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Environmental filtering and competitive exclusion drive biodiversity-invasibility relationships in shallow lake plant communities

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Abstract

1. Understanding the processes that influence the diversity of ecological communities and their susceptibility to invasion by exotic species remains a challenge in ecology. In many systems, a positive relationship between the richness of native species and exotic species has been observed at larger spatial (e.g., regional) scales, while a negative pattern has been observed at local (e.g., plot) scales. These patterns are widely attributed to (1) biotic interactions, particularly biotic resistance, limiting

invasions in high-diversity locations, producing negative local-scale relationships, and (2) native and exotic richness covarying at larger spatial scales as a function of environmental conditions and heterogeneity, producing positive large-scale relationships. However, alternative processes can produce similar patterns and need to be critically evaluated to make sound inferences about underlying mechanisms.

2. We aggregated a large dataset of aquatic vegetation surveys from 1,102 Minnesota shallow lakes collected over 13 years to quantify spatial and temporal patterns of community composition. Using those data and additional information on environmental conditions we evaluated evidence for four distinct mechanisms that could drive patterns of native and exotic species richness: biotic resistance, competitive exclusion, environmental filtering, and environmental heterogeneity.
3. We found the classic pattern of a negative native-exotic richness relationship at local scales and a positive relationship at lake scales. However, we found no evidence for local-scale biotic resistance; instead, competitive exclusion by invasive species appeared to reduce native species richness after locations became invaded. Evaluating the influence of environmental filtering and heterogeneity, we found that native and exotic species occupied somewhat different niches. Invaders were less sensitive to environmental gradients and more tolerant of a wider range of conditions. This segregation of habitat preferences alone could produce a negative local native-exotic richness relationship and a positive regional pattern without the involvement of biotic interactions.
4. *Synthesis:* Our findings conflict with established expectations, which come from research predominantly conducted in terrestrial ecosystems. This illustrates the

importance of explicitly evaluating underlying mechanisms in diversity-invasibility research and for comparisons across different types of ecosystems. Identification of different drivers of diversity also has direct implications for decisions about management of freshwater plant communities.

Keywords: Invasion ecology, Biodiversity, native-exotic richness relationship, biotic resistance, competitive exclusion, environmental filtering, heterogeneity, aquatic plants

Introduction

The relationship between the diversity of ecological communities and their propensity to be invaded by exotic species has been heavily debated (Levine & D’Antonio 1999; Levine 2000; Wardle 2001; Kennedy *et al.* 2002; Fargione & Tilman 2005). Much research, particularly modeling and small-scale experiments, has supported a negative relationship between diversity and invasibility. However, at larger (e.g., regional) scales the opposite pattern is frequently observed, with more diverse communities having more exotic species (Levine & D’Antonio 1999; Stohlgren *et al.* 1999; Cleland *et al.* 2004). This scale-dependent shift in the native-exotic richness relationship (NERR) remains difficult to explain, with multiple processes potentially interacting to produce overall patterns. At the same time, invasive species are a global ecological threat (*MEA* 2005, Bellard et al. 2016); thus, improving understanding of biodiversity-invasibility relationships is important for supporting conservation and management.

A common explanation for scale-dependent NERR differences is that separate processes drive local and regional patterns (Levine & D’Antonio 1999; Stohlgren *et al.* 1999). It has been posited that at local scales high diversity confers biotic resistance to invasion (Kennedy *et al.*

2002; Fargione & Tilman 2005), but that at broader scales, incorporation of new habitats that are favorable for native and invasive species alike increases diversity of both in parallel (Levine & D'Antonio 1999; Naeem *et al.* 2000). However, further work has highlighted other processes that may influence NERRs (Fridley *et al.* 2007). Spatial heterogeneity in environmental conditions may support positive NERRs (Davies *et al.* 2005) by increasing avenues for coexistence (e.g., Chesson 2000; Tilman 2004). The strength or direction of a local-scale NERR can also shift as a function of productivity, disturbance, or environmental gradients (Davies *et al.* 2007; Belote *et al.* 2008). For example, invaders that have broader environmental tolerances or prefer less productive conditions may occur, on average, in less diverse localities (e.g., Paavola, Olenin & Leppäkoski 2005) because those conditions tend to correlate with lower diversity. In such cases, negative NERRs may arise through a sampling effect without the need for any particular biotic interaction to be involved.

The management implications of an NERR can differ depending on its underlying mechanism(s). For example, a negative NERR resulting from diversity-driven biotic resistance would argue for efforts to create or maintain diversity to pre-empt invasion. In contrast, if such patterns are a result of competitive exclusion by the invader, efforts to increase diversity may offer little protection against invasion. At the regional scale, if a positive NERR arises because invasive and native species share environmental preferences, then the most resource-rich environments may be at the greatest risk of invasion. Alternatively, if heterogeneity is the driving mechanism for an NERR, the most variable locales may be most vulnerable.

Even in a single system, NERRs are likely to arise from multiple processes, especially across local and regional scales (Fridley *et al.* 2007). However, there is a growing consensus that biotic interactions tend to be key drivers of community structure at local scales while environmental conditions become more influential as spatial scale increases (Fridley *et al.* 2007). Thus a more mechanistic perspective that evaluates multiple processes at multiple scales is needed. Such studies are logistically difficult to conduct as experiments, but large-scale, long-term monitoring datasets offer an alternative means to address these dynamics.

Here we focus on four mechanisms that could influence native or exotic species diversity, three of which we could evaluate at multiple spatial scales. *Biotic resistance* to invasion has long been considered a potential benefit of diverse communities (Elton 1958) and is well-supported by experimental work (Stachowicz, Whitlatch & Osman 1999; Levine 2000; Naeem *et al.* 2000; Kennedy *et al.* 2002; Fargione & Tilman 2005), though the universality of this mechanism has been questioned (Capers *et al.* 2007). Invasive species can also *competitively exclude* resident species after establishment (Casas, Scrosati & Luz Piriz 2004; Yurkonis, Meiners & Wachholder 2005), producing a pattern of native and invader richness similar to biotic resistance but with a different temporal signature, i.e., loss of native diversity following invasion rather than lower likelihood of subsequent invasion in diverse locales. Thirdly, *environmental filtering* influences species' abilities to establish and persist in particular localities. Alignment of preferences between natives and invaders could produce positive regional NERRs, while competitive interactions determine local-scale outcomes (Davies *et al.* 2005; Cavender-Bares *et al.* 2009). Alternatively, if invaders have wider environmental tolerances than natives (Richards *et al.* 2006; Vazquez 2006), a negative local NERR could be produced by invaders establishing in marginal habitat with few native species. Lastly, *environmental heterogeneity* in conditions or habitat types is a key mechanism supporting overall diversity that can increase both native and invader richness (Davies *et al.* 2005). This effect is likely to become more pronounced over larger spatial scales as greater variability is accrued (Huston 1999).

