

## Research Article

## Weak non-linear influences of biotic and abiotic factors on invasive macrophyte occurrence

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**Citation:** Fleming JP, Wersal RM, Madsen JD, Dibble ED (2021) Weak non-linear influences of biotic and abiotic factors on invasive macrophyte occurrence. *Aquatic Invasions* 16(2): 349–364, <https://doi.org/10.3391/ai.2021.16.2.09>

**Received:** 24 April 2020

**Accepted:** 7 December 2020

**Published:** 19 February 2021

**Handling editor:** Carla Lambertini

**Thematic editor:** Elena Tricarico

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### Abstract

Aquatic plants (macrophytes) are important components of freshwater ecosystems and serve numerous functions, both physical and biological, that help to structure aquatic communities. However, invasive macrophytes may negatively alter ecosystem properties. Non-native invasive species have been identified as a major cause of biodiversity loss and the increasing prevalence of invasive species has prompted studies to help understand their impacts and to conserve biodiversity. Studying mechanisms of invasion also gives ecological insight into how communities are structured and assembled. This study examined a set of potential factors influencing invasion including biotic resistance, exposure, and water depth using mixed-effects models on macrophyte survey data collected from twenty-nine lakes across the United States. The results of this study indicated that biotic resistance measured from native species richness, exposure due to fetch, and water depth interact, often in non-linear ways to influence probability of invasive species occurrence at a given location; however, models explained a relatively low percentage of variation in probabilities. It is likely that strong predictive principles governing macrophyte invasions do not exist, at least among comparisons across a range of ecosystem types and environmental conditions. However, ecologists should continue to search for general patterns within definable ecosystem units to increase understanding about factors contributing to invasibility.

**Key words:** invasive species, aquatic plant ecology, niche theory, biodiversity, disturbance, biotic resistance

### Introduction

Invading plants have become pervasive in a vast number of ecosystems and their negative impacts on ecosystem processes have been studied by numerous researchers (Parker et al. 1999; Mack et al. 2000; Hershner and Havens 2008). Invasive species may alter ecosystem functioning, in some cases disrupting ecosystem services, food web interactions, and native species diversity (Shea and Chesson 2002). Species invasions are one of the least reversible forms of human caused degradation and not only impact

local ecosystems, but also local economies (Pimentel et al. 2005; Rahel 2007; Rahel and Olden 2008). For this reason, identifying the mechanisms governing invasions has become an urgent need (Dietz and Edwards 2006; Kueffer et al. 2013).

Development of a general theory of invasions would be helpful in developing both mitigation strategies to lower invasion risk, and management plans to enhance biodiversity conservation. Unfortunately, ecological theory has struggled to find general principles that predict these invasions (Dietz and Edwards 2006). Still, many hypotheses have been presented to identify potential mechanisms that lead to ecological invasion. Of these hypotheses, two major themes have emerged. First, the probability of successful invasion may be dependent on a species' biological traits (e.g., high reproductive output, competitive superiority, dispersal ability; Cadotte and Lovett-Doust 2001; Kolar and Lodge 2001; Cadotte et al. 2006; Mathukrishnan et al. 2018). One of the most widely hypothesized mechanisms of invasion success (or lack of success) is biotic resistance. This hypothesis, based in niche theory, predicts that as more species accumulate in an area, available environmental space (micro habitat) decreases and therefore increased interspecific interference (i.e., competition) is better able to exclude invaders (Petruzzella et al. 2018). In contrast, successful invasion may be a property of the community or environment where an introduction occurred (Levine 2000; Chadwell and Engelhardt 2008; Jacobs and MacIsaac 2009). This second theme of environmental determinants of invasibility is likely the most intuitive for synecologists because it explicitly considers interactions among and between organisms and their environment in a given location.

Early hypotheses in invasion ecology promoted the idea that biological diversity may mitigate potential invasion success (e.g., Elton 1958). Although diversity of a community may be an important determinant of invasion success, results of experimental and observational studies have often been inconclusive and differed across spatial scales of study (e.g., Kennedy et al. 2002; Stohlgren et al. 2003; Fleming et al. 2015; Pulzatto et al. 2019). Fridley et al. (2007) reviewed evidence for native-exotic richness relationships and found that, in general, small scale studies reported a negative relationship whereas large scale studies reported the opposite, and these findings align with other more recent studies as well (e.g., Pulzatto et al. 2019). These conflicting results, known as “invasion paradox” (*sensu* Fridley et al. 2007), open new doors for inquiry into the causes of these seemingly scale-dependent patterns.

