

Assessing ecosystem vulnerability to invasive rusty crayfish (*Orconectes rusticus*)

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Abstract. Despite the widespread introduction of nonnative species and the heterogeneity of ecosystems in their sensitivity to ecological impacts, few studies have assessed ecosystem vulnerability to the entire invasion process, from arrival to establishment and impacts. Our study addresses this challenge by presenting a probabilistic, spatially explicit approach to predicting ecosystem vulnerability to species invasions. Using the freshwater-rich landscapes of Wisconsin, USA, we model invasive rusty crayfish (*Orconectes rusticus*) as a function of exposure risk (i.e., likelihood of introduction and establishment of *O. rusticus* based on a species distribution model) and the sensitivity of the recipient community (i.e., likelihood of impacts on native *O. virilis* and *O. propinquus* based on a retrospective analysis of population changes). Artificial neural networks predicted that ~10% of 4200 surveyed lakes ($n = 388$) and ~25% of mapped streams (23 523 km total length) are suitable for *O. rusticus* introduction and establishment. A comparison of repeated surveys before vs. post-1985 revealed that *O. virilis* was six times as likely and *O. propinquus* was twice as likely to be extirpated in streams invaded by *O. rusticus*, compared to streams that were not invaded. Similarly, *O. virilis* was extirpated in over three-quarters of lakes invaded by *O. rusticus* compared to half of the uninvaded lakes, whereas no difference was observed for *O. propinquus*. We identified 115 lakes (~3% of lakes) and ~5000 km of streams (~6% of streams) with a 25% chance of introduction, establishment, and extirpation by *O. rusticus* of either native congener. By identifying highly vulnerable ecosystems, our study offers an effective strategy for prioritizing on-the-ground management action and informing decisions about the most efficient allocation of resources. Moreover, our results provide the flexibility for stakeholders to identify priority sites for prevention efforts given a maximum level of acceptable risk or based on budgetary or time restrictions. To this end, we incorporate the model predictions into a new online mapping tool with the intention of closing the communication gap between academic research and stakeholders that requires information on the prospects of future invasions.

Key words: crayfish; invasive species; *Orconectes propinquus*; *Orconectes rusticus*; *Orconectes virilis*; prevention of extinction; risk assessment; Wisconsin.

INTRODUCTION

Invasive species are a leading threat to freshwater ecosystems, with ecological impacts ranging from behavioral shifts by native species to the complete restructuring of food webs (e.g., Simon and Townsend 2003, Eby et al. 2006, Cucherousset and Olden 2011). Continued increases in commerce and climate change will likely further accelerate the arrival and spread of invasive species (Rahel and Olden 2008, Hulme 2009). In response, governments are designing management strategies aimed at reducing the environmental, economic, and human health impacts of invasive species by better integrating the efforts of academia, natural resource agencies, local governments, and citizen groups (Lodge et al. 2006).

Prevention is widely recognized as the cornerstone of invasive species management strategies, as decades of experience have demonstrated that, following establishment by nonnative species, eradication or control is costly and difficult (Myers et al. 2000, Simberloff et al. 2005). Two important aspects of invasive species prevention involve prohibiting the entry of species into a new country or region, and containing the spread of species that have already established in a region, but have not reached their full distributional potential. For example, the Laurentian Great Lakes are home to >180 nonnative species, many of which were transported from abroad on transoceanic vessels (Holeck et al. 2004). A number of these species have begun to spread to inland lakes and streams as “hitchhikers” via a variety of human-related vectors, including with recreational and fishing boats. For some species, there may be thousands of suitable, though currently uninvaded freshwater ecosystems, yet the geographic scope for future spread

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remains poorly known (Vander Zanden and Olden 2008).

Preventing the spread of nonnative species to new ecosystems requires predictive tools that can be used to help guide resource allocation and prioritize management activities (Ricciardi and Rasmussen 1998, Vander Zanden and Olden 2008). Our ability to confront this challenge may be enhanced if the invasion process is considered as a stepwise progression of events in which individuals of some species are introduced or disperse to a novel location, establish a self-sustaining population, spread beyond the initial colonization location, and integrate into the receiving ecosystem, possibly causing ecological effects (Sakai et al. 2001). Fundamental to this process is the recognition that not all individuals successfully pass through each of these filters, such that only a fraction of the species that are moved by people will transit through all stages to be considered "invasive." To date, research efforts in freshwater systems (and elsewhere) have focused on the first two stages of the invasion process: initial introduction (e.g., Buchan and Padilla 1999, MacIsaac et al. 2004, Cohen et al. 2007), and potential for successful establishment based on where a species can survive and reproduce (e.g., Drake and Lodge 2006, Mercado-Silva et al. 2006, Herborg et al. 2007). By contrast, our quantitative understanding of the entire invasion process, including the likelihood of ecological effects, is limited (Parker et al. 1999, Strayer et al. 2006). Previous research efforts have also rarely focused on the site scale at which management strategies are designed and implemented (i.e., lake or stream reach), choosing instead to model at a spatial grain (i.e., latitude–longitude grids) in which environmental data are readily available but have little ecological and management relevance for freshwater species (e.g., Drake and Lodge 2006, Loo et al. 2007). Unfortunately, this disconnect has only broadened in recent years because of the growing automation of ecological niche models embedded in geographic information systems (Elith and Leathwick 2009).

In this study, we assessed the vulnerability of freshwater ecosystems to the multiple stages of invasion, from arrival to establishment and ecological impacts, by a problematic nonnative species, rusty crayfish (*Orconectes rusticus*). Our modeling approach is novel in that we combined a species distribution model for predicting rusty crayfish occurrence in both lakes and stream reaches of Wisconsin with a retrospective analysis of impacts on ecologically similar native congeners at invaded and uninvaded sites. This approach provides probabilistic, spatially explicit predictions of vulnerability to *O. rusticus* invasion as a function of exposure risk (i.e., likelihood of introduction and establishment of *O. rusticus*) and the sensitivity of the recipient community (i.e., likelihood of impact on native species). We incorporated the model predictions into a new online mapping tool with the intention of shortening the communication gap between academic

research and resource managers (who must prioritize monitoring and prevention efforts), concerned citizens, and environmental groups seeking information on the prospects of future invasions. Our study aims to inform proactive management strategies for stemming the further spread and ecological impacts of invaders on freshwater ecosystems, and also providing a general framework that can be applied to other nonnative species and regions.