In this study, we used an exceptionally large data set of aquatic vegetation surveys from Minnesota shallow lakes to characterize NERRs at local and regional scales and examine evidence for alternative mechanisms. Using data from sites with repeated sampling over time we tested for (1) native species richness conferring *biotic resistance* to invasion and (2) invaders *competitively excluding* native species after establishment. We used environmental data to (3) correlate native and invasive species richness with abiotic conditions to evaluate if *environmental filtering* acted similarly on both groups and (4) evaluate how native and invasive species responded to *environmental heterogeneity* as a potential driver of regional scale diversity.

Methods

Survey data

Vegetation data for the study were aggregated from 1,662 grid-based, point-intercept surveys conducted by the Minnesota Department of Natural Resources in 1,102 shallow lakes from 2002–2014. The lakes represent a broad range of shallow lakes across the state with varying levels and types of nearby land use, human activity, and management. Surveys were conducted with a thrown rake that was pulled along the benthic surface to collect vegetation. All macrophytes (aquatic vascular plants and macroalgae) were identified to species or lowest feasible taxon. For simplicity we refer to all taxa as “species,” i.e., including those identified only to genus (See Supplementary Table 1 for a full list of taxa). The number of survey points varied between lakes (61.7 ± 37.9; mean ± SD), scaling with lake size.

We used these data to calculate species richness at point and lake scales. We distinguished species considered invasive in Minnesota based on established lists (Milburn, Bourdaghs & Husveth 2007; USDA 2016), and six were present in our surveys: *Lythrum salicaria* (purple loosestrife), *Myriophyllum spicatum* (Eurasian watermilfoil), *Phalaris arundinacea* (reed canarygrass), *Potamogeton crispus* (curly-leaf pondweed), *Typha angustifolia* (narrow-leaf cattail), and *Typha* × *glauca* (hybrid cattail). In cases where identification was resolved to a taxonomic level encompassing both invasive and native species (e.g., *Typha* sp. is ambiguous with the native *Typha latifolia*) we conservatively assumed the native form. Similarly, while invasive European genotypes of *Phragmites australis* occur in Minnesota, lineages were not discriminated in our dataset. Thus we treated all *P. australis* as comprising the widespread native subspecies *P. australis* ssp. *americanus*. In a small number of lakes, invasive *Typha* was recorded both to species and to the grouped category "*T. angustifolia* or × *glauca*." We counted these as representing only a single invader species.

Using these data, we evaluated NERRs at local (individual sampling point) and regional (whole-lake) scales. All analyses were performed in R version 3.1.2 (R Core Team 2014). Using point-level data, we estimated the relationship between native and exotic species richness. To account for the integer nature of the response variable, we used a generalized linear model (GLM) with a Poisson error distribution (using the 'glm' function from the stats package) and evaluated significance using the 'summary.glm' function (this approach was used for all GLMs). We then calculated lake-level richness values and constructed a separate GLM for lake-level native and exotic species richness.

Biotic interaction mechanisms

To calculate the potential for native diversity to confer biotic resistance to invasion and for invasive species to competitively exclude native species, we analyzed temporal patterns in lakes that had been repeatedly sampled over multiple years. Because temporal analyses would be sensitive to changes in sampling effort or locations, we only included data from lakes where the same grids of sampling points were used among years; this comprised 179 lakes, each with 2-9 interannual surveys (mean = 3.22).

To quantify biotic resistance, we compared the relationship between native species richness and the probability of a sampling point becoming invaded at subsequent sampling times. Because invasive species themselves can potentially increase the likelihood of further invasions (via an invasional meltdown; Simberloff & Von Holle 1999) or increase resistance (Henriksson *et al.* 2016), we focused only on initial invasions, excluding all locations that were already invaded. While the potential effects of initial invaders on secondary invasions are of interest, the number of such records was insufficient to address this issue. Additionally, some locations may have been generally unsuitable for vegetation, producing zero values for richness that could artificially reduce estimates of species richness, thus we excluded from our analysis points lacking vegetation at any sampling time. We also excluded locations from lakes that did not contain any invasive species at the initial sampling point. Invasion in such cases would require colonization from another lake, a highly stochastic process that could bias estimates. We analyzed data from the remaining sites using a generalized linear mixed effects model (from the binomial family). Whether or not an uninvaded point was subsequently invaded was used as the response variable, native species richness was treated as a fixed effect, and lake identity was included as a random effect. The model was fit using the ‘glmer’ function from the lme4 package (Bates *et al.* 2015) and using the “bobyqa” optimizer (with the argument control=glmerControl(optimizer="bobyqa")); significance was evaluated using a parametric bootstrap. This approach first estimates the full mixed model with the variable of interest included, then a reduced model with the variable removed; change in fit between models was assessed using the ‘PBmodcomp’ function (from the pbkrtest package with 1000 simulations; Halekoh & Højsgaard 2014). We also evaluated biotic resistance at the lake scale, evaluating how whole-lake native species richness influences the probability of becoming invaded using a GLM from the binomial family.

To evaluate whether invaders competitively excluded native species, we estimated rate of change in native species richness for each sampling point by estimating a linear regression for native species richness with sampling year as the single independent variable. For each model, the coefficient for the time parameter provides an estimate of the average yearly change in species number, with negative values indicating species loss. Differences in average coefficient values were compared between sites that were invaded and those that remained uninvaded through all surveys, also using a linear model. We again excluded locations where no vegetation was recorded during any survey and used a linear mixed effect model (with the ‘lmer’ function from the lme4 package) to compare rates between invaded and uninvaded sites while accounting for lake as a random effect. Statistical significance was again evaluated using the same parametric bootstrap approach as above. Competitive exclusion was also evaluated at the lake scale using a standard linear model (with the “lm” and “summary.lm” functions) to compare rates of change in species richness between invaded and uninvaded lakes.

Environmental mechanisms of invasion

To investigate how environmental conditions influenced patterns of diversity, we collected data on a range of environmental parameters at both point and lake scales. During surveys, point-level measures of bottom depth and Secchi depth were recorded. We used GLMs to estimate influence of depth and Secchi depth on native and invasive species richness, assuming Poisson distributions for species richness. We calculated these relationships at point and whole-lake scales (using mean values across points). Because depth and Secchi depth were correlated, we used separate models to independently evaluate their relationships with richness rather than including both parameters in a single analysis. The total possible richness of invasive species was much lower than that of native species, thus we conducted analogous analyses using invader presence as a binomial response in GLMs to test for environmental preferences of invasive species in general. Additionally we calculated standard deviations (SD) of depth and Secchi depth for each lake as measures of within-lake heterogeneity and used these data to estimate GLMs testing relationships between lake heterogeneity and native and invasive species richness at the lake scale, again assuming Poisson distributions for species richness. We also conducted an additional analysis of invader response with invader presence as a binomial response in a GLM.