Given the ostensibly conflicting results of previous studies, it may be that a general theory of invasibility does not exist (Colautti et al. 2004; Hierro et al. 2005; Mitchell et al. 2006). However, this may be true in the theoretical domain only for comparisons among ecosystem types, where communities are structured through diverse mechanisms due to

environmental heterogeneity, as opposed to comparisons within the same model system (e.g., forest *vs.* grassland *vs.* lake; Kueffer et al. 2013). This is especially important in aquatic environments which are particularly prone to invasion but have received less study than terrestrial systems (Shea and Chesson 2002; Capers et al. 2007; Petruzzella et al. 2020). Species invasions are highly non-random in freshwater ecosystems (Strayer 2010), yet ecologists who specialize in aquatic systems, and particularly aquatic plants, will note that there are limited studies regarding the development and testing of invasion hypotheses (e.g., biotic resistance) for invaded aquatic plant assemblages in lentic aquatic systems that cross a variety of regions (Capers et al. 2007; Thomaz and Michelan 2011; Fleming and Dibble 2015).

Aquatic plants (macrophytes) provide important ecosystem services (Carpenter and Lodge 1986), and although native macrophytes are beneficial in aquatic ecosystems, invasive aquatic plants can cause significant ecological and economic harm. High densities of macrophytes such as invasive *Myriophyllum spicatum* and *Hydrilla verticillata* interfere with foraging and spawning of some fish species (Valley and Bremigan 2002; Theel and Dibble 2008). Canopy forming plants reduce light transmittance and oxygen diffusion into the water column which can lead to anoxic zones unsuitable for other aquatic organisms (Caraco and Cole 2002). Because of differences in the physiology of introduced plants, nutrient cycles may be altered in some systems (Templer et al. 1998; Angeloni et al. 2006). In addition, invasive aquatic plants may hybridize with native species, threatening native diversity (Boylen et al. 1999; Houlahan and Findley 2004; Moody and Les 2007). They may also interfere with recreational opportunities and navigation, and can block water intakes. Artificial reservoirs and impoundments may facilitate invasion (Havel et al. 2005; Johnson et al. 2008), and therefore, understanding the factors that lead to increased probability of invasion is of high importance to ecologists and aquatic resource managers alike.

Numerous factors influence the distribution of aquatic plants and may also contribute to species invasion. Abiotic factors such as water depth and clarity (Ogdahl and Steinman 2015; Verhoeven et al. 2020) may lead to stresses on aquatic plants due to light attenuation, along with surface and benthic disturbances caused by wind exposure (Koch 2001; Pulzatto et al. 2019). Because disturbance is thought to contribute to invasions by opening niche space or altering resource availability that allows pre-adapted species to succeed (Davis et al. 2000; Havel et al. 2005; Facon et al. 2006), potential stresses and disturbances (such as interactions among water depth, clarity, and wind exposure in lakes and reservoirs) may make these ecosystems especially susceptible to aquatic plant invasion. In fact, it has been suggested that interspecific competition may play a lesser role in structuring submersed macrophyte assemblages because of environmental influences such as those caused by increased stress or disturbance

(McCreary 1991; Wilson and Keddy 1991). These environmental influences may alter or become synergistic with factors such as biotic resistance from native species in determining invasion success (Thomaz et al. 2003; Capers et al. 2007; Strayer 2010; Muthukrishnan et al. 2018).

The goal of this research is to investigate hypotheses that the probability of invasion by an exotic aquatic plant is a function of biotic factors, namely biotic resistance from native species (measured here by native species richness), abiotic factors including water depth and exposure (measured by fetch) as a potential disturbance, or a combination of these biotic and abiotic factors at a small local (sampling point) scale. These three factors are all potential factors in major hypotheses that attempt to explain invasion success (Mitchell et al. 2006), and also possibly influence the distribution of aquatic plants within lentic aquatic systems. Based on previous studies of biotic resistance, a negative association is expected between probability of an invasive species occurring at a small scale and number of native species occurring at that site (Muthukrishnan et al. 2018). In addition, probability of invasion is expected to increase with disturbance (e.g., exposure due to fetch; Pulzatto et al. 2019), but may be non-linear based on intermediate disturbance hypothesis (assuming interspecific biotic interaction also occurs). We investigated these hypotheses using a combination of field data, geographic information systems, and statistical modeling to address whether native species richness, water depth, fetch, and/or interactions between abiotic factors (depth and fetch) contributed to the probability of invasive species occurrence at a small (point) scale, whether relationships were positive, negative, or non-linear, and additionally to what degree each of these factors contributed to the probability of invasive species occurrence.