METHODS

Ecology of rusty crayfish, Orconectes rusticus

The rusty crayfish, *Orconectes rusticus* (Girard 1852), is native to the Ohio River Basin, but has been widely introduced throughout the United States and Canada (Taylor et al. 2007, Olden et al. 2009, Phillips et al. 2009). In Wisconsin, long-term records show that *O. rusticus* have increased from 7% of all crayfish records collected during the first 20 years of their invasion (1965–1984) to 36% of all records during the most recent 20 years (Olden et al. 2006b). Major vectors of *O. rusticus* introductions include bait bucket discharge from recreational anglers, intentional releases by lake-users for nuisance weed control, biological supply and pet trades, and natural dispersal (Lodge et al. 2000, Puth and Allen 2005). Once established, *O. rusticus* has resulted in numerous ecological impacts manifested across entire lake food webs. *O. rusticus* commonly reach high densities and cause the displacement of native congeners, particularly the northern crayfish *Orconectes virilis* and the northern clearwater crayfish *Orconectes propinquus* (e.g., Capelli 1982, Lodge et al. 1986, Olsen et al. 1991, Hill and Lodge 1999, Perry et al. 2001). They are voracious omnivores and cause reductions in macrophytes, benthic invertebrates, and fish (Lodge et al. 1986, 1994, Olsen et al. 1991, McCarthy et al. 2006, Rosenthal et al. 2006).

Long-term crayfish database

We assembled a comprehensive data set of crayfish occurrence records from the state of Wisconsin, USA (169652 km² total area) for six native species (*O. virilis*, *O. propinquus*, *O. immunis*, *Cambarus diogenes*, *Procambarus acutus*, and *P. gracilis*), and nonnative *O. rusticus*. Note that *O. propinquus* is presumed native to southern and eastern drainages of the state, and therefore it is considered native to Wisconsin (Hobbs and Jass 1988). The data set contains >3000 crayfish locality records for lakes and streams collected primarily from 1965 to 2006 throughout the entire state, including tributaries of the Upper Mississippi River Basin, Lake Superior Basin, and Lake Michigan Basin. *O. rusticus*, *O. propinquus*, and *O. virilis* constitute >95% of all records. Records include incidence, identity, and collection information for the complete holdings of major regional museum collections, numerous smaller holdings, records from peer-reviewed and unpublished literature sources, university theses and dissertations,

and recent field surveys by University of Wisconsin (Center for Limnology) and the Wisconsin Department of Natural Resources (WDNR). Our aim was to maximize the use of the available crayfish occurrence data, recognizing that diverse sampling methodologies were used, and that crayfish species at very low abundances might not be detected. We refer the reader to Olden et al. (2006a, b) for additional information regarding data sources and standardized collection techniques of recent surveys.

Species distribution modeling

Predictors of crayfish occurrence.—We selected surrogates that are likely to reflect key factors influencing crayfish introduction and establishment success in lakes and streams. The lake analysis included nine variables describing human visitation, lake morphology, water chemistry, and hydrologic type. We used the number of boat landings per lake as a proxy for the popularity of recreational boating and fishing, because previous studies have found that boat landings offer a useful estimate of human visitation rates and invader propagule pressure (e.g., Buchan and Padilla 1999). In support of this, we found a strong positive relationship ($r = 0.69$, $P < 0.01$) between the number of boat landings and human visitation for 937 water bodies, according to boater movement data from a randomized survey of >50 000 registered Wisconsin boaters (Johnson et al. 2008). We also classified lakes into three human accessibility categories according to whether they had a public boat landing or were reachable by a navigable waterway (“boat access”), if they were reachable by wilderness trail (“trail access”), or if they were inaccessible (“no access”). Information on the number of boat landings and accessibility per lake was obtained from WDNR, DeLorme Gazetteers (Yarmouth, Maine, USA), and regional sportfishing guides. Lake physical and water quality variables included lake surface area (in square kilometers), shoreline perimeter (kilometers), maximum depth (meters), mean summer water clarity (Secchi depth, in meters), specific conductance (micro-mhos per centimeter), hydrologic type (seepage with no connecting stream vs. drainage with connecting stream(s)), and water body type (natural lake vs. impoundment). Water conductivity is considered a strong indicator of hydrologic connectivity in midwestern lakes (Martin and Soranno 2006). These data were collated from the WDNR Register of Waterbodies, the Wisconsin Lakes Book, and the Surface Waters of Wisconsin volumes. Estimates of Secchi depth were obtained from Landsat imagery according to methods outlined in Chipman et al. (2004). This technique is correlated with direct empirical estimates of Secchi depth but offers more extensive coverage and a standardized time scale of measured values. Critical thresholds for crayfish presence in lakes according to dissolved calcium (>2–3 mg/L) and pH (>5.5) were not examined because previous analyses for Wisconsin

suggest that the large majority of lakes fall above these thresholds, indicating little potential to limit *O. rusticus* establishment (Olden et al. 2006b).

The stream analysis included 11 variables describing channel characteristics, flow regime, land use, superficial geology, and regional climate. Channel characteristics included Strahler stream order, channel gradient (meters per meter, with the resulting angle expressed in degrees), and an index of stream baseflow according to the 90% exceedance derived from mean daily discharge (in cubic meters per second). We quantified the upstream riparian area (30-m buffer width, expressed as a percentage) into the following categories: agricultural row crops, urban land use, forested wetlands, carbonate bedrock (indicative of limestone, dolomite, and marl bedrock that is rich in calcium), and lacustrine clay and silt (a strong predictor of alkalinity/pH). We focused on the riparian zone because it exerts a disproportionately large influence on streamwater chemistry by acting as a mediator of geological, soil, and land use influences (Mulholland 1992). Previous studies have demonstrated that the proportion of lacustrine clay material, carbonate bedrock, forested wetlands, and row crop agriculture immediately adjacent to the channel are strong predictors of water calcium concentrations and alkalinity in midwestern streams (e.g., Johnson et al. 1997). At the watershed scale, we quantified mean soil permeability (in millimeters per hour) and mean annual air temperature (°C) and precipitation (millimeters) for the period 1960–1990 (as a measure of primary productivity and stream runoff). All variables were quantified as part of the Great Lakes Aquatic GAP project (information available online).⁵

Modeling crayfish occurrence.—We used a multi-response artificial neural network (MANN) trained by the backpropagation algorithm to model crayfish occurrence in 292 lakes and 546 stream sites using the entire database of records (using the most recent record when multiple records existed) (Fig. 1). Neural networks provide a flexible framework in which to model multiple response variables, are capable of modeling nonlinear associations with a variety of data types, require no specific assumptions concerning the distributional characteristics of the independent variables, robust to multicollinearity among variables (although $r < |0.75|$ for all pairwise variable comparisons), and can accommodate interactions among predictor variables without any a priori specification (Olden et al. 2006a). The architecture of MANNs consisted of single-input, hidden, and output layers, where the input layer contained one neuron for each of the environmental variables and the output layer contained one neuron for each crayfish species representing the probability of species' occurrence. The number of neurons in the hidden layer was chosen to minimize the trade-off

⁵ (<http://www.glsc.usgs.gov/GLGAP.htm>)

between network bias and variance by comparing the performances of different cross-validated networks, with 2–50 hidden neurons, and choosing the number that produced the greatest external network performance. This resulted in a 9–3–3 (input–hidden–output) and 11–7–3 network structure for lakes and streams, respectively. Variable contributions in the neural networks were quantified by calculating the product of the input–hidden and hidden–output connection weights between each input neuron and output neuron and then summing the products across all hidden neurons (Olden et al. 2004). All neural network analyses were conducted using computer macros written in the MatLab (MathWorks, Natick, Massachusetts, USA) programming language.