To estimate additional environmental parameters for lakes, we aggregated data from two publicly available sources. We collected measurements of lake area and long-term average Secchi depth (m) for ~11,000 lakes derived from remote sensing data by the University of Minnesota Remote Sensing and Geospatial Analysis Laboratory (Olmanson, Bauer & Brezonik 2008; Olmanson, Brezonik & Bauer 2014). In addition, the Minnesota Pollution Control Agency (MPCA) manages a large dataset of direct lake measurements (~6 million records) collected by state, local, and citizen-based organizations on a wide variety of environmental parameters. We focused on five parameters likely to influence macrophyte distribution that were sampled in large numbers of lakes: pH, conductance (µS), total Kjeldahl nitrogen (N; mg/L), total phosphorus (P; mg/L), and chlorophyll *a* concentration (µg/L). Data were heterogeneous in space and time and collected by groups with differing technical proficiency, thus we took several steps to assure data quality. We limited environmental measures to only those collected since the year 2000 and during the growing season (June–September). To remove data likely to be erroneous we calculated mean and SD for each variable across all lakes and excluded any samples with values >5 SD from the mean. Because SD was sometimes strongly influenced by extreme outliers, we then recalculated SD with outliers removed and repeated the process a second time. This left us with 139 lakes in the dataset with values for all parameters. For these lakes we aggregated all measurements of a given parameter into a single mean.

For surveyed lakes with data for all environmental parameters, we used GLMs with multiple fixed effects to identify environmental conditions associated with native or invasive species. GLMs included 6 environmental parameters as potential predictors (N, P, pH, conductance, chlorophyll *a*, and Secchi depth). Native and invasive species richness and invasion status were modeled as responses in separate analyses, using a Poisson error distribution for richness measures and invader presence/absence as a binomial response.

Results

Overall patterns

Vegetation data comprised 56,134 sampling points from 1,662 surveys in 1,102 lakes. Across surveys, 150,318 individual vegetation samples were identified to 172 taxa (generally species; Table S1). Invasive species were identified in nearly half of the lakes (546) and invaded lakes spanned the entire range of native species richness (Fig. 1). The average number of species at a sampling point was 2.69 ± 1.83 (mean ± SD) and within a lake was 10.13 ± 7.23. Consistent with the “invasion paradox” (Fridley *et al.* 2007), we observed a negative NERR at the point scale and a positive relationship at the whole-lake scale (Table 1, Fig. 2).

Biotic resistance

At the local scale, we observed no significant relationship between species richness and the probability that a location would become invaded in the subsequent survey (Table 1, Fig. 3a), i.e., no support for local-scale biotic resistance. Results showed high variability with many lakes showing positive relationships, while others displayed negative relationships, indicating very noisy data with little pattern rather than a consistent but small effect. At the lake scale, we also did not see a significant relationship between species richness and invasion, though the parameter estimate was positive (0.028; Table 1). Thus, while non-significant, the trend followed the opposite pattern, with higher species richness being associated with a greater propensity for invasion. However, this pattern may be largely noise.

Competitive exclusion

Our analyses did provide support for competitive exclusion of native species by invaders at the local scale (Table 1). Based on parameter estimates of the linear mixed effects model, species richness decreased at invaded sampling points by 0.02 species per year (after accounting for lake-to-lake differences; Fig. 3b), while at uninvaded points richness increased by 0.08 species per year. At the lake scale, there was no significant difference in rates of richness change between invaded and uninvaded lakes; richness tended to increase in both over time (Table 1).

Environmental filtering

At the local scale, both native and invasive species richness significantly varied with environmental conditions (Table 1; analyses using binomial GLMs based on invasive species presence generally show the same directionality and significance patterns as the analyses using invader richness, results can be seen in Table S2 and figures S1 and S2 in online Supporting Information). Native and invasive species had significant, but opposing, relationships with depth (Fig 4a-b); native richness decreased with greater depth, while invasive richness increased, though less strongly. Both native and invasive richness increased with water clarity (Fig 4c-d), but this relationship was much stronger for native (z =40.17) than invasive species (z = 3.897), suggesting weaker light limitation in invaders. At the lake scale, native richness increased with mean lake depth and mean Secchi depth (Fig 4e,g). Invasive richness did not significantly differ with either parameter (Fig 4f,h), again suggesting broader tolerance.

Analyzing the larger set of environmental variables, we identified many significant relationships between lake-level environmental parameters and species richness (Table 1), but the significant variables differed between native and invasive species. All environmental conditions except N were significant predictors of native richness. In contrast, only pH and Secchi depth were significant predictors of invasive richness. Furthermore, directionality of some strong predictors of richness were reversed between native and invasive species. For example, native richness had a strong negative relationship with P, while the pattern was positive (though not significant) for invasive species. The opposite pattern was seen for Secchi depth; invasive richness decreased and native richness increased with greater clarity. Conductance and chlorophyll *a* were significant negative predictors of native richness and negatively correlated but not significant for invaders. The generally weaker responses of invasive richness to environmental conditions suggest that invaders had broader environmental tolerances. At the lake scale these patterns are potentially confounded by the general correlation of average depth and lake size. However, both lake size and average depth (as opposed to depth at a particular location), are likely proxies for overall habitat variability, which in turn drives increased native species richness rather than a direct influence of average depth or size. Thus the general pattern of stronger environmental constraints on native species than invaders exists independent of whether lake size and average depth are confounded.

Heterogeneity

Within-lake heterogeneity in depth and Secchi depth were significant positive predictors of native richness (Table 1, Fig 5a,c) but had no influence on invasive richness (Table 1, Fig 5b,d). This further supports the contention that invaders have lower sensitivity to environmental conditions.

Discussion

The aquatic plant communities we studied showed a strong negative relationship between native and invasive species richness at local (point) scales, but a positive relationship at regional (lake-wide) scales, matching patterns observed in numerous systems. However, when we evaluated mechanisms that could generate these patterns, we found varying levels of support, indicating that not all mechanisms were of equal importance. Similarly, no mechanism dominated and any given factor explained only a small amount of the patterns observed in native and invasive species richness. In contrast to many terrestrial systems (Naeem *et al.* 2000; Kennedy *et al.* 2002; Levine, Adler & Yelenik 2004), we found no evidence for local-scale biotic resistance. Our results also indicate a strong influence of environmental constraints on local-scale richness patterns, counter to general expectations that environmental filtering becomes more important at broader spatial scales (Fridley *et al.* 2007). Our findings illustrate that similar NERR patterns can be produced by different underlying mechanisms that can be difficult to discriminate. These alternative mechanisms may have very different implications for conservation and management of aquatic plant communities, underscoring the value of applying a mechanistic lens to evaluating patterns of community structure and diversity.