## Materials and methods

### *Study Areas and Design*

The study area spanned the conterminous United States, where lakes and reservoirs (hereafter lakes;  $n = 29$ ) were surveyed once at various times from 1997 to 2011 (Figure 1; Supplementary material Table S1). Lakes represented a variety of temperate freshwater environments ranging from 7–36,000 ha and nine freshwater ecoregions (Appalachian Piedmont 1, Chesapeake Bay 2, Colorado 1, Columbia Glaciated 3, Laurentian Great Lakes 8, Lower Mississippi 7, St. Lawrence 1, Upper Mississippi 3, and Upper Missouri 3). Lakes were publicly accessible and used for various recreational activities (e.g., water-sports, fishing). Like many publicly accessible lakes, these may have exhibited increased risk of species introductions due to human use, and therefore were also in need of a management plan for detection and control of problematic species. Each lake was originally surveyed for a specific project goal to obtain a baseline



**Figure 1.** Location of 29 lakes surveyed in the conterminous United States for aquatic invasive plants from 1997–2011.

of invasive and native species occurrence and distribution using the point-intercept method (Madsen 1999). Time since invasion was unknown when each survey was conducted and could not be determined; however, a snapshot of the macrophyte composition across this diversity of lakes allowed investigation of occurrences of invasives relative to biotic and abiotic environmental factors.

For each lake, a grid of points was generated in a GIS and integrated with field GPS to navigate to each point by boat. Point spacing varied and scaled by lake area to ensure representative sampling in each lake. At each sample point, a rake was tossed and retrieved to collect plants occurring at that location. Rake tosses generally collect plants directly under the boat and are dragged 1–2 m along the bottom. This method allowed a large number of samples to be collected and insured that all plants occurring in an area are accounted for. Each plant collected was identified to species and recorded as present (1) at the location.

Water depth at each point was collected using depth sonar to the nearest 0.1 ft and converted to meters. Fetch, the distance over which wind can travel across open water, was used as a measure of potential wind exposure (Mason et al. 2018). To calculate fetch, angle of wind direction was collected for each day in the given year of the lake survey (if available) at the nearest weather station (NOAA weather stations accessed through [weatherunderground.com](http://weatherunderground.com)). If wind direction data were not available for the survey year, we used the closest year available. Angular measurements of wind direction were rounded to the nearest 30-degree angle and the mode calculated to estimate prevailing wind direction for the entire year.

Prevailing wind directions were used to calculate fetch distance with 10-meter resolution raster surface following Finlayson (2005). Using this method, radials ( $n = 9$ ) spaced every three degrees on each side of the input degree of wind direction is weighted by the cosine of angle deviation. Effective fetch for each pixel was calculated using:

$$L_f = \sum x_i * \cos\gamma_i / \sum \cos\gamma \quad (3.1)$$

where  $L_f$  is the effective fetch,  $x_i$  is the distance to land for a given angle, and  $\gamma_i$  is the deviation angle. The resulting raster surface contains fetch distances for each location and accounts for potential variation and uncertainty in prevailing wind direction. ArcGIS (ESRI 2018; Redlands, CA, USA) was used to extract fetch values to each survey point for use in analysis.

### *Modeling*

To estimate probability of an invasive aquatic macrophyte occupying a given sampling location, generalized linear mixed models with environmental (abiotic) and native species richness (biotic) data were used and their performances were compared to select models that included the most appropriate variables and to infer the relative importance of biotic resistance, water depth, and exposure. Models were developed using the lme4 package in R (R Development Core Team 2012), and all models were fit using the binomial family and a logit link function (presence/absence of invasive species was coded as a binary response) with lake as a random effect to account for potential spatial autocorrelation within lakes and differing species pools among lakes.

Model terms specific to the original hypotheses (native species richness, depth, and fetch as determinants of the probability of occurrence of an invasive species) were selected. Survey data used in this study represent a snap-shot of species present at the time of sampling and abiotic factors that represent average conditions throughout a year. For presence of an invasive species, NSPP (native species richness), NSPP<sup>2</sup>, DEPTH (water depth), DEPTH<sup>2</sup>, FETCH (effective fetch distance), FETCH<sup>2</sup>, and the interaction term DEPTH × FETCH were used. Quadratic terms for native species richness, depth, and fetch were included to test for potential non-linear effects on probability of occurrence of invasive species. The interaction between depth and fetch was also included because of potential modification of effects by one term on the other. For the set of models, a global model was included which contained all terms relevant to the hypotheses, and a null (intercept only) model. All relevant combinations of these model terms were fit to separate models because we made no *a priori* assumptions that a particular subset of these model terms would provide more explanatory power than another.

