Title: Integrating landscape connectivity and habitat suitability to guide offensive and defensive invasive species management

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Summary

1. Preventing the arrival of invasive species is the most effective way of controlling their impact. Preventative strategies may be "offensive" aimed at preventing the invader leaving colonised locations, or "defensive" aimed at preventing its arrival at uninvaded locations. The limited resources for invasive species control must be prioritized, particularly for numerous vulnerable locations or uncertainty about which sites are already invaded.
2. We developed an integrative modelling framework to prioritise locations for either strategy by incorporating connectivity and habitat suitability. We applied this framework to a dataset comprising 5 189 water bodies in Wisconsin and Michigan, U.S.A, for zebra mussels *Dreissena polymorpha* and Eurasian watermilfoil *Myriophyllum spicatum*. We developed the framework with a spatial graph based on recreational boater movement and habitat suitability models.
3. An historical graph comprised 3105 natural lakes connected in one of 18 components, whereas a total of 3944 water bodies (lakes and reservoirs) were connected in one of 13 separate components in a graph of the contemporary system. Habitat suitability models accounted for around half of the deviance in the distribution data for each species.
4. There was a distinct spatial pattern in the levels of risk and subsequent recommended allocation of management interventions across several levels of investment. Higher risk water bodies were generally found in the largest component of the spatial graph.
   At comparatively low levels of investment, where managers target 5% of all locales to control *D. polymorpha*, the results suggested that 71% and 27% of this effort should be committed to defensive and offensive strategies respectively, in the largest component. For *M. spicatum*, 92% and 8% of this effort should be allocated in this component to

defensive and offensive strategies, respectively. It is only with much greater investment that water bodies in other components should be targeted.

5. *Synthesis and applications*. Allocating limited resources to prevent the spread of invasive species is a challenge that transcends ecosystems and geography. We successfully identified a reduced number of locations to target for offensive and defensive intervention strategies for two species. This framework is readily applicable to other aquatic and terrestrial ecosystems vulnerable to invasive species.

Keywords: invasive species management, risk assessment, graph theory, generalised additive models, zebra mussels, Eurasian watermilfoil, spatial graph, connectivity.

Introduction

Mounting theoretical and empirical research has revealed numerous challenges in modelling pathways that might promote invasive species (Hastings *et al.* 2005; Wilson *et al.* 2009) while illustrating the opportunity for this knowledge to inform management strategies (Vander Zanden & Olden 2008; Hulme 2009). Accordingly, the prevention of initial invasions is now a clear priority in emerging management policies (Lodge *et al.* 2006; Hulme *et al.* 2008). Attempts to prevent the secondary spread of an established invasive species, however, are complicated by the landscape context of vulnerable habitats and what may be arbitrary management jurisdictions – the so called "management mosaic" (Epanchin-Niell *et al.* 2010). As contemporary landscapes are managed for a variety of uses and outcomes, effective local-scale prevention measures can be undermined by lack of action at neighbouring source habitats (Peters & Lodge 2009), particularly when such source habitats occur in a separate management district. This challenge is particularly acute in fragmented or patchy environments where the natural and human-mediated connectivity may have changed over both space and time (von der Lippe & Kowarik 2007; Fausch *et al.* 2009; Rahel 2013).

Strategies for the prevention of secondary spread in patchy environments can broadly be considered as either offensive or defensive (Drury & Rothlisberger 2008). Offensive strategies aim to contain potential invaders at source locations, whereas defensive strategies aim to prevent the arrival at currently uninvaded locations. It remains a challenge to identify the most effective location and scale at which to apply these preventive measures; each strategy might be required depending on the suitability of the habitat to the invader (target defensive) or the probability of dispersal from an invaded site (target offensive). Simulation models support the intuitive prediction that defensive strategies are likely to be more effective once more than half of the habitats are invaded (Drury & Rothlisberger 2008). However, where invasive species management is coordinated at a regional scale and includes

hundreds or even thousands of locales, often with imperfect knowledge of invasive species distributions, such general findings may be difficult to implement. A multiscale approach that incorporates the functional connectivity of the entire system with the suitability to potential invaders of specific locations would represent an important step in addressing this challenge.

Graph theoretic methods have received growing attention in ecological applications as a way to visualise and quantify connections between habitat nodes in space (Dale & Fortin 2010). A spatial graph consists of nodes – representing habitat patches – that may be connected by arcs or links that depict pathways of potential for movement of a focal species, genes or populations (Urban & Keitt 2001; Galpern, Manseau & Fall 2011; Erős *et al.* 2012). Links within a graph may be binary, indicating the presence of a connection or quantitative, representing actual distance or the probability of connectivity between two nodes (Fortin & Dale 2010). Analyses of the topology of a graph provide insight into the connectivity of the landscape under study (Galpern, Manseau & Fall 2011; Erős *et al.* 2012). Additionally, there is capacity to incorporate the habitat quality of each location to weight the nodes of the graph, either explicitly or implicitly (Dale & Fortin 2010). In the context of invasive species management, such information may provide a way to identify specific habitats as well as broader regions that would be most suitable for offensive or defensive strategies. The value of this type of analysis may be enhanced when combined with habitat suitability modelling to allow concurrent analysis of the probability of arrival and establishment of invasive species in new locales.

Recent years have seen ecologists combine multiple models into integrative frameworks to model and forecast invasive species distributions and for risk assessment (Ibáñez *et al.* 2014; Franklin 2010). These approaches typically include empirical or phenomenological models, such as gravity models, spatial statistical models or machine learning methods (Leung and Mandrak 2007; Vander Zanden & Olden 2008; Rothlisberger & Lodge 2009), which may be

coupled with dynamic population models (Franklin 2010; Gallien *et al.* 2010). Although there are many advantages to these approaches, the use of dynamic population models may only be feasible when life history parameters and specific habitat requirements are well understood (Keith *et al.* 2008; Ibáñez *et al.* 2014). Dispersal events by invaders are often highly stochastic, therefore it can be difficult to define dispersal parameters and thus accurately predict colonisation (Rothlisberger & Lodge 2009). In the absence of suitable data to estimate such parameters, quantifying the different axes of invasion risk with empirical models may offer a way forward when urgent management interventions are required.