Strong, opposing roles of environmental drivers on native and invasive species

Contrasting patterns of negative NERRs at local scales and positive NERRs at regional scales have been seen in a variety of systems; we saw similar patterns in Minnesota aquatic plant communities. While it is recognized that multiple processes can influence NERRs, there is a general expectation that biotic interactions dominate at local scales but are supplanted by abiotic determinants at broader scales (Fridley *et al.* 2007). Our data do not support this prediction. Rather we found that environmental conditions were relatively important predictors of richness at regional *and* local scales while effects of biotic interactions were relatively weak. However, there was still substantial unexplained variance that may be influenced by environmental factors not considered as part of this study or by alternative ecological mechanisms.

Native and invasive species were sensitive to different environmental factors; in some cases even showing opposing responses to the same environmental gradients. For example, native richness was associated with lower water depth and P while invasive richness was associated with greater depth and P. For water clarity, native and invasive species both showed positive relationships at the local scale, but the relationship was weaker for invasive species.

These divergent preferences suggest that native and invasive species occupied somewhat different niches. Such niche segregation alone could produce a negative NERR without biotic interactions being involved.

The patterns we observed indicate that invasive species gained advantage over native species under more eutrophic conditions. This is presumably due to these species being better adapted to exploit higher resource availability and tolerate lower light levels (Nichols & Shaw 1986; Woo & Zedler 2002). Alternatively, it is also possible that poor water quality increased with greater human activity, and that human activity was the proximate cause of greater invasion rates via increased transmission opportunities.

Furthermore, while greater environmental heterogeneity was associated with increased richness of native species—consistent with a large body of ecological theory and literature (Pickett & Cadenasso 1995; Larkin, Bruland & Zedler 2016)—there was no such response by invasive species. This suggests that native species were more specialized to depth and light niches within lakes, while invasive species occupied broader niches and were thus able to exploit more marginal habitat. However, our analyses were limited to water depth and Secchi depth; it is possible that invaders may have exhibited greater responsiveness to heterogeneity in other environmental factors. Greater responsiveness to increased resource availability and broader environmental tolerances appear to be attributes of successful invasive plants in general (Davis, Grime & Thompson 2000; Zedler & Kercher 2004), and global drivers of change reinforce these advantages (Thompson & Davis 2011). In northern shallow lakes, recent findings point to persistent, anthropogenic shifts to more nutrient-rich, turbid alternative states (Ramstack Hobbs *et al.* 2016). Our findings suggest these changes will exacerbate aquatic plant invasions.

Invasive species win biotic interactions—competitive exclusion but not biotic resistance

How new invasions affect native plant communities depends on biotic interactions between resident native vegetation and invading species. We analyzed repeated surveys in the same locations to investigate biotic interactions and found mixed support for their importance. After sampling locations were invaded, native species richness tended to decrease over time, while uninvaded locations gained species. This supports the competitive exclusion hypothesis, i.e., that invaders reduce local-scale diversity by displacing native species. In contrast, when we evaluated biotic resistance, we found no evidence that more-diverse sites were less likely to be subsequently invaded. A caveat is that invasions are highly stochastic processes punctuated by relatively few invasion events (Mack *et al.* 2000; Simberloff 2009). Furthermore, it is difficult to resurvey precise locations over multiple years and imperfect detection may confound species' presence/absence records (Chen *et al.* 2013). These factors can result in noisy datasets and as such, the likelihood of type II errors (false negatives) may be particularly high and the ability to detect a signal low. Yet our ability to still identify competitive exclusion despite such noise suggests that our general approach is valid and that biotic resistance is likely weaker or potentially absent in this system, though it is difficult to make a direct comparison of process strengths. Thus while we found evidence of influential biotic interactions at the local scale, as expected (Fridley *et al.* 2007), we did not observe biotic resistance, which is often considered to be the key driver for a negative NERR (Levine *et al.* 2004; Fargione & Tilman 2005). Instead we found statistically significant evidence for competitive exclusion, which is less often cited as a driver of negative NERRs. Though the effects we observed were relatively modest, on the order of one more species being lost per decade in invaded sites relative to uninvaded sites, and there was high variability with many individual sites and lakes exhibiting the opposite pattern.

Over time, biotic resistance and competitive exclusion can produce similar negative NERR patterns. Studies in which richness is examined at only a single time point are inherently unable to discriminate these two processes. Yet the two mechanisms have different implications for conservation and management. A system with strong biotic resistance will be resilient to invasions (Naeem *et al.* 2000; Fargione & Tilman 2005) and managing for diversity can minimize risk. But where biotic resistance is weak and competitive exclusion likely, uninvaded communities are vulnerable and biodiversity will not reduce invasion risk.

The combination of broader environmental tolerance of invasive species and the potential for competitive displacement of native species may provide an important pathway for invasion. By taking advantage of marginal habitat for native species, invaders can establish in new areas without facing competition. Once established, propagule pressure can then promote spread into nearby habitat preferred by native species (Lockwood, Cassey & Blackburn 2005). Propagule pressure from nearby sources will far exceed that associated with rare long-distance dispersal events (Simberloff 2009) and could swamp effects of biotic resistance (Thomsen *et al.* 2006). This "leapfrogging" of invasive plants from marginal to preferred habitat has been demonstrated in invasion of European *Phragmites australis* in North America, which spreads across the landscape via highway corridors and anthropogenic habitat (Lelong *et al.* 2007; Taddeo & De Blois 2012), providing propagules that can then invade intact natural wetlands and displace native species (Price, Fant & Larkin 2014; Fant, Price & Larkin 2016). The importance of environmental conditions in determining native and invasive species richness suggest that management of those factors may be a key strategy for limiting invader establishment.

At the larger spatial scale of whole lakes, our findings more closely match expectations from other systems (Levine & D'Antonio 1999; Davies *et al.* 2005; Fridley *et al.* 2007). Our lake-scale analyses showed no evidence of biotic resistance or competitive exclusion, instead native and invasive species richness increased in concert. This is consistent with NERRs not being driven by biotic interactions at large spatial scales but instead broader environmental, historical, or biogeographic factors (Ricklefs 2004; Fridley *et al.* 2007; Cavender-Bares *et al.* 2009). Native species richness increased with environmental heterogeneity, which aligns with the expectation that the inclusion of broader environmental conditions drives regional-scale diversity patterns (Levine & D'Antonio 1999; Davies *et al.* 2005; Fridley *et al.* 2007), though we did not observe a similar pattern for invasive species with the environmental factors we evaluated. Nonetheless, even if invasive species have broad environmental tolerances and are not influenced by heterogeneity, stochastic processes could still lead to increased invader richness at larger spatial scales, resulting in a positive NERR (Fridley, Brown & Bruno 2004).

Is biotic resistance "all dry"?