We used MANNs to simultaneously predict the probability of contemporary (1985–2006) occurrence of *O. rusticus* and two common native crayfishes, *O. propinquus* and *O. virilis*, as a function of environmental and anthropogenic factors describing the likelihood of introduction and establishment. We modeled these invasion stages together because we recognize that many of the aforementioned factors influence both the probability of introduction and establishment of *O. rusticus* (Johnson et al. 2008). N-fold (leave-one-out) cross-validation was used to generate model predictions and assess classification performance of the neural networks according to overall classification performance (percentage of sites where the model correctly predicts species' presence–absence), sensitivity (percentage of the sites where species' presence was correctly predicted), and specificity (percentage of the sites where species' absence was correctly predicted) (Fielding and Bell 1997). Optimal decision thresholds to classify species' presence–absence were determined using Receiver Operating Characteristic (ROC) curves. We applied Cohen's kappa statistic (Titus et al. 1984) to assess whether model performance differed from expectations based on chance alone.

Quantifying impact of O. rusticus on native crayfishes

Long-term monitoring programs or repeated sampling events provide the opportunity to quantify changes in crayfish populations over time (Edwards et al. 2009). We conducted a retrospective analysis of population change by identifying all lakes ($n = 64$) and stream sites ($n = 119$) whose crayfish fauna was sampled in two periods: pre-1985 (i.e., historical records) and post-1985 (i.e., contemporary records); and for which there was at least 10 years between the sampling dates. In order for a survey to be considered the same stream site, the samples had to be separated by no more than one kilometer, and not bisected by a perennial tributary. We calculated events describing colonization (gains) and extirpation (losses) between historical and contemporary time periods for each of the three species of crayfish. Using this information, we estimated the probability of native species extirpation by *O. rusticus* by contrasting the

frequency of species gains and losses for each native species (N) at sites that were invaded vs. uninvaded by *O. rusticus* (OR) between historical and contemporary time periods as follows:

$$\text{Freq}(\text{Loss})_N = \text{Freq}(\text{Loss}_N | \text{Inv}_{\text{OR}}) - \text{Freq}(\text{Loss}_N | \text{Un-Inv}_{\text{OR}}) \quad (1)$$

$$\text{Freq}(\text{Gain})_N = \text{Freq}(\text{Gain}_N | \text{Inv}_{\text{OR}}) - \text{Freq}(\text{Gain}_N | \text{Un-Inv}_{\text{OR}}) \quad (2)$$

$$P(\text{Extirpation})_N = \text{Freq}(\text{Loss})_N - \text{Freq}(\text{Gain})_N \quad (3)$$

where Loss indicates the historical presence and contemporary absence of a native species at a lake/site, Gain indicates the historical absence and contemporary presence of a native species at a lake/site, Inv indicates the gain (or establishment) of *O. rusticus*, and Un-Inv indicates the contemporary absence of *O. rusticus*. The difference between the frequency of loss and the frequency of gain was used as an estimate of extirpation probability associated with establishment of *O. rusticus*. Two components of our calculation are notable. First, we accounted for losses and gains of native species associated with factors (e.g., habitat modification, climate change) other than *O. rusticus* invasion by examining population changes in uninvaded sites. Second, by including $\text{Freq}(\text{Gain})$ in the estimation of $P(\text{Extirpation})$ we allow for the possibility of *O. rusticus* reducing the likelihood of native populations colonizing new sites over time (e.g., biological exclusion).

The ecological impacts of *O. rusticus* were explored by categorizing the response of *O. propinquus* and *O. virilis* by invasion history of *O. rusticus* (invaded vs. uninvaded) and by testing the χ^2 goodness-of-fit of the resultant 2×2 contingency table (with the Cochran-Haber correction) using Fisher's exact test (Zar 2010). Specifically we asked whether lakes/streams invaded by *O. rusticus* exhibited greater levels of native species loss over time compared to uninvaded lakes/streams, and whether lakes/streams invaded by *O. rusticus* exhibited lower levels of native species gain over time compared to uninvaded lakes/streams.

Quantifying vulnerability to O. rusticus invasion

Vulnerability to an invasion event is determined by the level of exposure to a risk factor, the degree of intrinsic sensitivity of the recipient community to that risk, and the extent to which adaptive capacity enables these potential impacts to be offset. There are no objective, independently derived measures of exposure, sensitivity, or adaptive capacity in invasion biology, and so their relevance and interpretation depend on the scale of analysis, the particular species under consideration, and the type of data available (Parker et al. 1999, Strayer et al. 2006). We chose measures of exposure and sensitivity that incorporated all stages of the invasion

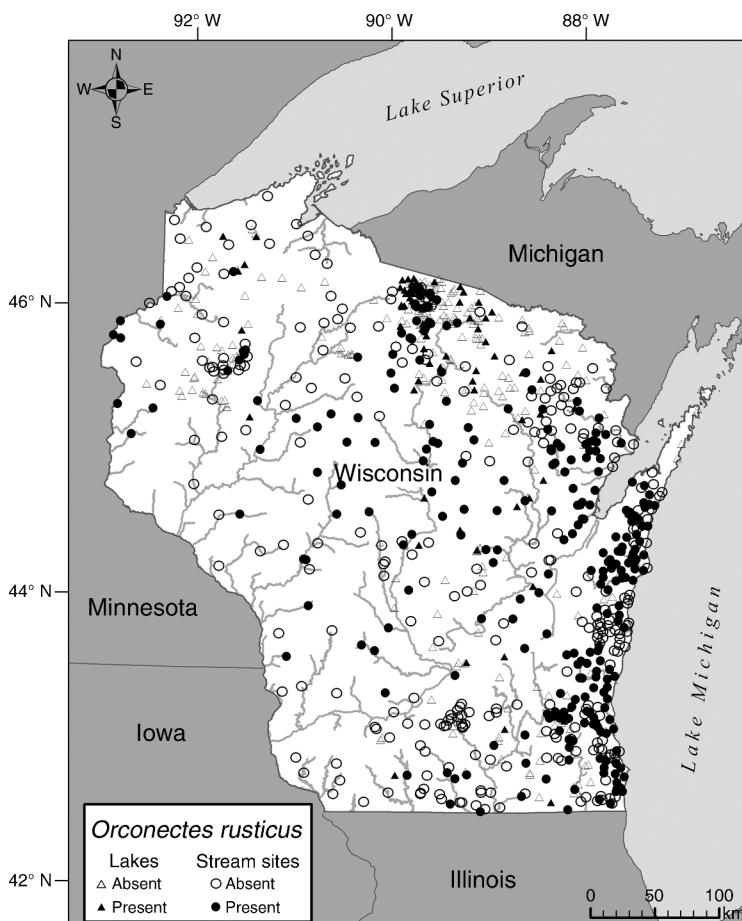


FIG. 1. Map of study lakes (triangles) and streams (circles), indicating sites with detected occurrences of the rusty crayfish *Orconectes rusticus* (solid symbols).

process (i.e., introduction, establishment, and impact). Using the MANNs, we predicted the probability of occurrence for *O. rusticus*, *O. propinquus*, and *O. virilis* for 4200 lakes and 35 856 stream segments (representing 90 360 river kilometers) as a function of the environment/spatial predictors across the entire state of Wisconsin. The overall vulnerability of *O. rusticus* invasion was calculated as the product of: (1) the probability of *O. rusticus* occurrence (range: 0–1) representing exposure; (2) the probability of native species occurrence (range: 0–1); and (3) the probability of native species extirpation given *O. rusticus* establishment (range: 0–1) representing sensitivity. Current data availability precluded us from incorporating the capacity of native crayfish to adapt to the invasion of rusty crayfish at the landscape scale, but we do acknowledge its potential role in the study region (Hayes et al. 2009).