Native species richness, depth, and fetch values were centered and standardized by 2 standard deviations (Mean = 0, Stand. Dev. = 0.5; Gelman 2008) to improve model convergence and parameter interpretation, and to avoid large differences in scale due to the ranges of values. Only sites with depth > 0 and where a plant occurred (whether native or invasive) were included in the analysis. Because all growth forms of aquatic plants encountered in the survey were included, using only sites where depth > 0 insured that submersed species could potentially co-occur there, even if an emergent plant was present (for example, if an emergent plant was recorded on the shoreline at depth = 0 it was excluded from analysis, but included if recorded in deeper water). Likewise, sampled sites where no plants occurred were excluded because it is possible that no plants can occur at those locations due to environmental limitations.

Seventeen models were created (including a null model). All models converged after variables were standardized. Performance of each model was evaluated by calculating Pseudo- $R^2$  values and model comparisons were made using Akaike Information Criterion (AIC). Akaike weights ( $w$ ) were calculated to measure model support and model selection uncertainty. Using ranked AIC scores and Akaike weights, a 95% confidence set of models was selected and the relative importance of each variable was estimated. Model averaging was used for models contained within the 95% confidence set to estimate model parameters, decrease model selection uncertainty, and evaluate the relative strength of each predictor (Burnham and Anderson 2002).

## Results

Surveys were performed in 29 lakes containing invasive macrophytes between 1997–2011 (Figure 1; Table S1). Ninety-one species were identified including 14 species considered invasive (Table S2). A total of 10,486 surveyed points were included in the dataset. Of these, 4,169 (approx. 40%) had at least one species and had a depth greater than zero. Invasive plants occurred at 1,846 of these sample points. Total number of points surveyed averaged 361.6 (SD = 425.1) per lake ranging from 62 to 1,614. Total number of points used in the analysis ( $N = 4,113$ ) averaged 141.8 (SD = 120.7) per lake ranging from 24 to 636. Sites with depth greater than zero and where plants occurred had a mean depth of 2.26 m and a mean fetch of 761.2 m. Sites where an invasive species occurred had 2.2 native species on average with mean depth 2.1 m and mean fetch 657.1 m.

Seven models were included in the 95% confidence set which included the global model (Rank = 2; Table 1). Native species richness, quadratic native species richness, depth, fetch, quadratic fetch, and the interaction between depth and fetch were included in the highest ranked model (Rank = 1) which was also the most parsimonious model (Rank = 1,  $\Delta AIC < 2$  and contained the least number of model parameters). However, model performance was

**Table 1.** Model results for factors influencing probability of occurrence of an invasive macrophyte from 29 lakes surveyed across the United States, 1997–2011.

Model <sup>a</sup>	$K^b$	AIC <sup>c</sup>	$\Delta AIC^d$	$w_i^e$	Pseudo- $R^2$	Rank
NSPP + DEPTH + FETCH + NSPP <sup>2</sup> + FETCH <sup>2</sup> + DEPTH × FETCH	6	3875.301	0.000	0.478	0.03	1
NSPP + DEPTH + FETCH + NSPP <sup>2</sup> + DEPTH <sup>2</sup> + FETCH <sup>2</sup> + DEPTH × FETCH	7	3877.051	1.750	0.199	0.03	2
NSPP + FETCH + NSPP <sup>2</sup> + FETCH <sup>2</sup>	4	3878.432	3.131	0.100	0.02	3
NSPP + DEPTH + FETCH + NSPP <sup>2</sup> + DEPTH <sup>2</sup> + FETCH <sup>2</sup>	6	3879.138	3.837	0.070	0.03	4
NSPP + DEPTH + NSPP <sup>2</sup>	3	3879.331	4.030	0.064	0.02	5
NSPP + DEPTH + FETCH + NSPP <sup>2</sup> + DEPTH <sup>2</sup> + DEPTH × FETCH	6	3880.467	5.166	0.036	0.03	6
NSPP + DEPTH + NSPP <sup>2</sup> + DEPTH <sup>2</sup>	4	3881.331	6.030	0.023	0.02	7

<sup>a</sup> Model terms are native species richness (NSPP), water depth (DEPTH), and fetch distance (FETCH). Input variables were all standardized to 2 SD.

<sup>b</sup>  $K$  = no. of parameters in model.

<sup>c</sup> Akaike's Information Criterion Score

<sup>d</sup>  $\Delta AIC$  = the difference between the AIC value of the best supported model and successive models.