While our results regarding the relative importance of biotic interactions vs. abiotic drivers run counter to previous findings—particularly with respect to the absence of biotic resistance—the cause of that inconsistency remains uncertain. It may be partly due to few studies simultaneously investigating multiple alternative mechanisms of NERRs (but see Fargione & Tilman 2005) or to patterns being attributed to mechanisms that are presumed to be common but have not been explicitly tested.

It is also possible that the preponderance of diversity-invasibility research that comes from terrestrial systems biases expectations. Strong (1992) asked whether trophic cascades were "all wet." Is biotic resistance "all dry?" Nearly all evidence for local-scale biotic resistance comes from grassland or other terrestrial systems (Naeem *et al.* 2000; Levine *et al.* 2004;

Fargione & Tilman 2005; Fridley *et al.* 2007; but see Stachowicz *et al.* 1999). Relatively little research has been conducted in aquatic plant communities and some past findings have run counter to terrestrial expectations. Capers et al. (2007) found no evidence of biotic resistance in lake plant communities in the northeastern U.S. In lakes across the U.S., Fleming et al. (2015) tested Darwin's naturalization hypothesis that niches being occupied by close relatives would repel invaders; they found no evidence of such resistance. Ström et al (2014) experimentally demonstrated a local-scale but *positive* NERR in boreal wetlands.

Why would diversity-invasibility relationships differ between land and water? There is some evidence that aquatic plant communities are more strongly structured by abiotic environmental constraints (Santamaría 2002; Heino *et al.* 2017). Difficult environmental conditions in aquatic communities, particularly at higher latitudes, may impose such a strong filter on the macrophyte habitat species pool that species interactions have limited influence on community assembly (Santamaría 2002). Similar patterns have been observed in aquatic invertebrate communities (Peckarsky, Horn & Statzner 1990; Milner *et al.* 2001), suggesting that this may be a common pattern for freshwater systems. If the relative importance of abiotic and biotic processes in NERRs systematically varies between terrestrial and aquatic systems, then the limited research performed in the latter could bias our general understanding of the ecological mechanisms contributing to these patterns.

Implications for biodiversity conservation and invasive species management

Invasive species are one of the most important drivers of global change and can drastically restructure ecosystems (Vitousek *et al.* 1997; W. H. Mason, Bastow Wilson & B. Steel 2007; Tylianakis *et al.* 2008). The relationship between diversity and composition of native communities and their invasibility has been a fundamental area of inquiry in ecology going back to Elton (1958) and even Darwin (Daehler 2001). Understanding the conditions that allow invasive species to establish and that mediate their impacts remain critical issues for conservation and management (Mack *et al.* 2000; Byers *et al.* 2002). Studying the relationship between diversity of native species and invasive species can offer important insights into these questions by helping to identify the factors that support or deter invasions. In particular, the idea of biotic resistance suggests a "virtuous cycle" wherein efforts to support biodiversity also help repel invasions. However, the patterns we observed suggest that watershed management to support water quality may be a more effective means of mitigating invasions and their impacts. Nonetheless, it is clear that diversity-invasibility patterns can be driven by multiple mechanisms and recognizing the context-specific importance of these different mechanisms can help refine management strategies.

Our analysis of alternative mechanisms underlying NERRs in shallow lakes reveals several concerning trends: (1) environmental conditions consistent with broad patterns of anthropogenic change benefit invasive species, (2) lakes with higher biodiversity value are more likely to become invaded, and (3) biotic interactions represented a "bad news-bad news" scenario wherein local-scale diversity does not confer resistance to invasion but invasion does reduce local-scale diversity via competitive exclusion. However, our results do support continued effort toward established strategies for invasive species management. Specifically, efforts to maintain or improve lake condition, reduce spread of invasive species, and restore diverse plant assemblages where they have been lost are needed to slow the erosion of native plant diversity in these important ecosystems.

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Author Contributions

NH-W managed data collection. RM and DJL designed the study and analyses. RM analyzed the data and wrote the initial draft of the manuscript. All authors participated in data interpretation and revising the manuscript.

Data Accessibility

Macrophyte community data, environmental data, and analysis scripts for this study are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.19cf1c2 (Muthukrishnan, 2018)

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Figure Captions

Figure 1. Frequency of lakes with different native species richness. Dark gray portions of bars indicate lakes that had no invasive species present and light gray portions indicate lakes with at least one invasive species.

Figure 2. Relationship between richness of native species and invasive species identified in individual samples (a) or aggregated to the lake level (b). Points are jittered along the y-axis to increase visibility of overlapping points. The solid red lines indicate the estimated value and dashed lines are the 95% confidence interval for the estimate.

Figure 3. Biotic resistance (a) is indicated by an estimate of the probability of invasion of individual sampling locations as a function of native species richness. Colored lines indicate the trends for individual lakes with purple lines indicating lakes where invasion risk decreases with greater native species richness (indicating biotic resistance) and green lines indicating higher risk of invasion. The dashed portions of lines indicate estimates calculated for native species richness beyond the range where actual data was observed. The solid black lines indicate the overall estimates after accounting for autocorrelation within lakes and the dashed lines indicate the 95% confidence interval for those estimates. Competitive exclusion (b) is evaluated by a comparison of the rate of change in native species richness between locations that are uninvaded across all sampling time points and those where an invader is present. Here green lines indicate lakes with higher values at invaded points while purple lines are lakes with lower values at invaded sites and the black lines again show the overall estimates with a 95% confidence interval.

Figure 4. Relationships between depth (a-b, e-f) or Secchi depth (c-d, g-h) and the richness of native species and invasive species at individual sampling locations (a-d) and aggregated across entire lakes (e-h). Points are jittered along the y-axis for clarity and red lines indicate the mean and 95% confidence interval of the estimated value.

Figure 5. Relationships between the heterogeneity of depth or Secchi depth in a lake and the richness of native species (a,c) and invasive species (b,d). Points are jittered along the y-axis for clarity and red lines indicate the mean and 95% confidence interval of the estimated value.