The aim of this study was to develop an integrative modelling framework that effectively operationalized the concepts of offensive and defensive management strategies for invasive species management. To quantity where and how to prioritise these strategies we developed a risk metric based on emerging graph-theoretic techniques and habitat-suitability models. This metric simultaneously integrated the effects of habitat quality, spatial proximity and the probable connectivity of each potential locale. Importantly, our approach provides an avenue to make recommendations for interventions at both local and landscape scales. To demonstrate the utility of this approach, we examined the diverse freshwater landscapes of the mid-western United States, which has a high concentration of both natural lakes and artificial reservoirs that have been invaded by numerous non-native species (Vander Zanden & Olden 2008). Lake systems are exemplary of fragmented landscapes with suitable habitats nested within a broader habitat matrix that is unavailable to resident biota; best illustrated by the “lakes-as-islands” analogy (Keddy 1976; Arnott *et al.* 2006). Today, water bodies in the region are invaded by species such as zebra mussels *Dreissena polymorpha* and Eurasian watermilfoil *Myriophyllum spicatum* ; two highly invasive species with respect to ecological and economic impacts (Johnson, Olden & Vander Zanden 2008).

Materials and Methods

Study region and species

We compiled species and environmental data for 5 189 water bodies representing 4 183 lakes and 1 006 reservoirs (≥0.04 km^2 in surface area and ≥2 m in maximum depth) distributed across Wisconsin and the upper peninsula of Michigan, U.S.A (Johnson, Olden & Vander Zanden 2008). Historical connectivity in this system is a function of lake hydrology, with drainage lakes having clear movement corridors along stream channels and the many seepage lakes being historically disconnected. However, contemporary connectivity is also influenced by human activity; the construction of artificial reservoirs has created barriers to in-channel movement (Johnson, Olden & Vander Zanden 2008) whereas the entrainment of invasive species on recreational boating and fishing equipment (so-called "hitchhiking") has facilitated the overland dispersal of many species (Buchan & Padilla 1999; Johnson & Carlton 1996). We broadly classified reservoirs to include hydroelectric reservoirs, impoundments created by damming a river or flooding a low-lying area, lakes equipped with stabilizing dams or created through soil excavation, and mill, irrigation or stock ponds.

Occurrence of *D. polymorpha* and *M. spicatum* were obtained from the Wisconsin Department of Natural Resources (WDNR), Michigan Department of Environmental Quality (MDEQ), the Great Lakes Indian Fish & Wildlife Commission (GLIFWC), and the Center for Limnology at University of Wisconsin (CFLUW) according to strict inclusion criteria (see Johnson, Olden & Vander Zanden 2008). Distributional data were collected primarily during broad-scale field surveys, rather than through isolated accounts, thereby reducing the likelihood of any systematic biases in the data. Environmental characteristics used for habitat suitability modelling were obtained from the WDNR Register of Waterbodies, the Wisconsin Lakes Book, the Surface Waters of Wisconsin volumes, and the MDEQ.

Dreissena polymorpha are relatively small (25–35 mm length) suspension-feeding mussels that commonly reach densities exceeding 10 000 individuals m^{-2} (Berkman *et al.* 1998). *Dreissena polymorpha* can dramatically affect phytoplankton abundance, nutrient cycling and water clarity, and are associated with declines in native biota (Higgins & Vander Zanden 2010) as well as significant economic damages via fouling and water treatment (Connelly *et al.* 2007). The invasion of *D. polymorpha* into North America was facilitated through the ballast water of trans-Atlantic ships, and was first identified in the western basin of Lake Erie during 1986 (Carlton 2008). Within a few years of establishment, *D. polymorpha* expanded its range to include all five of the Laurentian Great Lakes, reached the upper Mississippi River by 1991, and currently has expanded its range southward to the Gulf of Mexico (Benson 2013). Secondary spread of *D. polymorpha* has been largely facilitated by entrainment on recreational boats by encrusting on hulls and entanglement on engine propellers and fishing equipment (Rothlisberger *et al.* 2010). Data used in our analysis included verified reports of established adult populations, standardized visual and substrate sampling by the WDNR, and veliger larvae sampling by the WDNR (1998–2006) and GLIFWC (2003-2006). Briefly, veliger sampling involved epilimnetic vertical tows of a 50–64 micron mesh zooplankton net (50 cm opening) performed at three sites per water body and on three different dates during the summer season (late June to August). Preserved samples were subsequently examined for the presence of *Dreissena* veliger larvae (Johnson, Olden & Vander Zanden 2008).

Myriophyllum spicatum was first introduced to the United States in the 1940s and presently occupies 44 states and several Canadian provinces from Québec to British Columbia (Zhu *et al.* 2006). Initially introduced accidentally via the plant aquarium trade, human transport of plant fragments on boating equipment is now cited as the most important vector of dispersal among water bodies for *M. spicatum* (Madsen & Smith 1997; Rothlisberger *et al.* 2010). This

species is a perennial herbaceous submersed plant which forms a dense canopy of branches, and causes marked changes in macrophyte cover, light penetration, nutrient cycling, and invertebrate and vertebrate communities (Smith & Barko 1990). *Myriophyllum spicatum* was first found in southeastern Wisconsin in the mid-1960s and has since spread northward and westward. Distribution data for *M. spicatum* in Wisconsin and Upper Peninsula Michigan, came from surveys conducted by the WDNR (and its volunteer monitoring program), GLIFWC and CFLUW. We relied heavily on broad-scale survey data collected by Stanley Nichols and colleagues between 1976 and 2000 (Nichols & Martin 1990). Sampling methodologies involved a fixed number of rake throws along transects in the littoral zone (http://lter.limnology.wisc.edu/protocols.html).

Spatial graphs

As the principal vector of dispersal of invasive species in this system is entrainment on recreational boating equipment, we developed a spatial graph for the 5189 water bodies (i.e. graph nodes) with binary links derived from a probability of connectivity via road travel. Recent surveys suggest that up to 30% of recreational boaters in the region seldom or never wash down their equipment after use, while 32% may at times travel directly between lakes on the same day (Peterson & Nelson 2008). Nonetheless, the majority of boat users visit one water body per trip (Buchan & Padilla 1999), which means that most hitchhiking propagules are not transported directly from one water body to another. Rather, potential introductions most likely occur on subsequent trips to uninvaded water bodies within a time frame that propagules remain viable. To accommodate this, we used the centroid of each county in the region as a surrogate for boaters' residences (given that boater' addresses were not collected) and routed all road distances through these locations.

We began by generating a matrix of road distances between each water body and all of the county centroids. We then converted these road distances to probabilities based on an empirical distribution of boater travel in Wisconsin, which was highly correlated with the observed pattern of spread of *D. polymorpha* (Buchan & Padilla 1999). This provided an estimate of the probability of travel to each water body from each of the county centroids in the region. We used these probabilities to derive a probability of connectivity between each pair of water bodies. For a pair of water bodies in the same county, the probability of connectivity was simply the product of the probability of travel from the centroid to each water body. For a pair of water bodies in different counties (lake 1 in county A and lake 2 in county B), we calculated two estimates of the probability of connectivity. The first of these being the product of the probability of travel from each lake to the centroid of county A and the second being the product of the probability of travel from each lake to the centroid of county B. We set the probability of connectivity between the two lakes as the maximum of these two values. This resulted in a pairwise matrix of probabilities of connectivity among all water bodies in the dataset from which we built a contemporary spatial graph using all water bodies including artificial reservoirs. We subsequently identified the proportion of probable connections to define two water bodies as "connected" via a sensitivity analysis that varied the possible threshold between 0.025 and 0.975.