All models in the 95% confidence model set are included

<sup>e</sup>  $w_i$  = Akaike model weight.

**Table 2.** Model averaged parameter estimates of invasive species occurrence, from 29 lakes surveyed across the United States, 1997–2011.

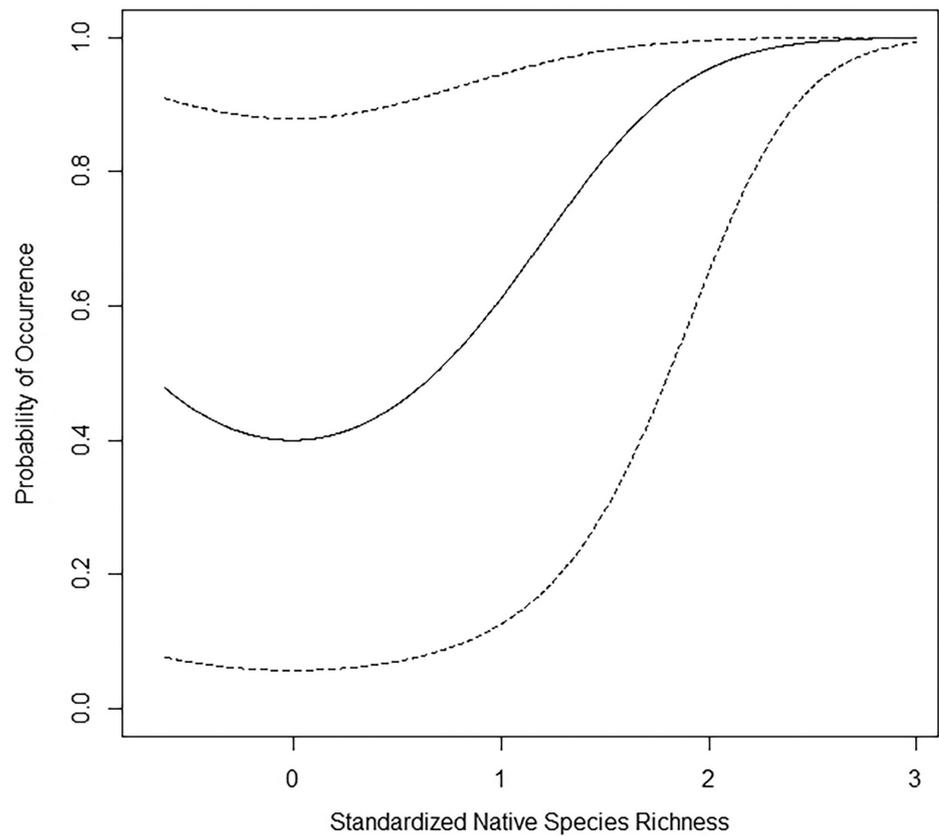
Model Term <sup>a</sup>	Parameter Estimate	Standard Error	95% Confidence Limit		Relative Importance
			Upper	Lower	
NSPP <sup>2</sup>	0.837	−0.123	0.597	1.078	0.970
NSPP	0.032	0.128	0.282	−0.218	0.970
FETCH <sup>2</sup>	0.208	−0.088	0.035	0.380	0.883
FETCH	−0.353	−0.194	−0.733	0.027	0.883
DEPTH <sup>2</sup>	−0.030	−0.076	−0.179	0.120	0.329
DEPTH × FETCH	−0.399	−0.203	−0.797	0.000	0.713
DEPTH	−0.207	−0.149	−0.499	0.084	0.870

<sup>a</sup> Model terms are native species richness (NSPP), water depth (DEPTH), and fetch distance (FETCH). Input variables were all standardized to 2 SD

relatively low, accounting for only a small proportion of variance (Pseudo- $R^2 = 0.03$ ). In each of the top two models ( $\Delta AIC < 2$ ), all terms were significant at  $P < 0.1$  except for depth and quadratic depth in the global model. Although depth and quadratic depth were included in the 95% confidence set, depth was not significant in 4 of the 6 models that included it and quadratic depth was not significant in any of the 4 models that included it ( $P > 0.1$ ).

Based on averaged parameter estimates and relative importance calculated from AIC weights for the 95% confidence set, native species richness and quadratic native species richness were the most important variables included in the model (Table 2). Fetch and quadratic fetch were the next most important followed by depth. Although quadratic depth was included in the model averaged estimates, it had the least importance.