RESULTS

Species distribution modeling

Crayfish occurrence was highly predictable according to the MANN relating species presence–absence to the

suite of environmental descriptors (Table 1). The cross-validated neural network correctly predicted *O. rusticus*, *O. propinquus*, and *O. virilis* in >90% of the 292 lakes and >93% of the 546 stream sites (cross-validated estimates). Model performance was significantly greater than random for all species in both lakes and streams. The high levels of sensitivity (77–94%) demonstrate the utility of the network for predicting the potential presence of all crayfish species (Table 1). Applying this model to the entire state showed that 388 lakes (9.9% of unsurveyed lakes) and 23523 stream kilometers (25% of mapped streams) were predicted to be suitable for both the introduction and establishment of *O. rusticus* (based on a probability decision threshold of >0.30 for lakes and >0.50 for streams). *O. propinquus* and *O. virilis* were predicted to occur (based on environmental suitability) in 475 and 2729 lakes, respectively, and 40 992 and 39 573 stream kilometers, respectively (Table 1).

The probability of *O. rusticus* occurrence was predicted to be higher in drainage lakes (i.e., those containing an outlet) with greater maximum depths and a higher number of boat landings/ramps (Fig. 2). Impoundments were predicted to be invaded at a higher

TABLE 1. Performance of the multi-response artificial neural network for predicting presence–absence of crayfish (*Orconectes*) species in the 292 study lakes and 546 stream sites.

Species	Freq.	CC	SE	SP	κ	Z	P	Suitable
Lakes								
<i>O. rusticus</i>	0.27	93.2	85.9	95.8	0.93	57.9	<0.001	388 lakes
<i>O. propinquus</i>	0.23	90.8	77.3	94.7	0.91	68.1	<0.001	475 lakes
<i>O. virilis</i>	0.58	92.8	94.0	91.1	0.89	21.6	<0.001	2729 lakes
Streams								
<i>O. rusticus</i>	0.49	94.3	93.2	95.4	0.92	39.5	<0.001	22 337 km
<i>O. propinquus</i>	0.34	91.9	88.6	93.6	0.90	58.9	<0.001	40 992 km
<i>O. virilis</i>	0.38	93.0	88.5	95.8	0.93	53.3	<0.001	39 573 km

Notes: Reported values are frequency of occurrence (Freq.), percentage of correct classification (CC), sensitivity (SE), specificity (SP), Cohen's kappa statistic (κ), Z score approximation, and associated P value. "Suitable" indicates the predicted number of lakes and total stream kilometers that are environmentally suitable for species establishment; optimal decision thresholds to predict species' occurrence were determined using ROC plots. (See *Methods* for further definitions of these parameters.)

rate compared to natural lakes, and lakes with no boat access were less likely to support *O. rusticus* populations. For stream sites, *O. rusticus* was predicted to occur in low-gradient channels with high baseflow, draining watersheds with high percentages of agricultural row crops, urban land use, and carbonate bedrock.

Impact of *O. rusticus* on native crayfishes

We found substantial changes in the occurrence of the three crayfish species when comparing historical and contemporary time periods. For *O. rusticus*, 17 lakes gained populations over time, while only two lakes lost populations. By contrast, *O. virilis* was lost in 29 lakes and was gained in only a single lake. There was little change in the number of lakes supporting *O. propinquus* (Table 2). Overall, the net change in lake occurrences over time was a 58% increase for *O. rusticus*, while *O. virilis* and *O. propinquus* declined by 78% and 8%, respectively. Significant changes in crayfish occurrence were also observed for streams. *O. rusticus* was gained in 58 stream sites over time, while only three sites lost populations. *O. virilis* was gained at 7 streams and lost at 50 streams, and similarly, 9 streams gained *O. propinquus*, while 30 streams lost this species (Table 2). On balance, the stream occurrence of *O. rusticus* increased by 500%, whereas the occurrence of *O. virilis* and *O. propinquus* decreased by 58% and 35%, respectively.

Changes in native crayfish occurrence corresponded with the invasion of *O. rusticus*, particularly in stream habitats (Fig. 3). *O. propinquus* was twice as likely to be extirpated in streams invaded by *O. rusticus* compared to streams that remained uninvaded (36.2% vs. 18.4%: Fisher's exact test, $P < 0.001$; Fig. 3B), and the frequency of *O. virilis* extirpation in streams was six times more likely for the same comparison (58.6% vs. 10.2%: Fisher's exact test, $P = 0.002$; Fig. 3D). No significant differences were found for either species in lakes (Fig. 3A, C), although *O. virilis* was extirpated in 76.5% of lakes invaded by *O. rusticus* compared to 50.0% of uninvaded lakes (Fig. 3C). With respect to patterns of species gain over time, the proportion of

streams and lakes that gained *O. propinquus* populations was considerably lower in those locations invaded by *O. rusticus* (Fig. 3A, B); no significant differences were observed for *O. virilis* (Fig. 3C, D). *O. propinquus* established in 18.8% of uninvaded lakes compared to zero invaded lakes (Fisher's exact test, $P = 0.023$, Fig. 3A), and was gained in four times more uninvaded vs. invaded streams (12.2% vs. 3.4%: Fisher's exact test, $P = 0.024$, Fig. 3B). In summary, *O. propinquus* populations were much less likely to be gained in streams and lakes between the historical and contemporary time periods compared to *O. virilis*.

Forecasting vulnerability to *O. rusticus* invasion

We combined predictions from the species distribution models with the retrospective results above (see Eqs. 1–3) to estimate the vulnerability of Wisconsin lakes and streams to *O. rusticus* invasion. According to the gains and losses of native species over time (Eqs. 1–3), the probability of native extirpation in the presence of *O. rusticus* was 0.33 in lakes and 0.43 in streams for *O. virilis*, and 0.06 in lakes and 0.27 in streams for *O. propinquus*. Notably, these estimates account for "background" patterns in native crayfish occurrence over time, or changes that are independent of *O. rusticus* invasion and likely the result of other drivers of environmental change.