Having determined a set of pairwise connections using the contemporary spatial graph, we constructed three additional graphs; 1) an historical graph represented by only natural lakes, 2) a contemporary high-use graph representing only water bodies with boat launches and 3) a contemporary low-use graph representing only water bodies without boat launches. This enabled us to evaluate the effect of the relatively recent construction of artificial reservoirs on the connectivity of the system, assuming contemporary boater movements, and examine the potential vulnerabilities in the system at high-use water bodies.

To assess network topology and quantify different elements of connectivity, we computed a series of graph theoretic indices for each graph. First, we calculated the number of components to quantify the connectivity of the spatial graphs as a whole. A component is a set of nodes (here, water bodies) in which there is a path, though not necessarily a direct link, between all pairs of nodes (Galpern, Manseau & Fall 2011). As such, all components are effectively disconnected from each other (Pascual-Hortal & Saura 2006) and could be used as discrete management units to guide local and landscape scale invasive species interventions. As the connectivity of the entire graph increases, the number of components decreases. Second, we computed the number of links in each graph. At the water-body level, we computed the node degree for each water body, which is the number of binary connections of that node. As the connectivity of a node increases, so does its degree. Third, we calculated the mean distance to an invaded water body in each graph. We calculated the number of components using Conefor Sensinode 2.2 (Saura & Torné 2009) while all other graph theoretic indices were calculated in the R statistical environment version 2.14.1 (R Development Core Team 2012).

Habitat suitability modelling

For each water body we estimated the suitability of habitat for *D. polymorpha* and *M. spicatum* by fitting logistic generalised additive models (GAMs) using presence/absence data from a subset of the water bodies (n=312 for *D. polymorpha* and n=601 for *M. spicatum*). Generalised additive models are a flexible non-parametric approach to regression modelling that can account for non-linear relationships via the use of splines (Hastie & Tibshirani 1990). The spatial GAMs were fit with a set of predictor variables and a smoothed spatial term, using splines on latitude and longitude, to account for residual spatial variation (Bivand, Pebesma & Gómez-Rubio 2008). The predictor variables included environmental characteristics deemed important for colonization and establishment based on previous

investigations (reviewed in Johnson, Olden & Vander Zanden 2008), including maximum depth (m), surface area (km^2), conductance (µmhos cm^{-1}), secchi depth (m), upstream watershed area (km^2), water body type (seepage or drainage), impoundment status (lake or reservoir), number of boat launches and the straight line distance to the nearest Great Lake (either Lake Michigan or Lake Huron). Predictor variables were selected using backwards elimination to remove statistically non-significant variables while minimising the AIC. The smoothness of the spatial spline was determined by minimising the unbiased risk estimator criterion (Wood 2011). The spatial GAMs were fit in the R statistical environment (R Development Core Team 2012) using the `mgcv` package (Wood 2011). We calculated the area under the receiver operating characteristic (ROC) curve using the `pROC` package (Robin *et al.* 2011).

Management recommendations

We combined the results of the GAMs with results of the spatial graphs to rank water bodies according to priority for management intervention relative to other water bodies on a continuous scale. First, each water body was identified as suitable for offensive or defensive strategies depending on its invasion status and subsequently prioritised according to a probabilistic estimate of risk based on combined connectivity and habitat suitability. We defined the risk of invasion at any given water body as a product of its habitat suitability and those to which it is connected, and its probable connectivity to other invaded or vulnerable water bodies:

$$R_i = H_i \times \sum_{j=1}^{J} \left(H_j C_{ij}\right)$$

Where R_i is the estimated risk at the *i*th lake, H_i is the estimated habitat suitability of the *i*th lake and H_j is the habitat suitability of each of the *j* connected lakes, and C_{ij} is the probability

of connection between the *i*th lake and all *j* lakes within the component. For lakes known to be invaded, we simply replaced the model-estimated habitat suitability H_i or H_j with 1. We used the components that were identified in the contemporary spatial graph to define a neighbourhood for each water body that provided the connections used to estimate our metric of risk. However, we used to the probabilistic connections to define C_{ij}, rather than the binary ones used to define the neighbourhood, which we scaled within each component to a unit sum. Thus, the sum of all C_{ij} in each component was 1, which ensured the estimate of risk, R_i, represented a probability that ranged from 0 to 1.

Under this model, the risk associated with known invaded water bodies can be interpreted as an offensive risk, and for water bodies that are uninvaded or unknown it can be interpreted as the defensive risk. We tested the risk metric by evaluating its capacity as a classifier of invasion status using the area under the receiver operating characteristic curve (AUC). An AUC of 1 indicates perfect classification while an AUC of 0.5 indicates no better than random classification (Fielding and Bell 1997). We compared the AUC for the risk metric with that of the spatial GAMs to assess the improvement in classification when combining connectivity with habitat suitability.

We prioritised local-scale measures under different budget constraints, or levels of investment, according to the spatial distribution of risk across the components. We quantified different levels of investment in terms of the proportion of all water bodies at which intervention measures could afford to be deployed. At each level of investment we allocated effort by ranking the water bodies by their risk and attributing effort accordingly. For example, if only 5% of the water bodies in the region could be targeted with a prevention measure, we identified the proportion of the water bodies above the 95th percentile of risk that fell in each component. These proportions identified the specific water bodies to be targeted and by extension the allocation of effort for that component. An additional step examining

high-use water bodies within the contemporary graph offers a further filter to assist prioritisation. This would identify potential habitats that are highly connected to both high and low-use water bodies that may be more likely to act as source habitats for invaders.

In addition to prioritising local-scale offensive and defensive management, the multiscale nature of our approach, based on the use of the graph components, ensured we could make recommendations for additional landscape-scale interventions according to the overall risk among these groups of connected water bodies in the region. Network components that consisted of water bodies with high overall risk could then be prioritised for additional landscape-scale interventions.

Results

The sensitivity analysis to identify a suitable threshold of connectivity based on the contemporary graph, showed a distribution of numbers of components ranging from 1 to 60, with a clear jump from 13 to 60 components as the threshold is reduced from 0.9 to 0.875 (Fig. 2a). There was a subsequent decrease in the number of components to 3 and 1 for the thresholds 0.925 and 0.95 respectively. This suggested a reasonable cut-off would be to use 90% of the probable connections to define water bodies as connected via a county centroid. A slightly higher threshold, such as the intuitively appealing 0.95, would provide little value to guide management interventions as it would fail to identify any components. Equally, a slightly lower threshold results in such a large number of components as to have limited utility at the regional planning level. This provided a basis to develop the three subsequent graphs to compare connectivity through space and time.