Based on model results, biotic resistance (i.e., influence of native species richness) had a small, but statistically significant impact on the probability of an invasive species co-occurring at a survey point, but its influence changed at a threshold of native species richness (Figure 2). There was a slight decline in probability of occurrence of an invasive species with increasing native species richness but this relationship changed to a positive

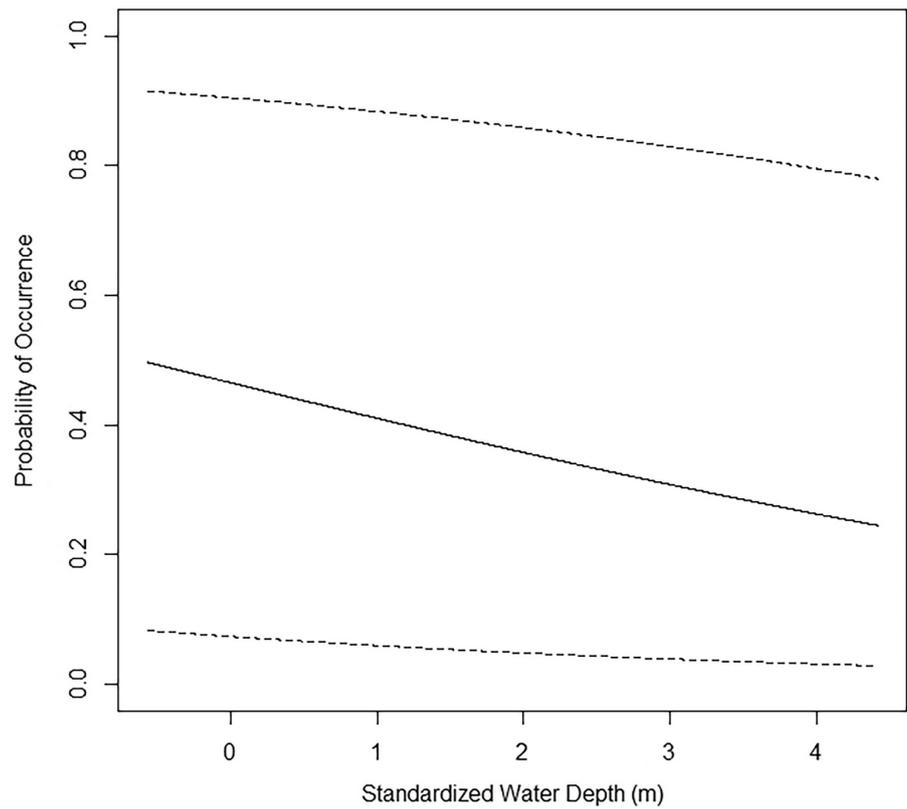


**Figure 2.** Probability of occurrence of an invasive species as a function of quadratic standardized native species richness based on the best model fit (Rank = 1) with 95% confidence intervals (dashed lines). Native species richness values were standardized to 2 standard deviations (For original values of native species richness, 1 SD = 1.79).

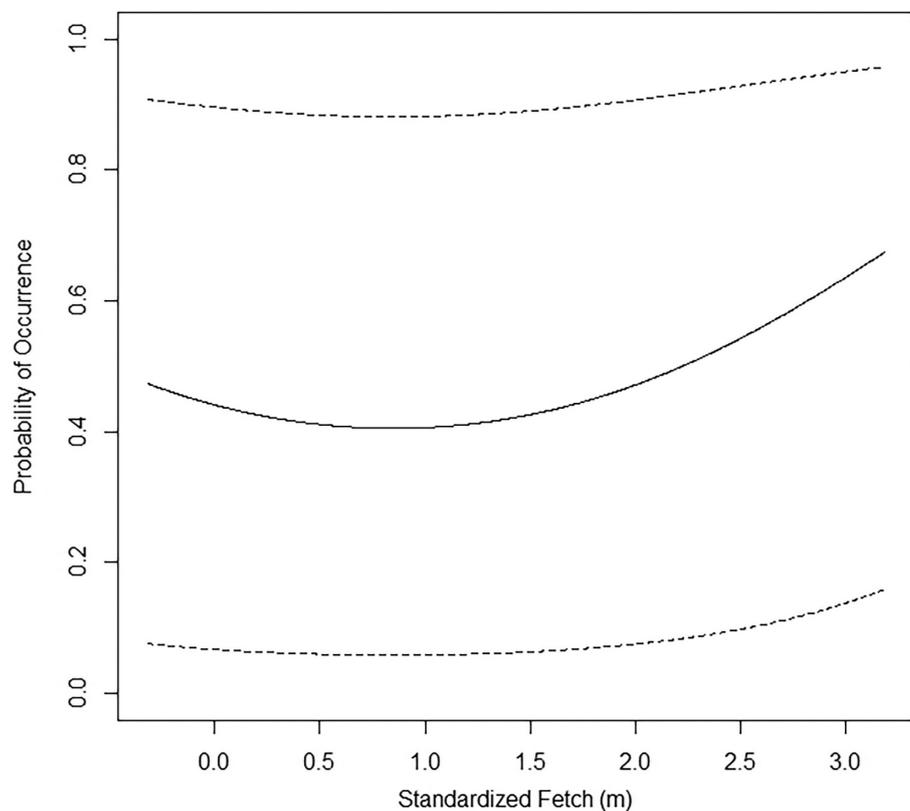
association as native species richness increased beyond the mean value. Water depth also appeared to be a significant factor and as depth increased, probability of occurrence of an invasive species decreased (Figure 3). Fetch and quadratic fetch were significant, indicating that as exposure increased, probability of occurrence of an invasive species decreased. However, beyond two standard deviations (1 SD = 1200 m), probability of occurrence increased with increasing exposure (Figure 4). Furthermore, the interaction between depth and fetch was significant, supporting the hypothesis that exposure becomes less important as depth increases; this is presumably because wind exposure has less direct impact on benthic areas in deeper water. These results suggest that potentially stressful or disturbed conditions, along with competition from native species, may act synergistically but in a non-linear way to affect colonization by an invasive macrophyte.

