 2005; Leung et al. 2002). In the long term, in the absence of prioritizing management efforts around a clearly defined strategy, legislators and the general public will perceive invasive species management programs and expenditures as ineffective and may be unwilling to commit additional resources. On the other hand, thoughtful and carefully targeted programs have the potential to garner broad support because they explicitly attempt to direct resources in the most cost-effective manner.

There are other major challenges involved in preventing or slowing the secondary spread of freshwater invasive species. Although identifying sites that are vulnerable to specific invasive species may improve the allocation of management efforts, it does not provide guidance in allocating effort among different management activities (prevention vs. control) or among different invasive species. Each invasive species will differ with regards to the potential for spread, stage in the invasion process, and responsiveness to prevention and control efforts. Because management funds are chronically limited, effort allocated to one species may be at the expense of dealing with others. This highlights the need to consider the management of any single invasive species within the context of other invasive species. We envision that the general approach presented here could ultimately integrate decision-making options for a suite of invasive species on a landscape. Such efforts should consider not only attributes of the sites and species, but also the extent of spread, the cost and likelihood of success at different sites, and the economic and ecological value of the recipient ecosystems. Certain management actions may simultaneously constrain the spread of multiple species. For example, a small number of lakes may act as invasion

“hubs” and should be the focus of efforts to prevent or slow the secondary spread of invasive species (Havel et al. 2005; Muirhead and MacIsaac 2005).

Another challenge involves interactions between biological invasions and other forms of environmental change. The spread and impact of invasive species may be amplified by current trends of land use, climate, and hydrologic alterations (Dukes and Mooney 1999; Mooney and Hobbs 2000). For example, reservoirs may serve as stepping stones for the progression of invasive species across landscapes (Johnson et al. 2009; Havel et al. 2005). Global climate change will fundamentally alter the nature of species interactions in ecosystems with profound and potentially unpredictable implications for the spread and ecological impact of invasive species (Rahel and Olden 2008). Fish species distributions in eastern North America are already shifting northwards as a result of recent warming trends (Jackson and Mandrak 2002), and climate warming is likely to promote the further invasion of fishes into the Laurentian Great Lakes (Mandrak 1989). Finally, invasions may create conditions that facilitate further invasions. For example, the presence of zebra mussels in the Great Lakes is thought to facilitate the subsequent establishment of round goby (*Apollonia melanostomus*; Ricciardi and MacIsaac 2000). Considering interactions among invasive species will become increasingly important as the number and geographic distribution of these species expand.

Conclusions

Invasive species research has been successful in describing the nature and magnitude of the problem. It has been less effective in providing guidance for invasive species management, and science has yet to achieve its full potential in terms of “turning the tide” of biological invasions (Hulme 2006). Though prevention is widely recognized as the cornerstone for successfully managing invasive species, the concept of prevention is multifaceted. Where the identity and basic biology of invasive species is known, recent studies have been successful in identifying vulnerable sites, such that prevention efforts can be targeted to where they are likely to produce the greatest benefit. The approach developed here for the Laurentian Great Lakes region may be transferable to other regions and ecosystem types, particularly where discrete sites or patches can be defined and modeled, such as islands or coastal harbors. A useful parallel is the emergence of the field of reserve design and conservation planning in recent decades. Conservation organizations and resource agencies have undertaken careful planning to set priorities for directing resources so as to best achieve biodiversity conservation goals, leading to more thoughtful allocation of conservation resources. An analogous “conservation planning” perspective can be used to guide efforts to prevent or slow the spread of invasive species. These advances are part of an ongoing transformation of the field of invasion biology from a descriptive science to a normative science capable of improving our ability to manage ecosystems.

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