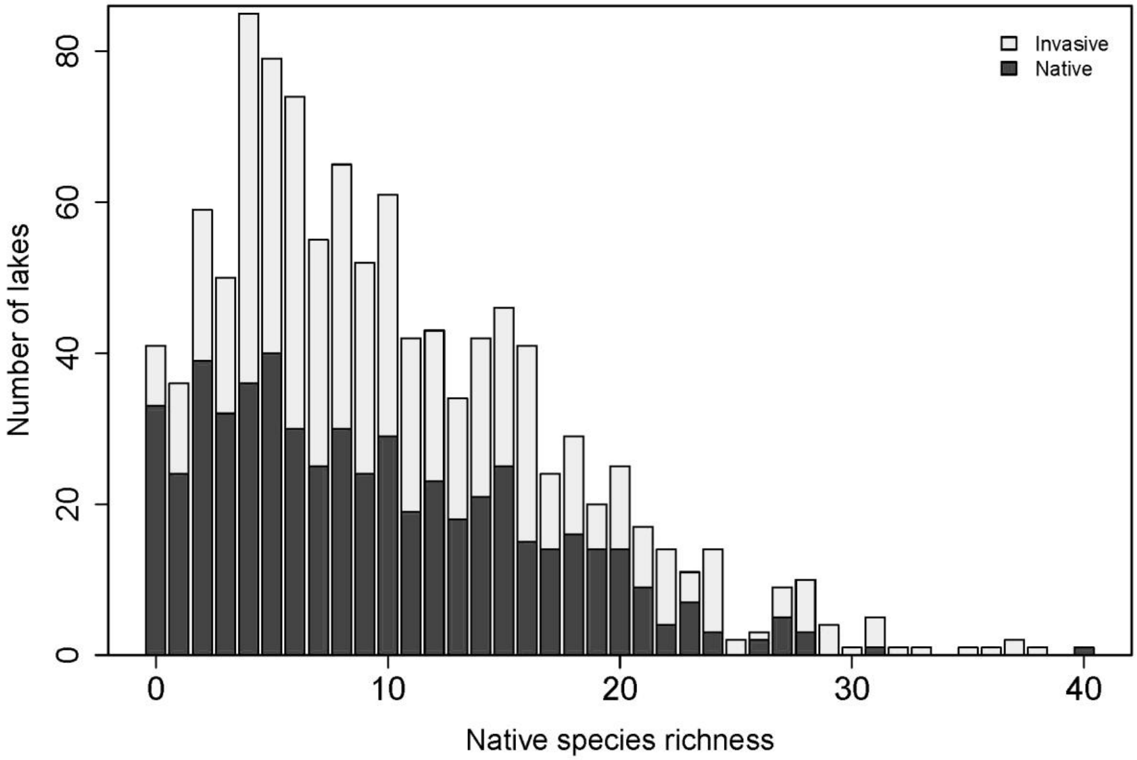
Tables

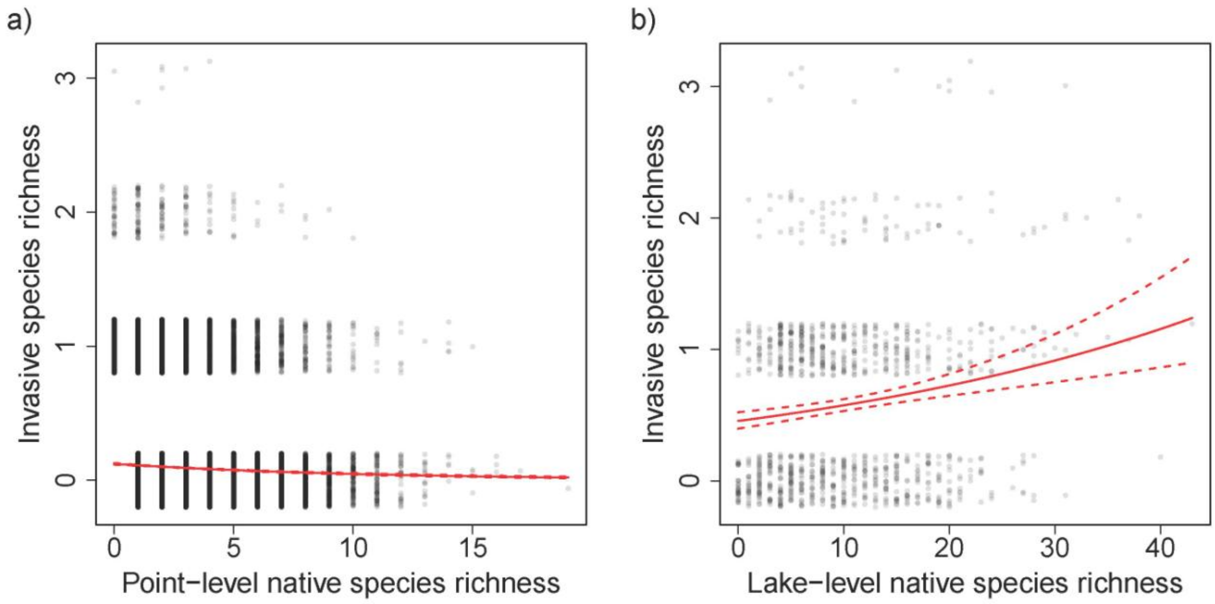
Table 1. Results of fixed effects from all statistical models. Generalized linear models were used in most analyses but mixed models were used for point scale analyses of biotic resistance and competitive exclusion to account for autocorrelation within lakes. Statistically significant results indicated with a “*”.

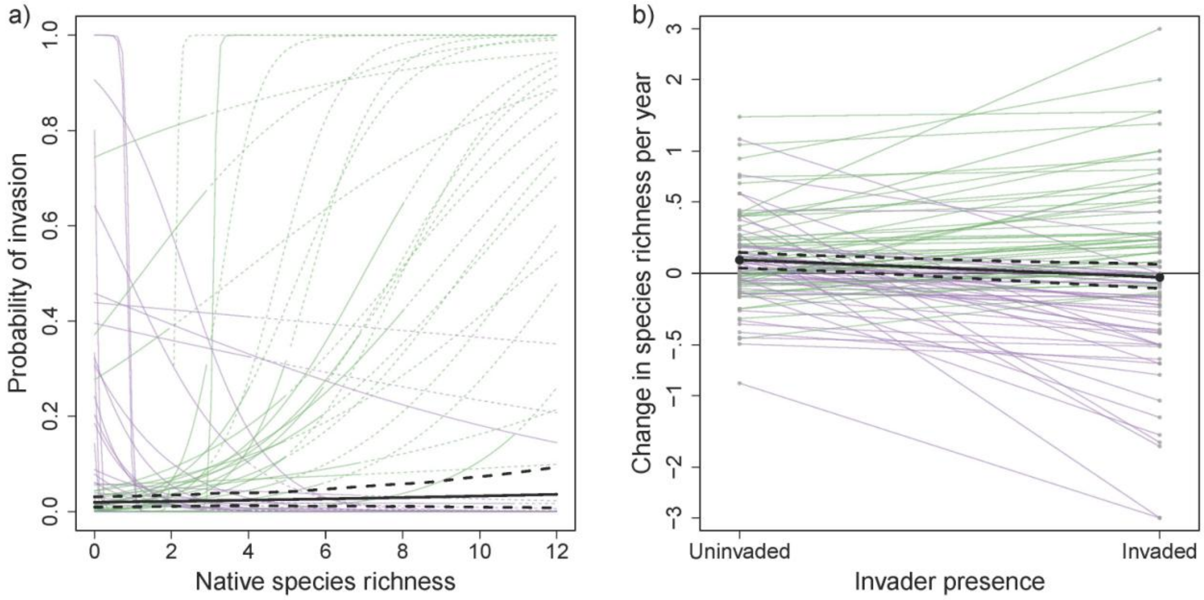
Analysis	Scale	Parameter	Estimate	Std. Error	Test statistic	p-value	Significant
Overall NERR	Point	Intercept	-2.103	0.024	-88.076	< 0.001	*
		Coefficient	-0.096	0.008	-11.308	< 0.001	*
	Lake	Intercept	-0.786	0.070	-11.277	< 0.001	*
		Coefficient	0.023	0.005	4.631	< 0.001	*
Biotic Interactions							
Biotic resistance	Point	Intercept	-3.921	0.286	-13.735		
		Coefficient	0.053	0.054	0.971	0.356	
	Lake	Intercept	-0.642	0.230	-2.798	0.005	*
		Coefficient	0.028	0.026	1.103	0.270	
Competitive exclusion	Point	Intercept	0.080	0.024	3.343		
		Coefficient	-0.101	0.025	-4.130	<0.001	*
	Lake	Intercept	0.021	0.182	0.114	0.910	
		Coefficient	0.239	0.221	1.080	0.282	
Environmental analyses							
Native richness ~ Depth	Point	Intercept	1.150	0.006	208.374	< 0.001	*
		Coefficient	-0.052	0.001	-40.172	< 0.001	*
	Lake	Intercept	2.268	0.020	114.602	< 0.001	*
		Coefficient	0.010	0.004	2.747	0.006	*