By accounting for the entire invasion process, we found marked differences in the system vulnerability to *O. rusticus* invasion across native species and habitat types (Fig. 4). For *O. virilis*, 130 lakes (or 3.1%) have a >20% vulnerability to *O. rusticus* invasion, whereas for *O. propinquus*, 21 lakes (or 0.5%) have a >5% vulnerability to *O. rusticus* invasion (Fig. 4A, B). These predictions are mapped in Figs. 5A and B. In stream habitats, 4050 km (or 4.5%) for *O. virilis* and 2500 km (or 2.8%) for *O. propinquus* exhibit >20% vulnerability to *O. rusticus* invasion (Fig. 4C, D). These predictions are mapped in Figs. 5C and D. For either native species, 115 lakes (2.7%) and 5000 stream kilometers (5.5%) have a 25% likelihood of being

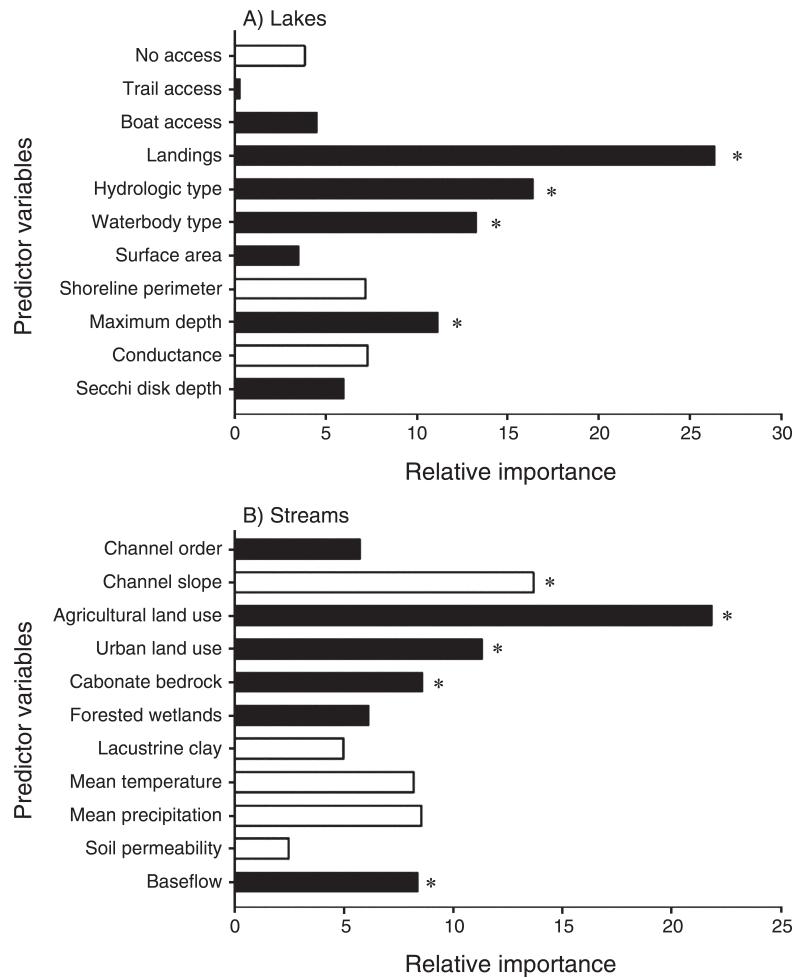


FIG. 2. Relative importance (%) of the environmental variables in the multi-response artificial neural network (MANN) for predicting *Orconectes rusticus* occurrence in (A) lakes and (B) streams. Positive contributions (i.e., increasing values of the variable enhance the probability of occurrence) are presented as solid bars, and negative contributions (i.e., increasing values of the variable decrease the probability of occurrence) as open bars. Asterisks indicate variables that significantly contribute to network predictions. Access variables refer to no (0) or yes (1), hydrologic type refers to seepage (0) or drainage (1), and water body type refers to natural lake (0) or impoundment (1).

* $P < 0.05$.

invaded by *O. rusticus* and causing native species extirpation. In all cases, lake and stream populations of *O. virilis* were more vulnerable to *O. rusticus* invasion compared to *O. propinquus*; a result due to both greater probability of occurrence (Table 1) and greater observed impacts by *O. rusticus* (Table 2).

For *O. propinquus*, vulnerability to *O. rusticus* invasion was generally low across lakes of northern Wisconsin, concentrated primarily in the Upper Wisconsin and Flambeau River Basins (north-central) (Fig. 5A). Risk from invasion was noticeably absent from lakes in central and southern Wisconsin. By

TABLE 2. Comparison of historical (pre-1985) and contemporary (post-1985) occurrences of crayfish (*Orconectes*) species in lakes and streams of Wisconsin.

Change (historical–current)	Lakes			Streams		
	<i>O. rusticus</i>	<i>O. propinquus</i>	<i>O. virilis</i>	<i>O. rusticus</i>	<i>O. propinquus</i>	<i>O. virilis</i>
No change (0–0)	16 (27%)	41 (69%)	22 (37%)	49 (41%)	49 (42%)	37 (31%)
No change (1–1)	24 (41%)	5 (8%)	7 (12%)	8 (7%)	30 (25%)	24 (20%)
Gain (0–1)	17 (29%)	6 (10%)	1 (2%)	58 (49%)	9 (8%)	7 (6%)
Loss (1–0)	2 (3%)	7 (11%)	29 (49%)	3 (3%)	30 (25%)	50 (43%)

Note: Reported values are the number of lakes/stream sites (with percentages in parentheses) for the three crayfish species.