Water body connectivity

The last century of river impoundment and proliferation of reservoirs has dramatically increased landscape connectivity of water bodies (Table 1). There were fewer components in the contemporary graph than the historical one, indicating a more interconnected present-day network. Three-quarters of the 5189 water bodies in the contemporary landscape (3144 lakes and 800 reservoirs) were connected in one of 13 separate components (numbered arbitrarily as 1–13), leaving 1039 and 206 unconnected lakes and reservoirs, respectively (Fig. 2b). By contrast, only 60% (or 3105) of lakes in the historical landscape (which excludes reservoirs) were connected in one of 18 separate components. There was also a higher number of connections in the contemporary graph and a significantly higher number of connections per water body (mean degree) compared to the historical graph (Table 1). In addition, the distance to the nearest water body invaded by *D. polymorpha* has also declined with reservoir construction (Table 1). In both networks, several of the components were relatively small and isolated with only six components in the contemporary network and eight in the historic network consisting of more than 15 water bodies.

The comparison of high-use vs. low-use water bodies in the contemporary graph (i.e. those with and without boat launches) yielded some counter intuitive results (Table 1). There were fewer high-use water bodies in the landscape, which resulted in a graph with more components and fewer links, indicating a less-connected network than that of low-use water bodies. However, the ratio of mean degree to the number of links was considerably higher for low high-use water bodies (Table 1) indicating relatively higher node-level connectivity. Interestingly, the distance to the nearest water body invaded by *D. polymorpha* is higher for high-use water bodies than low-use, while it is slightly lower for *M. spicatum*.

Habitat suitability modelling

The habitat suitability models accounted for more than half the deviance in spatial distribution of each species and showed quite different patterns of risk. The spatial GAM for *D. polymorpha* accounted for 53% of the deviance in the observed data with an area under the ROC curve of 0.94 and included a significant smooth spatial term as well as five environmental predictor variables (Table 2). Predicted habitat suitability decreased significantly with distance from the nearest Great Lake, whereas drainage water-bodies and those with larger watershed area, maximum depth and secchi depth showed significantly increased risk (Table 2). The predicted habitat suitability of all water bodies for *D. polymorpha* was generally quite low across the region (Fig. 3a). Generally, water bodies in component 1 showed the highest habitat suitability, however, there were several highly suitable water bodies in other components (Fig. 3a; Table 3).

By contrast, the spatial GAM for *M. spicatum* predicted relatively high habitat suitability for water bodies across the entire region (Fig. 3b). The model accounted for 59% of the deviance in the observed data with an area under the ROC curve of 0.95 and included a significant smooth spatial term and two marginally significant environmental variables (Table 2). Predicted habitat suitability for this species increased significantly with increased conductance and decreased with distance from the nearest Great Lake. In contrast to the model for *D. polymorpha*, component 8 had the highest mean suitability for *M. spicatum*; however, there were many water bodies in other components with a high suitability for this species (Fig. 3b, Table 3).

Management prioritisation

By combining the connectivity of each water body with the estimated habitat suitability from the spatial GAMs into our metric of risk, we identified a subset of water bodies to target for offensive and defensive management interventions. Our risk metric discriminated very well

between water bodies observed to be invaded and uninvaded by *D. polymorpha* (Fig. 4a), and had an area under the ROC curve of 0.97, which is slightly higher than the spatial GAM. This pattern was consistent for high-use water bodies (Fig. 4b). The spatial distribution of risk for *D. polymorpha* was heavily skewed toward the south-eastern part of the study region, which largely comprised component 1 (Fig. 3c; Table 3). This is due to the generally higher habitat suitability and connectivity in that part of the graph (Table 3). Subsequently, analyses for allocation of effort suggested component 1 should receive the greatest allocation of effort for both offensive and defensive strategies (Table 4). Should management budgets allow for only 5% of water bodies to be protected, 71% of this effort should be allocated to defensive strategies at water bodies in component 1, with 27% allocated to offensive strategies in component 1 and 2% allocated to defensive strategies in other components. As management budgets allow for a greater proportion of water bodies to be targeted, our results suggest that other components should receive allocation of effort for both offensive and defensive strategies. It is not until it is possible to target 50% of all water bodies that all components should receive some allocation of management effort for *D. polymorpha*.

The relatively high risk of invasion by *M. spicatum* was distributed across most components of the spatial graph with most of the high risk water bodies contained in components 1 and 8 (Table 3; Fig. 3d); a pattern consistent with the predictions from the habitat suitability models. As with *D. polymorpha*, our risk metric was able to discriminate well between water bodies observed to be invaded and uninvaded by *M. spicatum* (Fig. 4c), with an area under the ROC curve of 0.93, which is comparable to the spatial GAM. The distributions of risk for *M. spicatum* was also similar for high-use water bodies (Fig. 4d). Despite the more relatively even distribution of risk across the region, the water bodies with the highest risk were predominantly located in component 1. Consequently it is only under management plans that allow for more than 20% of the water bodies to be targeted for intervention that another

component, in this case component 8, should receive management activities targeting *M. spicatum* (Table 4).

Discussion

Increasing evidence of the ecological and economic impacts of species invasions has emphasized the urgent need for researchers to provide managers with meaningful recommendations for how to both prevent invasions and prioritize management of invasive species (Papeş *et al.* 2011). The notion of offensive and defensive strategies in invasive species management provides a very useful framework to guide preventive measures aimed at limiting the secondary spread of non-native species, but until now has not been operationalized with empirical data. Under simulated conditions, Drury & Rothlisberger (2008) identified stages of the invasion process when each strategy would be most effective in slowing the secondary spread across the landscape. However, neither the suitability of receiving habitats given the ecological niche of the invader, nor the connectivity among those habitats was considered. Further, the constraint of large numbers of potential habitats to protect with limited resources means that some form of prioritisation is required. Here, we developed and presented an approach that integrates the notion of offensive and defensive strategies into recent frameworks representing integrative approaches to risk assessment (Vander Zanden & Olden 2008; Leung *et al.* 2012; Ibáñez *et al.* 2014). Our goal was to demonstrate an integrated modelling approach that incorporated separate axes of the invasion process (i.e. colonization vs. establishment) and provided guidelines for management intervention at multiple scales. Because sufficient data to estimate population demographic parameters are often lacking, we sought an empirical approach that did not rely on dynamic

population models. Rather, we integrated estimated habitat suitability and probable connectivity based on empirical distribution of boater behaviour from the region.