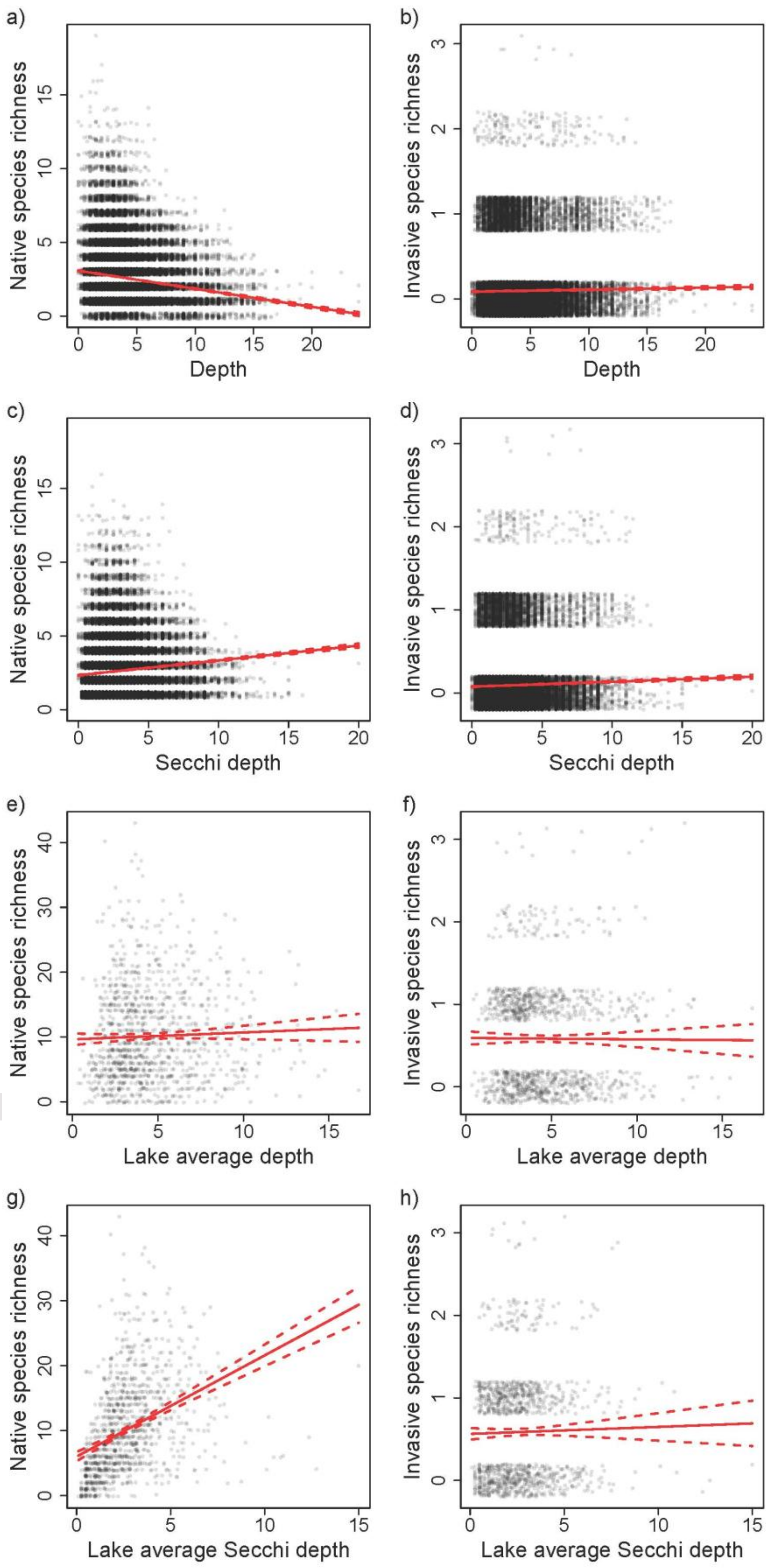
Invader richness ~Depth	Point	Intercept	-2.430	0.028	-87.339	< 0.001	*
		Coefficient	0.023	0.006	3.897	< 0.001	*
	Lake	Intercept	-0.524	0.083	-6.350	< 0.001	*
		Coefficient	-0.003	0.016	-0.178	0.859	
Native richness ~ Secchi depth	Point	Intercept	0.857	0.005	171.688	< 0.001	*
		Coefficient	0.037	0.001	25.767	< 0.001	*
	Lake	Intercept	1.957	0.016	119.019	< 0.001	*
		Coefficient	0.125	0.004	29.164	< 0.001	*
Invader richness ~Secchi depth	Point	Intercept	-2.545	0.026	-96.303	< 0.001	*
		Coefficient	0.059	0.007	8.107	< 0.001	*
	Lake	Intercept	-0.571	0.070	-8.144	< 0.001	*
		Coefficient	0.014	0.022	0.656	0.512	
Native richness ~ Environmental conditions	Lake	Intercept	2.283	0.357	6.388	< 0.001	*
		pH	0.087	0.043	2.006	0.045	*
		Conductance	-0.001	0.000	-6.518	< 0.001	*
		P	-1.359	0.380	-3.580	< 0.001	*
		N	0.028	0.051	0.550	0.582	
		Chlorophyll *a*	-0.006	0.001	-4.678	< 0.001	*
		Secchi depth	0.106	0.038	2.829	0.005	*
Invader richness ~ Environmental conditions	Lake	Intercept	-3.064	1.480	-2.070	0.038	*
		pH	0.412	0.175	2.355	0.019	*
		Conductance	0.000	0.000	-1.098	0.272	
		P	0.953	0.923	1.032	0.302	
		N	0.050	0.140	0.360	0.719	
		Chlorophyll *a*	-0.006	0.003	-1.866	0.062	
		Secchi depth	-0.316	0.157	-2.012	0.044	*
Heterogeneity analyses							