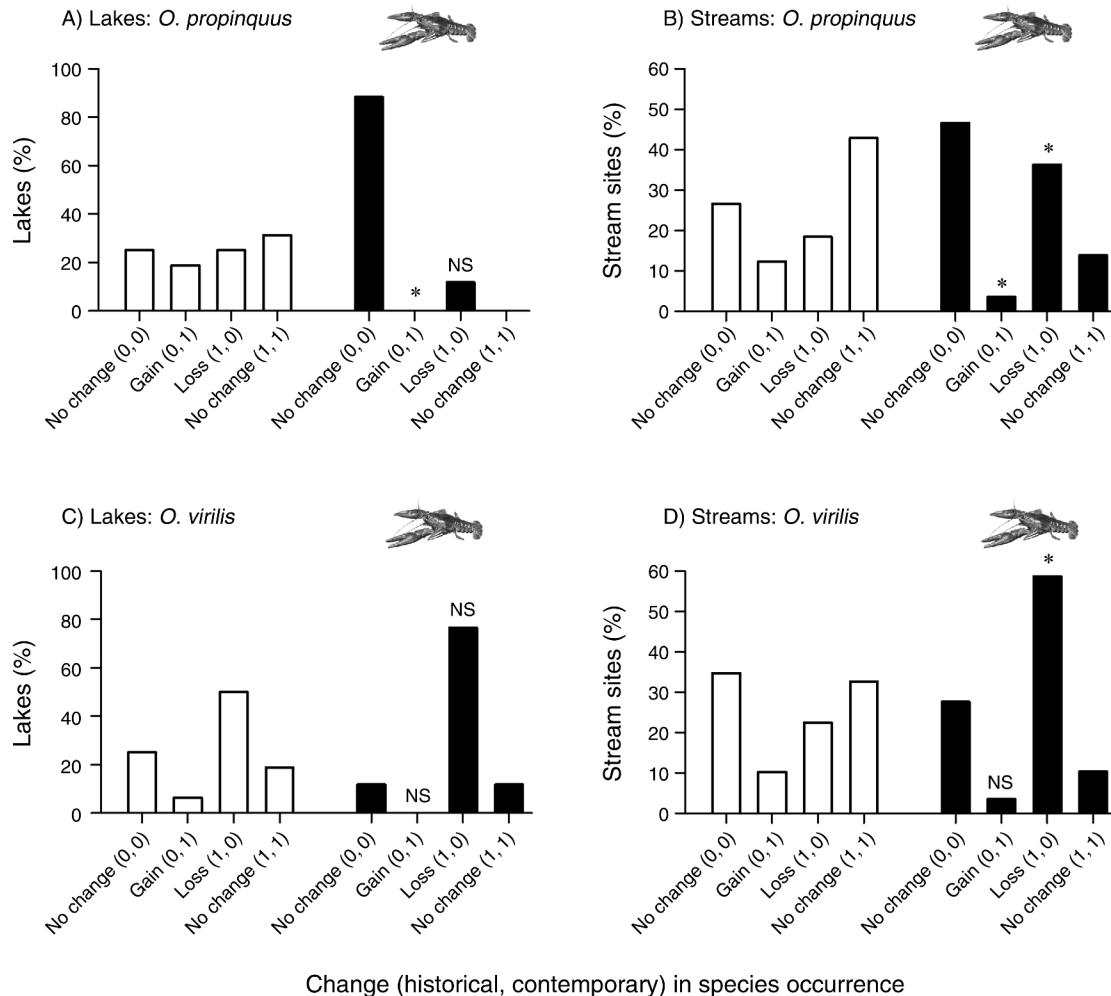


FIG. 3. Comparison of historical and contemporary occurrences of crayfish species in lakes and streams of Wisconsin. The bars represent colonization (gain) and extirpation (loss) between historical and contemporary time periods for (A, B) *O. propinquus* and (C, D) *O. virilis* at sites that were invaded (solid bars and indicated by crayfish photo) vs. uninvaded by *O. rusticus* (empty bars and indicated by no photo). The asterisks indicate significant differences between lakes/streams invaded vs. uninvaded by *O. rusticus* for the same category of change (historical, contemporary) in species occurrences. “No change (0,0)” and “No change (1,1)” refer to sites where the native species remained absent or present, respectively, between the historical and contemporary time periods.

* $P < 0.05$.

contrast, *O. virilis* lake populations are most vulnerable to *O. rusticus* invasion throughout Wisconsin, including in the Fox River Basin (southeast), Upper Chippewa River Basin and St. Croix River Basin (north-central), and the Duck-Pensaukee River Basin (north Lake Michigan Basin) (Fig. 5B). For streams, predicted invasion impacts on *O. propinquus* were highest in the Bad-Montreal Rivers (northwest Lake Superior Basin), Red Cedar, Fox, Upper Chippewa and Flambeau Rivers (north-central), Lower Wisconsin and Grant-Little Maquoketa Rivers (southwest), and Menominee and Brule Rivers (northeast Lake Michigan Basin) (Fig. 5C). *O. virilis* was predicted most vulnerable to *O. rusticus* invasion in streams of the Manitowoc-Sheboygan Rivers (north Lake Michigan Basin), Upper Rock River (south-central), Milwaukee River (southeast), Castle

Rock River (central) and Upper St. Croix River (Fig. 5D). Lake and stream probabilities of *O. rusticus* introduction and establishment and extirpation probabilities for *O. virilis* and *O. propinquus* are provided in the Supplement.

DISCUSSION

The idea that biological invasions are preventable is a dictum often repeated by natural resource managers, yet scientific tools to help managers more effectively undertake prevention efforts are sparse. To date, the implementation of management strategies to minimize the secondary spread of nonnative species is hindered by the simple facts that the landscapes to be managed are vast, there are numerous nonnative species, and resources available for prevention remain limited

(Simberloff et al. 2005). In an ideal world, ecologists would provide resource managers and conservation practitioners with timely information on the vulnerability of species invasions to the combined likelihood of introduction, establishment, and impact. This information would also be presented in a format that is immediately assessable to stakeholders (McNie 2007), and thus could be readily applied to help allocate limited funds effectively to the species most likely to invade and the ecosystems most vulnerable to impact (Vander Zanden and Olden 2008; Papeş et al., *in press*). Our study contributes to this goal by demonstrating the value of a probabilistic approach designed to predict the entire invasion process, from arrival to establishment and ecological impacts, and map ecosystem vulnerability, with the aim of informing on-the-ground management actions.

Despite the abundance of freshwater environments across Wisconsin, which by some estimates comprise one-fifth of the state's total area, 388 of 4200 surveyed lakes (~10%) and 23 523 of 90 360 stream kilometers (~25% of all mapped Wisconsin streams) are predicted to be suitable for both the introduction and establishment of *O. rusticus*. The habitats most susceptible to establishment included deep, drainage lakes with greater numbers of boat landings/ramps. Impoundments were predicted to be invaded at a higher rate compared to natural lakes, whereas lakes without boat access were less likely to support *O. rusticus* populations. These patterns highlight the key role of introduction "vectors" for predicting the likelihood of invasion. Anglers and the bait trade have been implicated in the introduction of *O. rusticus* throughout the midwestern United States (Taylor and Redmer 1996), and impoundments appear to be more susceptible to invasion compared to natural lakes, likely due to greater accessibility and disturbance regimes (Johnson et al. 2008). For stream sites, *O. rusticus* was predicted to occupy low-gradient channels with high baseflow, draining watersheds with high percentages of agricultural row crops, urban land use, and carbonate bedrock. Increasing urban land use is associated with enhanced opportunities for introduction from bait release and the biological supply and pet trades (Lodge et al. 2000, Puth and Allen 2005), and greater carbonate bedrock supports higher calcium concentrations that promote the growth, survival, and reproduction of crayfish (Cairns and Yan 2009). Low-gradient streams exhibiting more stable summer hydrology (i.e., baseflow conditions) may favor greater establishment success and enhanced opportunities for dispersal.