Using this approach for two different species, we identified an allocation of effort and a specific subset of water bodies for offensive and defensive strategies. This information can help ensure invasive species intervention measures are distributed most efficiently. Overall, the estimates of risk were much higher for *M. spicatum* than *D. polymorpha*, which reflects the generally higher predicted habitat suitability for *M. spicatum*. The improved classification accuracy of our risk metric for *D. polymorpha* and its comparable accuracy for *M. spicatum*, when compared to the spatial statistical models alone, provide strong evidence of support for this estimate of risk. Our approach provides flexibility for stakeholders to identify priority sites for prevention efforts given a maximum level of acceptable risk, or based on budgetary/time restrictions that may limit the number of locations that can be managed. Placing additional priority on high-use water bodies, reservoirs or those that are of high risk for both species would assist in identifying the highest priority water bodies for a given management plan. Finally, the water body and component level analysis provides a multiscale perspective to identify broader regions (network components) that may be suitable for larger-scale interventions such as component-wide boater education programs or wash down stations in population centres. Additionally, the 60 component graph could be used to guide meso-scale interventions, potentially administered at the local government level (i.e. county or lake districts).

The arrival of invaders at uninvaded habitat is arguably the most important step of the invasion process (Lockwood, Cassey, & Blackburn 2005), making attempts to quantify this process vital. We converted road distances to probabilities based on the empirical distribution of boater movements in the region reported by Buchan & Padilla (1999). By using road distances in this way we could more faithfully represent the dispersal process associated with

species' entrainment on recreational boats than if we had used some other distance measure, such as straight line distance (Drake & Mandrak 2010). We were required to assume that the county centroid represented the average boater's home to accommodate that the majority of recreational boating trips are to a single water body each day (Buchan & Padilla 1999). This assumption will almost certainly overestimate the connectivity of some water bodies and underestimate the connectivity of others. However, in the absence of information about specific trips or the physical addresses of registered boaters, this assumption is unavoidable at this stage. It is nonetheless, a reasonable one since the overwhelming majority of fishing trips are to a single water body and subsequent invasive species introductions occur on later trips to others (Peterson & Nelson 2008).

Improvements in the estimation of connectivity and its validation could come from data pertaining to the nodes (water bodies) or the links (the road network). Empirical data derived from surveys of patterns of use at specific water bodies, or probabilistic estimates of attraction similar to gravity models could be used to weight nodes according to their popularity. Equally, the distance between pairs of lakes could be weighted by the quality of the roads connecting them to derive connections based on distance and ease of access. In addition to these improvements, dispersal processes where the species move through the network of water bodies unassisted, either through drift or active dispersal along drainage channels, could be incorporated. We specifically looked at human-assisted movements to target under the risk assessment framework as this is generally the primary vector of spread for many species (Vander Zanden & Olden 2008). However, recent theoretical work predicting metapopulation persistence of several species, based on within network and overland dispersal of aquatic organisms demonstrated the likely importance of both processes to metapopulation persistence, particularly for *D. polymorpha* (Mari *et al.* 2014). Our

approach could be extended by developing a spatial graph of the drainage network and estimating connections according to empirical data on instream species movements.

Graph and network theoretic approaches offer a promising methodology to quantifying connectivity (or potential connectivity) in complex networks (Dale & Fortin 2010), especially freshwater ecosystems (Stewart-Koster *et al.* 2007; Erös *et al.* 2012; Rolls *et al.* 2014). A network approach to modelling dispersal has already demonstrated utility in understanding the spread of invasive species (e.g. Muirhead & MacIsaac 2005; Drake & Mandrak 2010). The development of numerous graph theoretic indices that describe the connectivity of a given system at a node and network level (e.g. Galpern, Manseau & Fall 2011) may provide further opportunity to advance invasive species research. Such indices can be used to identify important hubs in a network given their location and connectivity. The removal of such hubs from the network of invasive species spread (i.e. offensive or defensive protection) would reduce the connectivity of the system most substantially, thereby decreasing the vulnerability of the entire system (e.g. Florance *et al.* 2011). It may not necessarily be the most highly connected node that is most important, particularly for random as opposed to scale-free networks (Barabási 2009). In the present study, the difference between the historical and contemporary spatial graphs highlighted the importance of artificial reservoirs in reducing the average dispersal distance required for the invasive species to access uninvaded locations. These types of habitats are known to facilitate invasions into new locations (Johnson, Olden & Vander Zanden 2008). Expected changes to the system that improve accessibility such as such as the construction of new boat launches or additional reservoirs could also be incorporated into future spatial graphs of the system. Beyond invasion hubs, graph theoretic indices can be applied to links in the network to identify the most important potential invasion pathways, which if removed (i.e. offensive protection at appropriate invaded water bodies) would also reduce system-wide connectivity. These could also be applied to road

quality and accommodate new road developments that improve access to uninvaded water bodies.

Subsequent to the initial arrival of a species, the successful establishment of a population is dependent on several factors including the local habitat suitability. We quantified this component of the invasion process using spatial GAMs with environmental variables that may act as abiotic constraints on species establishment (Peterson & Vieglais 2001). These models, which accounted for approximately half of the deviance in the spatial distribution for each species, provided an avenue to predict invasion vulnerability at unsampled water bodies given local environmental conditions and any additional spatial processes not necessarily accounted for by the spatial graph. Improving the deviance explained and the predictive accuracy of the models would improve our approach and could be achieved through the use of additional predictor variables including biotic information, as well as mechanistic modelling approaches such as biophysical ecological models (Ibáñez *et al.* 2014). Additionally, modelling expected environmental and climate changes could facilitate a predictive risk assessment that accommodates how the invasion vulnerability of water bodies in the system may change.

Dreissena polymorpha and *M. spicatum* had quite different spatial distributions of predicted risk despite the dispersal of both being assisted via entrainment on boating and fishing equipment. This is no doubt a reflection of the different habitat requirements of each as well as the difference in time since initial invasion, *M. spicatum* arrived 20–30 years before *D. polymorpha* (see Materials and Methods). Nonetheless, component 1 in the contemporary spatial graph had the highest average invasion risk for both species. This is not entirely unexpected given its high number of reservoirs that are frequently associated with species invasions in this region (Johnson, Olden & Vander Zanden 2008) and its proximity to Lake Michigan, which acts as a key source habitat. It is also possible that both species are

approaching a point of saturation where invasion rates will start to decline because of some process not included in the model. If this were the case, the implicit assumption in the GAMs that the invasion vulnerability of each water body is defined only its location and the abiotic variables would result in the degree and extent of invasion vulnerability being overestimated. In such a scenario, the graph theoretic analyses still provide a useful first pass identifying vulnerability of water bodies to new and still spreading invaders given their potential connectivity (e.g. Johnson, Olden & Vander Zanden 2008; Olden, Vander Zanden & Johnson 2011). The economic and ecological impacts of these species make such assessments critical.