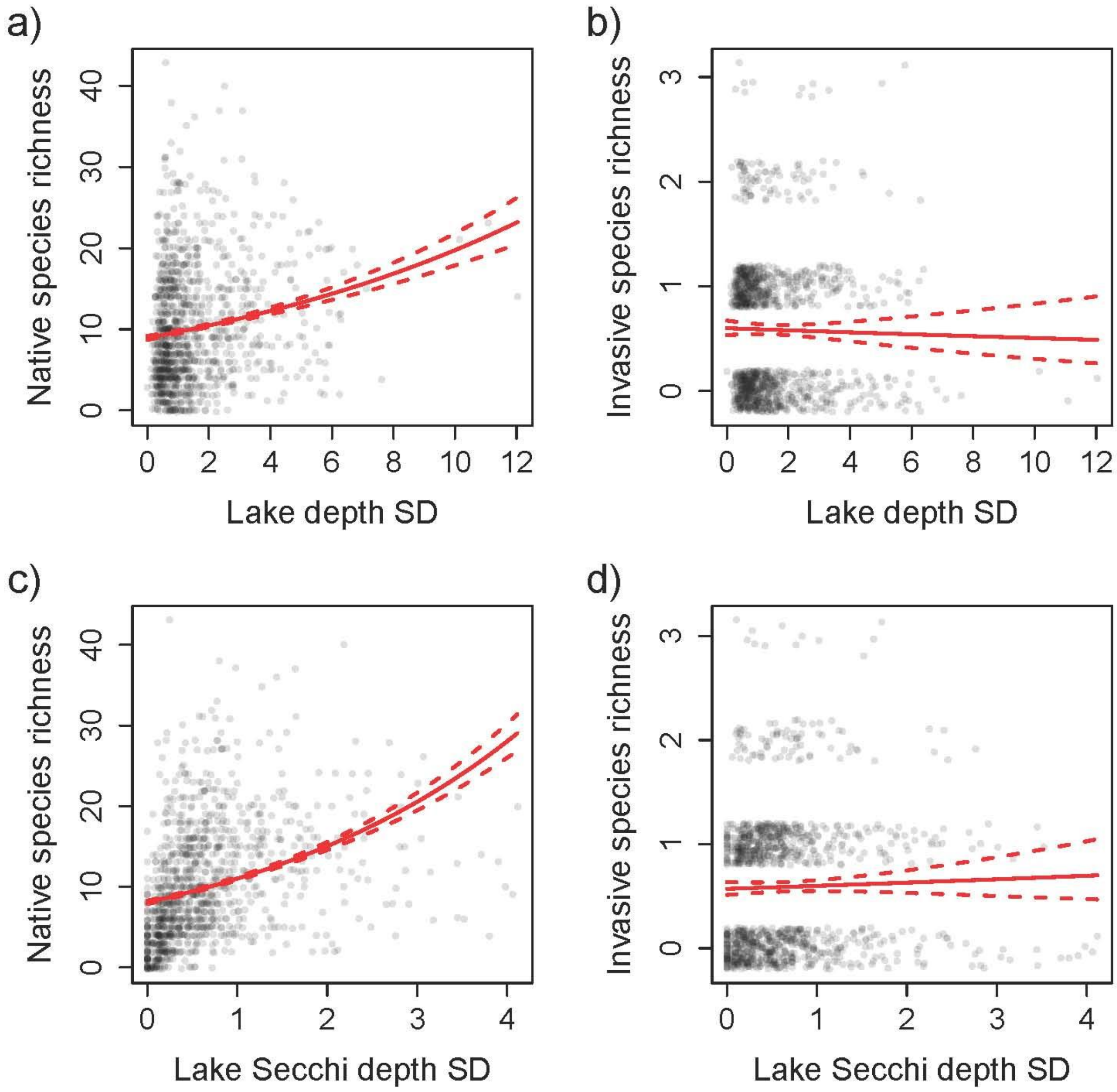
Native richness ~ Depth heterogeneity	Lake	Intercept	2.189	0.014	158.807	< 0.001	*
		Coefficient	0.079	0.006	13.223	< 0.001	*
Invader richness ~ Depth heterogeneity	Lake	Intercept	-0.510	0.058	-8.739	< 0.001	*
		Coefficient	-0.017	0.029	-0.576	0.565	
Native richness ~ Secchi depth heterogeneity	Lake	Intercept	2.089	0.013	155.818	< 0.001	*
		Coefficient	0.311	0.012	26.725	< 0.001	*
Invader richness ~ Secchi depth heterogeneity	Lake	Intercept	-0.561	0.055	-10.152	< 0.001	*
		Coefficient	0.050	0.058	0.856	0.392	


☐ Invasive
■ Native
Number of lakes
0
20
40
60
80
0
10
20
30
40
Native species richness


a)
Invasive species richness
0
1
2
3
0
5
10
15
Point−level native species richness
b)
Invasive species richness
0
1
2
3
0
10
20
30
40
Lake−level native species richness


a)
Probability of invasion
0.0
0.2
0.4
0.6
0.8
1.0
0
2
4
6
8
10
12
Native species richness
b)
Change in species richness per year
3
2
1
.5
0
−.5
−1
−2
−3
Uninvaded
Invaded
Invader presence


a)
Native species richness
0
5
10
15
Depth
0
5
10
15
20
b)
Invasive species richness
0
1
2
3
Depth
0
5
10
15
20
c)
Native species richness
0
5
10
15
Secchi depth
0
5
10
15
20
d)
Invasive species richness
0
1
2
3
Secchi depth
0
5
10
15
20
e)
Native species richness
0
10
20
30
40
Lake average depth
0
5
10
15
f)
Invasive species richness
0
1
2
3
Lake average depth
0
5
10
15
g)
Native species richness
0
10
20
30
40
Lake average Secchi depth
0
5
10
15
h)
Invasive species richness
0
1
2
3
Lake average Secchi depth
0
5
10
15


a)
Native species richness
0
10
20
30
40
0
2
4
6
8
10
12
Lake depth SD
b)
Invasive species richness
0
1
2
3
0
2
4
6
8
10
12
Lake depth SD
c)
Native species richness
0
10
20
30
40
0
1
2
3
4
Lake Secchi depth SD
d)
Invasive species richness
0
1
2
3
0
1
2
3
4
Lake Secchi depth SD