Widespread gains in *O. rusticus*-occupied systems paralleled sharp declines in both native congeners. *O. rusticus* exhibited a 58% increase in lakes (from 26 to 41 lakes) over time, whereas *O. virilis* and *O. propinquus* declined by 78% and 8%, respectively. These trends contrast those reported in lakes of south-central Ontario where net population losses from the early 1990s to mid-2000s were greater for *O. propinquus* (-15%) compared

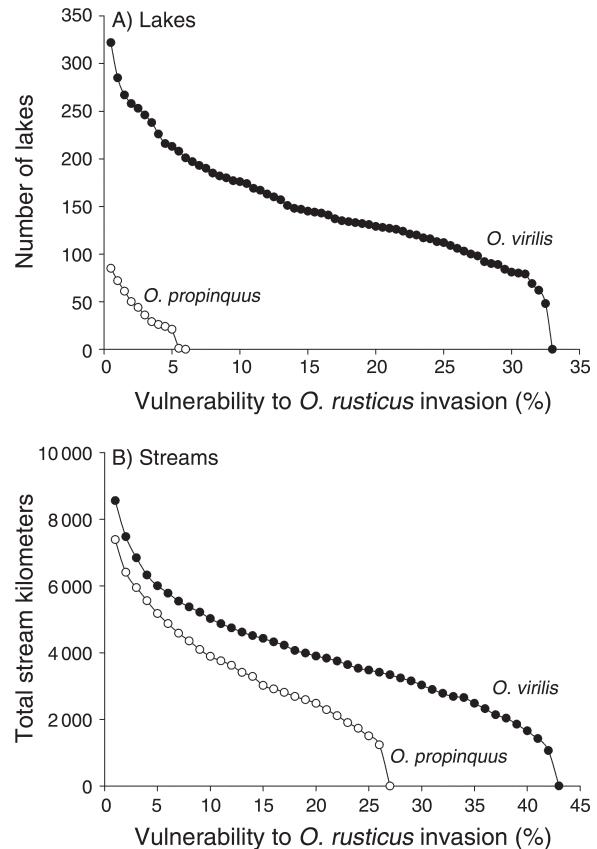


FIG. 4. The number of (A) lakes and (B) total stream kilometers considered vulnerable to *O. rusticus* invasion (introduction, establishment, and extirpation of native species) for *O. propinquus* (open circles) and *O. virilis* (solid circles). For the sake of clarity, data points for lakes exhibiting <0.5% vulnerability and streams exhibiting <1% vulnerability are not shown. For a particular level of vulnerability, the total number of lakes and stream kilometers at risk to *O. rusticus* invasion can be calculated (e.g., for *O. virilis*, 176 lakes have an invasion vulnerability of 10% or greater).

to *O. virilis* (-9%) (Edwards et al. 2009). Notably, *O. rusticus* is rare in this region, and exhibited declines similar in magnitude to native species, suggesting they are not a significant contributor to native species loss. Substantial changes in crayfish stream distributions were also evident: *O. rusticus* occurrence increased by fivefold, whereas the loss of *O. virilis* and *O. propinquus* exceeded one-half and one-third of their historical extents, respectively. The considerable declines of native *Orconectes* spp. in both lake and stream habitats over the past half-century is a matter of concern for the long-term persistence of these species.

Our historical comparison of crayfish occupancy suggests that *O. virilis* is more vulnerable than *O. propinquus* in response to *O. rusticus* invasion, and that stream reaches are more susceptible to native crayfish loss compared to lakes. *O. virilis* was six times and *O. propinquus* was twice as likely to be extirpated in streams invaded by *O. rusticus* compared to streams that

remained uninvaded. Similarly, *O. virilis* was extirpated in over three-quarters of lakes invaded by *O. rusticus* compared to half of the uninvaded lakes, whereas no difference was observed for *O. propinquus*. Multiple lines of evidence from laboratory and field studies further support the hypothesis that *O. rusticus* has greater impacts on *O. virilis* relative to *O. propinquus*. Laboratory experiments have demonstrated the dominance of *O. rusticus* over *O. virilis* in direct aggressive interactions and competition for shelter, whereas *O. propinquus* have been found to be intermediate in these interactions (Capelli and Munjal 1982). Competitive exclusion experiments have shown a dominance hierarchy defined by $O. rusticus > O. propinquus > O. virilis$ (Hill et al. 1993). Susceptibility to fish predation also varies greatly among the species. In mesocosm experiments, Hill and Lodge (1999) found that, in the presence of largemouth bass, *O. virilis* experienced the greatest mortality, followed by *O. propinquus* and *O. rusticus*, a result further supported by field experiments (DiDonato and Lodge 1993).

Our site-specific, probabilistic approach to predicting species invasions has direct utility for resource managers tasked with preventing the spread of *O. rusticus*. Model results identified 115 lakes (~3% of study lakes) and ~5000 stream kilometers (~6% of Wisconsin streams) that exhibited a >0.25 probability of introduction, establishment, and extirpation by *O. rusticus* of either native congener. This provides a tractable number of lakes and streams to prioritize for management action (Supplement), thus informing decisions regarding where and when resources would be most efficiently and effectively distributed (Vander Zanden and Olden 2008). Moreover, our results provide flexibility for stakeholders to identify priority sites for prevention efforts given a maximum level of acceptable risk (i.e., vulnerability) or based on budgetary/time restrictions (Fig. 4). For example, if a state agency deems a 30% probability of *O. rusticus* establishment and impact as acceptable, then management efforts should target 83 lakes and ~3000 stream kilometers (Fig. 5D). On the other hand, if a state agency was limited to managing 50 lakes due to funding or personnel considerations, then our model predictions suggest that they must tolerate invasion vulnerabilities up to 32%. Finally, our study quantified vulnerability based solely on two species of native crayfish, whereas *O. rusticus* also has demonstrable ecological impacts on macrophytes, benthic invertebrates, and fish (e.g., Olsen et al. 1991, Lodge et al. 1994, McCarthy et al. 2006, Rosenthal et al. 2006). Other measures of sensitivity to invasion could be incorporated into the estimation of ecosystem vulnerability and inform management actions.

Based on our findings, we highlight three potential management actions. First, public education and outreach could be targeted at high-risk locations (e.g., boat launches on drainage lakes and rivers) by increasing signage declaring the prohibited use of live crayfish for bait and

guiding boat inspection campaigns (Rothlisberger et al. 2010). In 1983, Wisconsin prohibited the use of crayfish as live bait and the introduction of live crayfish in inland waters; however, the impact of this law on slowing *O. rusticus* invasion is questionable. Waters containing highly valued sport fisheries can be further prioritized for prevention efforts given the likelihood of economic impacts associated with *O. rusticus* invasion (Keller et al. 2008). Second, those lakes identified at greatest risk of invasion could be used as sentinel locations for ongoing monitoring, increasing the chances of early detection by state and public surveys. Lake association groups should be engaged in this process, mirroring ongoing monitoring efforts by the public to detect other high-profile invaders such as zebra and quagga mussels. Third, voluntary or enforced catch-and-release programs for bass and sunfish could be implemented on those lakes most vulnerable to *O. rusticus* invasion, thereby helping to enhance the biotic resistance to establishment. For example, the Wisconsin Department of Natural Resources instated strict size and bag-limit regulations for smallmouth bass in Sparking Lake (Vilas County, Wisconsin) to assist manual trapping efforts to control the *O. rusticus* population. The combination of increased fish predation and intensive trapping resulted in population collapse, but not complete extirpation (Hein et al. 2007). Likewise, habitat enhancement to support bass and sunfish populations, such as installing log structures as fish habitat, in vulnerable lakes may also be a viable management strategy. Although fishery enhancement represents a novel management approach for invasive species prevention, careful consideration should be given to the potential consequences of such management actions for resident native crayfish (if present) and other native fauna.