In an age of limited public funds available for ecological protection, it is imperative that the implementation of invasive species management be targeted to locations of the highest priority in all ecosystem types (Papeş *et al.* 2011). A risk assessment framework that combines as many aspects of the invasion process as possible, such as that presented here, provides an avenue to guide such decisions. It is likely, given the already widespread spatial distribution of *M. spicatum*, that some of the water bodies with high and very high defensive priority are in fact already invaded by this species. As such, it would be prudent to conduct field sampling to determine the invasion status to further refine the prioritisation. It is also important to note that as with any risk assessment framework, we are not advocating that the invasion vulnerability at lower-priority habitats be ignored. Rather we are attempting to aid decision making as to where to apply limited resources for management. Clearly, it would be preferable to protect all uninvaded habitats and prevent the invaders from leaving already invaded ones. However, the reality of limited budgets and a growing number of invasive species introductions means that prioritisation is crucial to slowing or even stopping their spread. The approach presented here may assist with this process across many ecosystem types.

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Data accessibility

Water body locations, environmental conditions and estimated invasion risk, available at: http://dx.doi.org/10.6084/m9.figshare.1285847

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Table 1. Graph theoretic indices for each spatial graph. The historical graph included only natural lakes and the contemporary graph included all water bodies included reservoirs. The high use graph included only water bodies with boat launches and the low use graph included only water bodies without. Pairwise tests for significant differences in landscape-scale descriptors of each graph were only made between the historical and contemporary graphs and the high-use and low-use graphs. Pairs of indices in bold indicate a statistically significant difference determined by Wilcoxon rank-sum test

	Historical (lakes)	Contemporary (lakes & reservoirs)	High use (with boat launches)	Low use (w/o boat launches
Graph theoretic indices				
Total connected (N)	3 105	3 944	1 087	2 781
Total unconnected	1,078	1,245	334	987
Components	18	13	16	14

Number of links	170 155	223 418	16 388	123 105
Mean degree	**81**	**88**	**23**	**65**
(degree:links)*100	0.05	0.04	0.14	0.05
Distances to nearest invaded lake (km)				
Dreissena polymorpha	25	13	25	19
Myriophyllum spicatum	22	22	25	26

Table 2. Parameter estimates for the Generalised additive models of invasion vulnerability for the two invasive species. Only significant variables, as determined by analysis of deviance, were used in the final models

Species	Predictor variable	Estimate (SE)	Reduction in deviance	*p*-value
Dreissena polymorpha	Watershed area	0.87 (0.25)	12	<0.001
	Maximum depth	0.71 (0.27)	7.1	0.007
	Secchi depth	0.82 (0.31)	7.2	0.007
	Drainage lake	2.17 (0.61)	12.5	<0.001
	Distance to GL	-1.19 (0.57)	4.4	0.04
	S(longitude , latitude)		41.8	<0.001
Myriophyllum spicatum	Conductance	0.95 (0.47)	4	0.045
	Distance to GL	-1.28 (0.75)	3	0.085
	S(longitude , latitude)		77.1	<0.001

Table 3. Summary statistics of the major components in the contemporary spatial graph for both species, including the number of water bodies sampled (n_i), the proportion known to be invaded (p_i), predicted habitat suitability, and estimated invasion risk

	Dreissena polymorpha						*Myriophyllum spicatum*					
	Observations		Habitat suitability		Invasion risk		Observations		Habitat suitability		Invasion risk	
Component	n_i	p_i	Mean	Max	Mean	Max	n_i	p_i	Mean	Max	Mean	Max
1 (n=1 295)	163	0.42	0.14	0.99	0.04	0.71	326	0.97	0.84	1	0.75	1
2 (n=164)	13	0.08	0.02	0.58	0	0.01	7	0.71	0.29	0.96	0.06	0.23
4 (n=1 123)	28	0.07	0.007	0.77	0	0.02	64	0.41	0.34	0.99	0.13	0.7
5 (n=791)	55	0	0.004	0.17	0	0	142	0.2	0.24	0.93	0.08	0.56
6 (n=65)	1	0	0.003	0.02	0	0	3	0.33	0.61	0.93	0.38	0.62
7 (n=411)	21	0	0.006	0.54	0	0	28	0.14	0.25	0.81	0.08	0.39
8 (n=57)	9	0	0.004	0.03	0	0	7	1	0.92	0.99	0.86	0.96

Table 4. The recommended allocation of effort for both offensive and defensive strategies in each major component of the spatial graph, given several levels of investment. Each value represents the proportion of water bodies to be targeted based on the invasion risk of the lakes in each component relative to all others. For example, where the proportion of water bodies to be targeted is 5%, the values in the table represent the proportion of the water bodies above the 95th percentile of risk that fell in each of the major components. Major components of the contemporary spatial graph are defined as those with greater than 15 water bodies.

Proportion of water bodies	Defensive Allocations								Offensive allocations							
	Dreissena polymorpha								*Dreissena polymorpha*							
	1	2	4	5	6	7	8	other	1	2	4	5	6	7	8	other
5	0.71							0.02	0.27							
10	0.83		0.01					0.02	0.14							
20	0.87	0.02	0.02			0.01		0.01	0.07	0.01	0.02					
30	0.68	0.07	0.09	0.03		0.06		0.02	0.05							
40	0.55	0.06	0.15	0.08	0.01	0.09		0.02	0.04							
50	0.44	0.06	0.18	0.13	0.01	0.12	0.02	0.01	0.03							
	Myriophyllum spicatum								*Myriophyllum spicatum*							
5	0.92								0.08							
10	0.94								0.06							
20	0.87						0.06		0.07							
30	0.69		0.11	0.04	0.04	0.02	0.04	0.02	0.04							
40	0.55	0.01	0.22	0.08	0.03	0.04	0.03	0.01	0.03							
50	0.44	0.02	0.29	0.13	0.02	0.04	0.02	0.01	0.03							