## Discussion

Results of this study suggest there is weak or no support that biotic resistance from native macrophytes, water depth, or wind exposure influence the probability of invasive species occurrence in littoral areas of the U.S. lakes and reservoirs analyzed in this study. Model performances were relatively



**Figure 3.** Probability of occurrence of an invasive species as a function of water depth based on the best model fit (Rank = 1) with 95% confidence intervals. Water depth values were standardized to 2 standard deviations (For original values of water depth, 1 SD = 1.95 m).



**Figure 4.** Probability of occurrence of an invasive species as a function of quadratic fetch based on the best model fit (Rank = 1) with 95% confidence intervals. Fetch distance values were standardized to 2 standard deviations (For original values of fetch distance, 1 SD = 1200 m).

poor (Pseudo- $R^2$  0.02–0.03), indicating a large amount of unexplained variation in predicting probability of occurrence. Recent studies have found a similar lack of evidence for point scale biotic resistance and generally weak effects of environmental factors in explaining patterns of species invasion (e.g., Muthukrishnan et al. 2018).

Disturbance is widely regarded as a mechanism influencing invasions and it has been suggested that fetch, acting as disturbance, can indeed limit species occurrence or diversity in some reservoirs (Thomaz et al. 2003; Pulzatto et al. 2019). Although we did not assess the relationship between disturbance and overall species diversity, we did find a weak relationship between invasion probability and degree of exposure (fetch distance), a surrogate for disturbance. However, the relationship was non-linear and only negatively impacted invasion probability at relatively low exposures (i.e., shorter fetch distances). This result merits further study because intermediate disturbance hypothesis predicts greater species diversity at intermediate levels of disturbance. Taken in an ecosystem context, if disturbance facilitates invasion, and biotic resistance increases with diversity as has been hypothesized, a positive relationship between invasion probability and disturbance might be expected at lower and higher degrees of disturbance (Connell 1978). In addition, disturbances may open environmental space which can be exploited by species pre-adapted to those spaces or with inherent physiological traits that allow them to establish without interspecific interaction from natives (e.g., phenological differences; Davis et al. 2000).

We found no strong support that biotic resistance via native species richness decreased probability of occurrence of an invasive species, and it is likely the relationship is non-linear (i.e., does not hold true for locations with high native species richness). This should receive further investigation because most studies thus far in native/exotic richness relationships have simply identified a positive or negative relationship and have led to the popular notion of an “invasion paradox” (Fridley et al. 2007). However, results of this study indicate that even at small scales the relationship may not in fact be linear (or exist at all). Because this study used occurrence of invasive species at a point scale and all lakes in this study had at least one invasive species, multi-scale analysis was not possible. However, it is expected that species richness increases with area (Gleason 1925). Therefore, at larger scales and greater species richness, these results suggest there would indeed be a positive relationship between invasive species occurrence and native species richness. Thus, the invasion paradox may only reveal artifacts of a situation where environmental heterogeneity increases with area, species accumulation occurs at an expected rate, and non-random patterns indicate a particular phase in the relationship between invasion and native species richness.