Our study presents a general approach for assessing ecosystem vulnerability to the entire invasion process that is applicable to other nonnative species and regions. Greater availability of data and computer software has enhanced the opportunity for ecologists to develop distribution models for invasive species, though we recognize that ecological impacts of invasive species are difficult to predict and often remain poorly understood (Strayer et al. 2006, Pyšek et al. 2008). There are a number of approaches for estimating the probability of ecological impacts, ranging from intrinsic characteristics of nonnative species such as abundance, range size, and invasion history (e.g., Ricciardi 2003, Thiele et al. 2010) to extrinsic characteristics of the recipient ecosystems such as the presence/absence of sensitive species (e.g., Vander Zanden et al. 2004, Mercado-Silva et al. 2006) to probabilities of extirpation (this study). Qualitative or quantitative estimates of impacts could be readily incorporated into the framework presented here.

In conclusion, our study provides a perspective on the role of ecologists in informing management actions for invasive species. Although research on predicting the spread of invasive species through the use of habitat suitability (or ecological niches) models has surged over

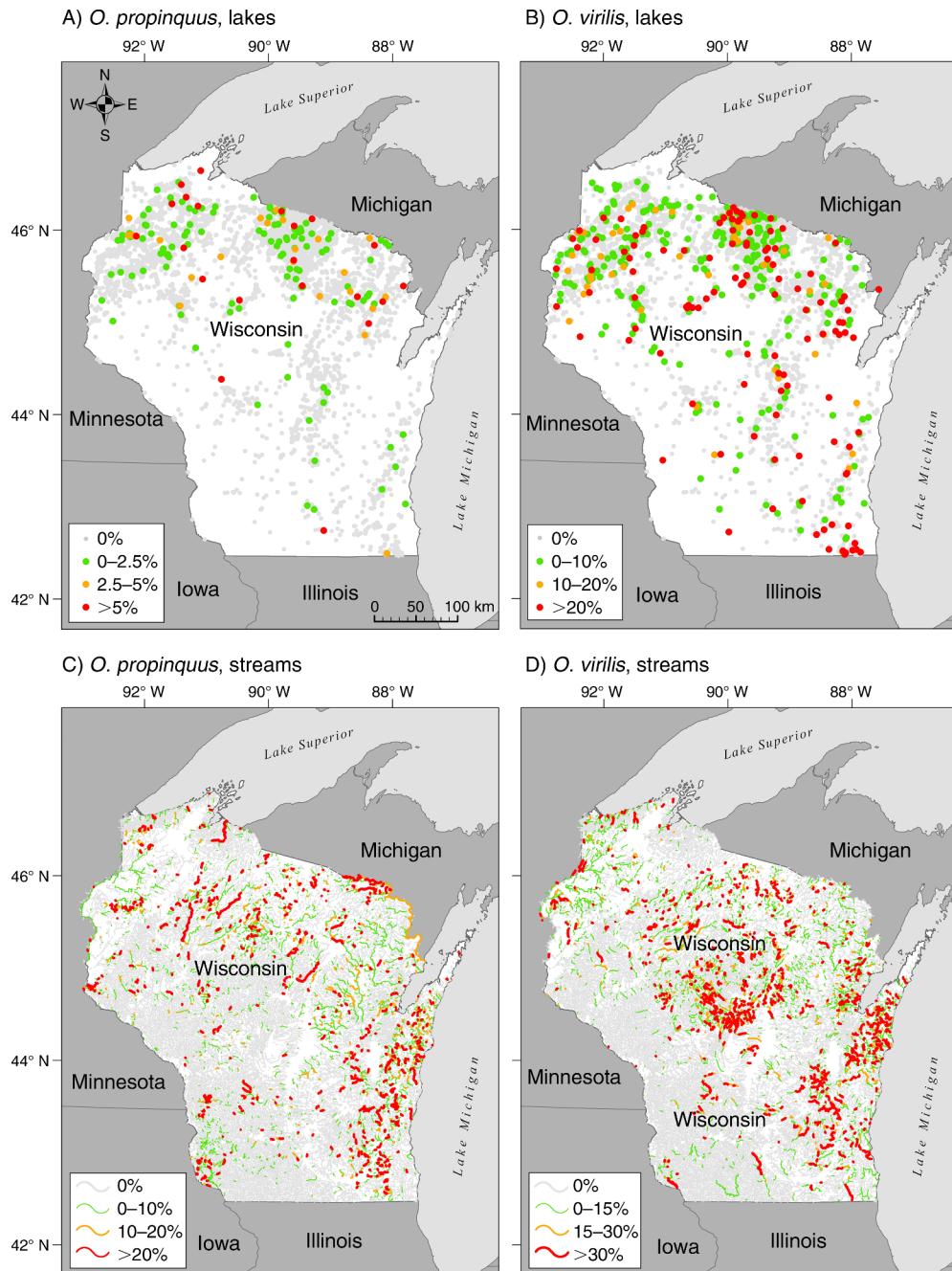


FIG. 5. Mapped vulnerability of (A, C) *O. propinquus* and (B, D) *O. virilis* to the combined probability of *O. rusticus* introduction, establishment, and the subsequent extirpation of native crayfish for lakes and streams of Wisconsin. Downloadable Google Earth files are available online: (<http://www.fish.washington.edu/research/oldenlab/outreach.html>).

the last decade (reviewed in Elith and Leathwick 2009), the application of these models for guiding on-the-ground resource management and invasive species prevention efforts remains poorly developed. This stems in part from disconnects between the spatial grain of model predictions (large scale) vs. management actions (local scale), as well as between where academic results are published (scientific journals) and the sources used by

stakeholders responsible for invasive species prevention (Arlettz et al. 2010). To help address this communication gap, our *O. rusticus* vulnerability assessment has been made available on an online aquatic invasive species management tool.⁶ These products are available to

⁶ (<http://www.aissmartprevention.wisc.edu>)

resource managers and concerned citizens in Wisconsin, and are designed to communicate site-specific information about vulnerability to invasion by aquatic invasive species with the ultimate goal of helping resource managers allocate their management efforts more effectively.

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SUPPLEMENT

Site-specific predictions of *Orconectes rusticus* establishment and vulnerability of *O. propinquus* and *O. virilis* in lakes and streams of Wisconsin (*Ecological Archives* A021-117-S1).