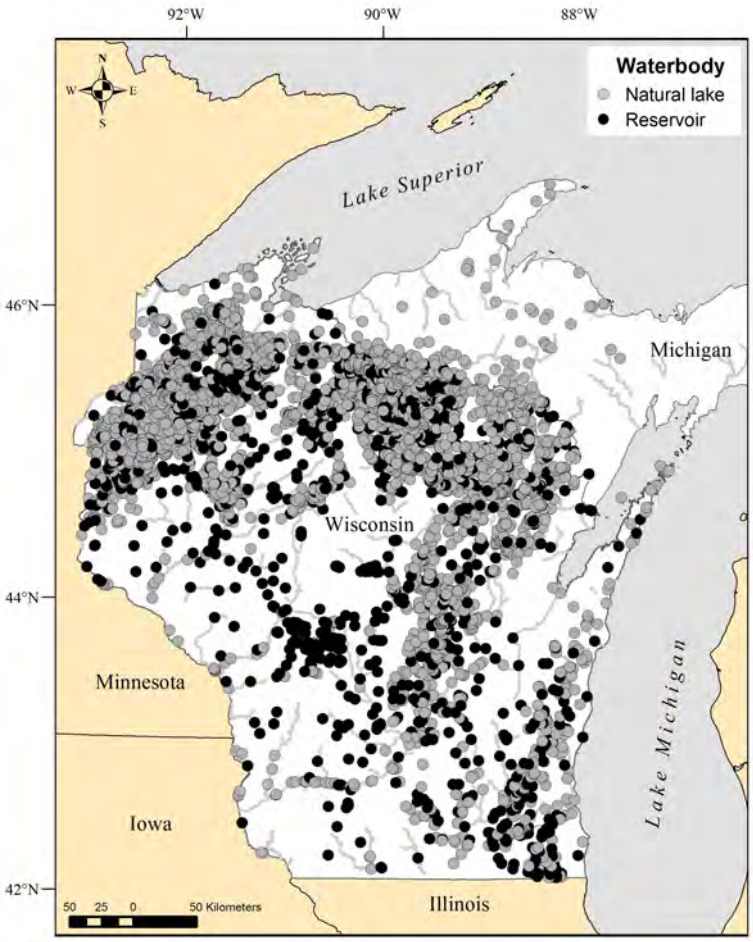

Fig. 1. Locations of water bodies in Wisconsin and the upper peninsula of Michigan classified as either lakes (black circles) or reservoirs (grey circles).

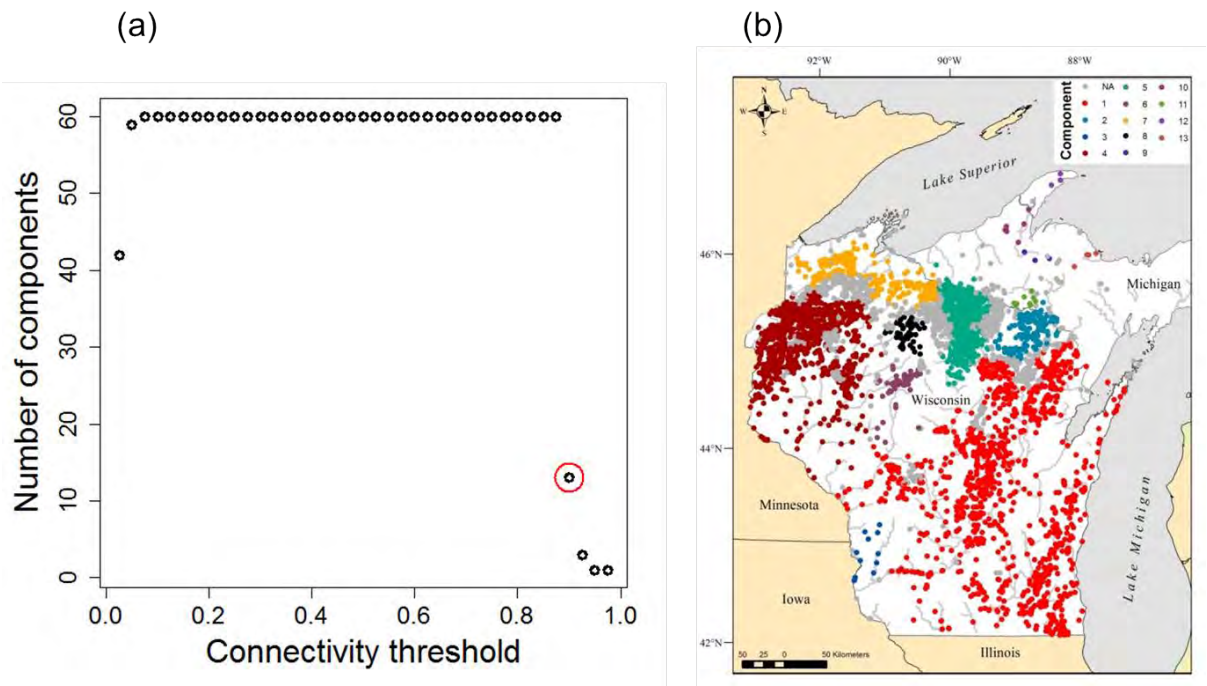

Fig. 2. The contemporary spatial graph including, a) the distribution of the number of components across all possible connectivity thresholds, with the selected threshold and number of components circled in red, and b) the contemporary graph built with lakes and reservoirs in the network using the connectivity threshold. Each water body is coloured according to its component. Grey water bodies are unconnected from all other water bodies. See the online version for the full colour figure.