There are several reasons these patterns could occur, even at small scales. First, with a limited number of native species, specialists (in a relative sense)

may be more suitably adapted to exploit limited resources in areas where they occur. However, as resources become plentiful and less limiting, or as environmental heterogeneity increases number of microhabitat types, invasive species may be able to co-exist with high numbers of native species (Pulzatto et al. 2019). With increasing species richness, likelihood of facilitation also increases. For example, as number of species increases, the physical complexity of the environment may also increase as species seek to exploit different volumes of space in the water column (Capers et al. 2007). This may result in increased likelihood that propagules of invasive species encounter reduced mobility through normal dispersal processes, become trapped, and have enough time to establish. Alternatively, as species richness increases, the likelihood of indirect effects such as apparent facilitation or competition may also increase and result in successful colonization by an invader (Thouvenot et al. 2013).

Another potentially significant component of biotic resistance not considered in this study is herbivory. Alofs and Jackson (2014) performed a meta-analysis of biotic resistance in freshwater environments and found that consumption through herbivory, not direct competition, was the driving factor. It is possible that generalist herbivores in some, possibly all, of our study sites play a direct role in where invasive species have been able to establish. The presence or absence of herbivores could explain the underlying mechanism for the weak non-linear relationship of invasion probability with native species richness that we detected. Herbivory may also play an indirect role through facilitation that manifests as biotic resistance (Petruzzella et al. 2017, 2020).

These results also lead to new questions with respect to which resources may be important in understanding invasion success. Although this study simply classified species as invasive or native, it may also be prudent to research species specific attributes within native and invasive communities to identify species and characteristics that influence invasion success in a more precise context (e.g., functional diversity, physical structure, phenology). In addition, density and biomass of plants (which naturally vary among species) may be a more important factor than richness per se (Petruzzella et al. 2018, 2020). Capers et al. (2007) found this in five of the six invasive aquatic plants they studied in Connecticut lakes. Likewise, recent studies have highlighted the importance of using fine-scale niche models incorporating species specific traits to predict impacts of invasion on native communities, as opposed to studying impacts based on whether a species is classified only as an invasive (Verhoeven et al. 2020).

Ecological effects of invasive species may either increase or decrease through time (Strayer et al. 2006; Gherardi 2007; Hawkes 2007). The invader or invaded community may evolve as species composition shifts toward species insensitive to the invaders, masking the real influence of native richness on invasiveness. The diversity of lakes and reservoirs used

in this study, and their distribution, may in fact also contribute to the limited support for the hypotheses we tested. Muthukrishnan and Larkin (2020) studied not only the relationship between native and invasive species, but also the influence of invasive macrophytes on biotic homogenization among lakes in Minnesota. Their results highlight the importance of studying species invasions at a community level while not only classifying communities based on richness and abundance of native or invasive species, but also the turnover of diversity among macrophyte communities across both space and time. The limitations of using a surveyed snap-shot of macrophyte communities in our study precludes this type of analysis, but future studies should take it into consideration.

There is still currently little predictive knowledge regarding what general factors or mechanisms lead to species invasions (Kueffer et al. 2013; Hierro et al. 2005). Nonetheless, it is imperative that future research efforts continue to test hypotheses for mechanisms that allow introduced species to establish. It is likely that understanding species invasions will depend on the context of model systems (Kueffer et al. 2013), and that universal principles across ecosystem types do not exist. However, ecologists should continue to search for general patterns within definable ecosystem units that increase understanding about factors contributing to invasibility.

## Acknowledgements

We would like to thank all individuals that contributed time and effort in collecting plant data used in this study. We would also like to thank Gary Ervin and Jerry Belant for reviewing earlier versions and four anonymous reviewers for suggestions that greatly improved this manuscript.

## Funding Declaration

The authors received no specific funding for this work. Contributed data were compiled for this study for the purpose of meta-analysis. Resources used during analysis were provided by the Forest and Wildlife Research Center and Department of Wildlife, Fisheries, and Aquaculture at Mississippi State University.

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#### Supplementary material

The following supplementary material is available for this article:

**Table S1.** Biotic and Abiotic characteristics of 29 lakes surveyed across the United States, 1997–2011.

**Table S2.** Species list for 29 lakes surveyed across the United States, 1997–2011.

This material is available as part of online article from:

[http://www.reabic.net/aquaticinvasions/2021/Supplements/AI\\_2021\\_Fleming\\_etal\\_SupplementaryTables.xlsx](http://www.reabic.net/aquaticinvasions/2021/Supplements/AI_2021_Fleming_etal_SupplementaryTables.xlsx)