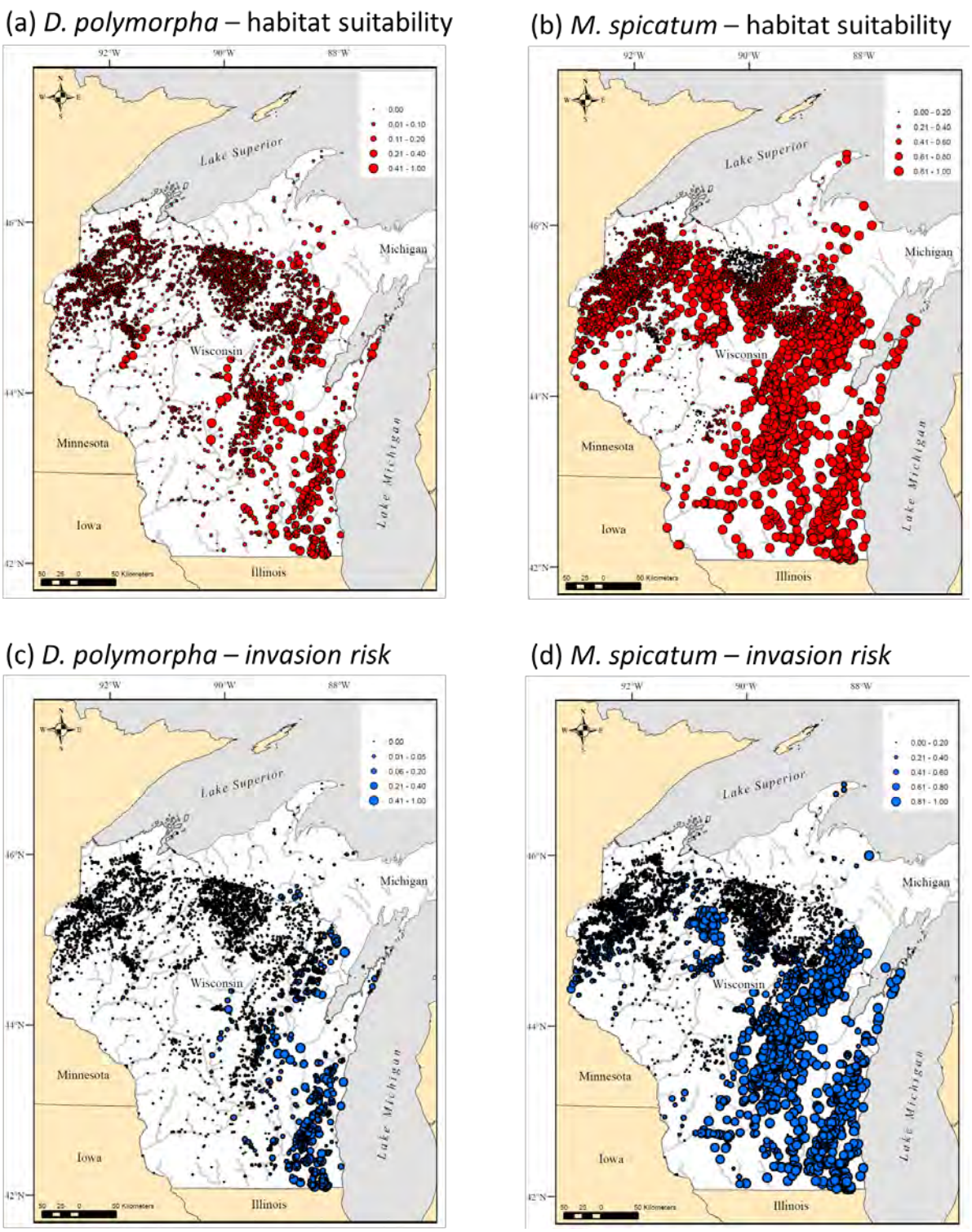

Fig. 3. Predicted habitat suitability as predicted by the spatial GAMs, for (a) *D. polymorpha* and (b) *M. spicatum*, and estimated invasion risk for (c) *D. polymorpha* and (d) *M. spicatum* integrating habitat suitability and probable connectivity of each water body. Symbol size reflects habitat suitability or invasion risk.

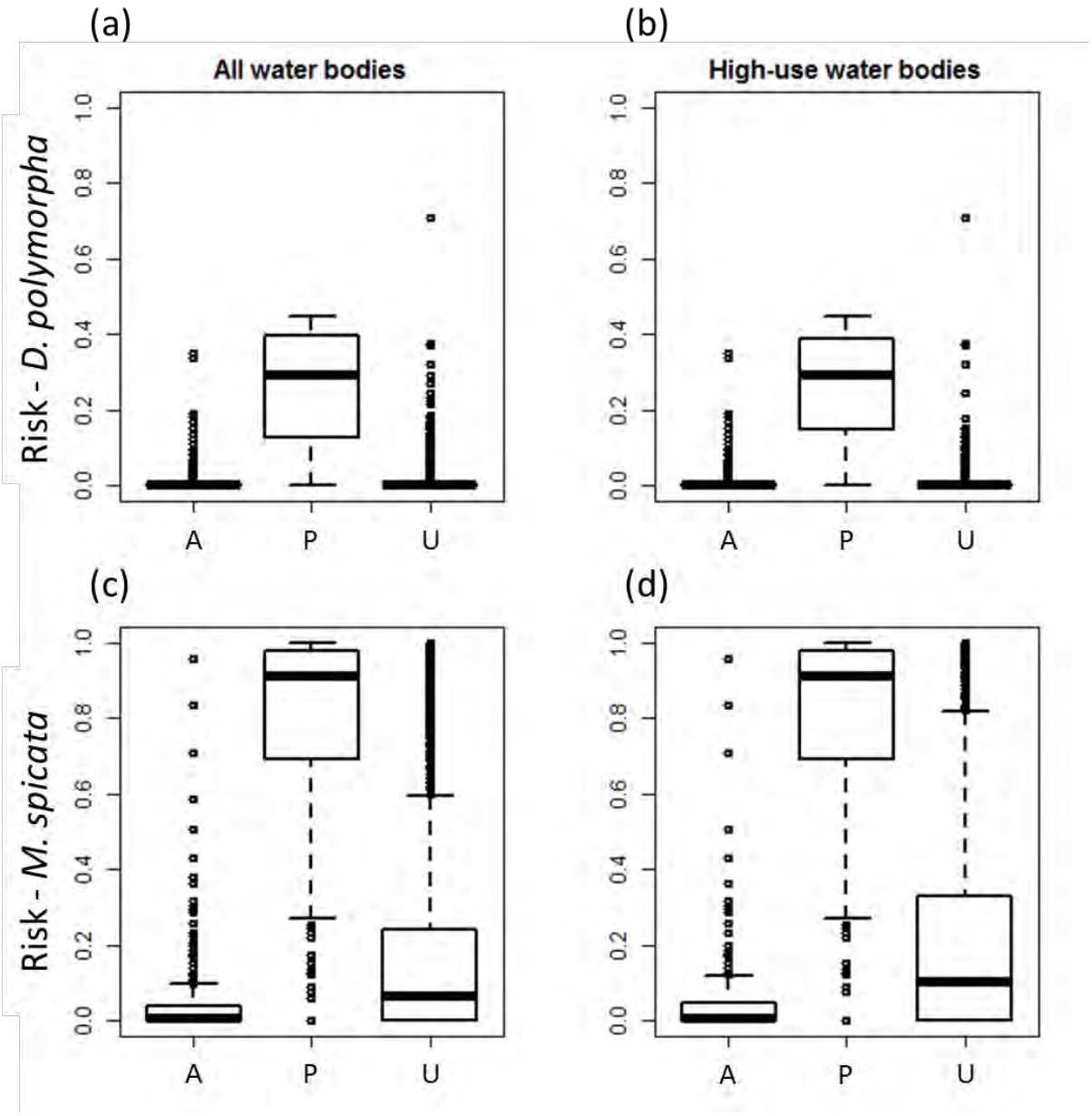

Fig. 4. The distributions of invasion risk plotted against invasion status, for *D. polymorpha* across (a) all water bodies and (b) high-use water bodies, and for M. spicatum across (c) all water bodies and (d) high-use water bodies. At each water body each species is either absent (A), present (P) or unknown (U).