AQUATIC PLANT COMMUNITY INVASIBILITY AND SCALE-DEPENDENT PATTERNS IN NATIVE AND INVASIVE SPECIES RICHNESS

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Abstract. Invasive species richness often is negatively correlated with native species richness at the small spatial scale of sampling plots, but positively correlated in larger areas. The pattern at small scales has been interpreted as evidence that native plants can competitively exclude invasive species. Large-scale patterns have been understood to result from environmental heterogeneity, among other causes. We investigated species richness patterns among submerged and floating-leaved aquatic plants (87 native species and eight invasives) in 103 temperate lakes in Connecticut (northeastern USA) and found neither a consistently negative relationship at small (3-m^2) scales, nor a positive relationship at large scales. Native species richness at sampling locations was uncorrelated with invasive species richness in 37 of the 60 lakes where invasive plants occurred; richness was negatively correlated in 16 lakes and positively correlated in seven. No correlation between native and invasive species richness was found at larger spatial scales (whole lakes and counties). Increases in richness with area were uncorrelated with abiotic heterogeneity. Logistic regression showed that the probability of occurrence of five invasive species increased in sampling locations (3 m^2, $n = 2980$ samples) where native plants occurred, indicating that native plant species richness provided no resistance against invasion. However, the probability of three invasive species' occurrence declined as native plant density increased, indicating that density, if not species richness, provided some resistance with these species. Density had no effect on occurrence of three other invasive species. Based on these results, native species may resist invasion at small spatial scales only in communities where density is high (i.e., in communities where competition among individuals contributes to community structure). Most hydrophyte communities, however, appear to be maintained in a nonequilibrial condition by stress and/or disturbance. Therefore, most aquatic plant communities in temperate lakes are likely to be vulnerable to invasion.

Key words: beta diversity; biodiversity; biological invasion; density; exotic plants; invasion resistance; macrophytes; species richness.

INTRODUCTION

Invasive plants represent a global ecological and economic threat (Wilcove et al. 1998, Pimentel et al. 2000), but research has failed to reveal what conditions make particular communities vulnerable to invasion. Observational and experimental studies of individual plants and their immediate neighbors often have found a negative correlation between native species richness and invasive richness, suggesting that communities with many native species can resist invasion (Naeem et al. 2000, Kennedy et al. 2002, Gilbert and Lechowicz 2005). The idea that native species could confer resistance on a community was advanced by Elton (1958) and presumes that more species would more fully occupy available

niche space, limiting opportunities for additional species to establish and survive (Levine and D'Antonio 1999, Shea and Chesson 2002). At larger spatial scales, however, invasive species are most likely to be found in communities with the highest native species richness (Levine and D'Antonio 1999, Lonsdale 1999), suggesting that native and invasive species respond in similar ways to environmental conditions and that communities, no matter how speciose, do not resist invasion.

In one attempt to resolve this paradox, it has been suggested that competition, operating between individual organisms at small spatial scales, produces the negative correlation, but that native and invasive species richness rise in tandem at larger spatial scales because biotic and abiotic conditions become more variable at larger temporal and spatial scales, permitting more native as well as more nonnative species to occur (Levine and D'Antonio 1999, Shea and Chesson 2002). The hypothesis is plausible, but it rarely has been tested in natural systems (Davies et al. 2005). Furthermore, observational and experimental studies have been conducted primarily in systems such as grasslands where competition affects community composition (Von Holle

et al. 2003). Even in some of these studies, invasion success has depended on the invading and resident species (Meiners et al. 2004). In short, the consistency of the relationship between native and invasive species richness remains in doubt, even at small spatial scales, especially in systems where competition may not play a major role in determining community composition.

We examined the relationship between native and invasive species richness of submerged aquatic plants in and among 103 Connecticut lakes. We also evaluated the degree to which density of native aquatic plants, separate from species richness, was related to richness of invasive plants, and we tested the hypothesis that environmental heterogeneity increases at large spatial scales, and thus can explain a shift from a negative to a positive native/invasive species richness relationship.

Freshwater systems are particularly vulnerable to invasion (Shea and Chesson 2002), and aquatic plant communities provide excellent study systems because they are simple and typically have fewer species than forests and grasslands. Competition occurs among emergent macrophytes (McCreary 1991, Gopal and Goel 1993, Keddy et al. 1998, Engelhardt and Ritchie 2002), and floating-leaved species clearly interfere with plants growing under them. However, competition may be less important among submerged plants (McCreary 1991, Wilson and Keddy 1991) because of stress and/or disturbance. Freshwater plant communities often are disturbed by waves, ice scour, fluctuating water levels, boats that cut leaves and stir up sediment, grazing waterfowl, fish, and other agents (Jupp and Spence 1977, Murphy and Eaton 1983, Lodge 1991), which may keep these communities from approaching equilibrial conditions.

In this study, we investigated the following questions: Is the relationship between native and invasive aquatic plant species richness positive or negative at small spatial scales (in circular sampling plots with 2 m diameter) within lakes? What is the relationship when comparing native and invasive species richness among entire lakes, and when comparing across larger areas, aggregating lakes into counties? Do abiotic conditions become more variable at larger spatial scales? For variability to be associated with higher regional species richness and a change in the nature of the relationship between native and invasive species richness, beta diversity must increase (Shea and Chesson 2002, Davies et al. 2005). If all communities in a region are composed of the same species, they have equal alpha diversity (local species richness) values, and the total diversity in a region (gamma diversity) would equal alpha diversity as well. Gamma diversity rises as differences among communities (beta diversities) increase, whether gamma diversity is calculated additively ($\gamma = \alpha + \beta$) or multiplicatively ($\gamma = \alpha \times \beta$). We determined the degree of beta diversity among Connecticut lake plant communities and the degree to which this could be attributed to abiotic heterogeneity.

METHODS

Surveys

A total of 103 water bodies were surveyed for submerged and floating-leaved aquatic plants during the period from late June to late September in 2004 and 2005. Plants that often occur as emergents were recorded only if they were growing in a submerged condition. Lakes were selected nonrandomly, but included water bodies in all areas of the state and across the full range of sizes, development status, and environmental conditions. Lakes with state boat ramps were over-represented, and surveyed lakes were disproportionately large compared to the >3400 named ponds and lakes in Connecticut (89% of water bodies in a state database were <10 ha in area, compared with 37% of the lakes we surveyed), which may bias the results somewhat.

Surveys were conducted from small boats and involved slowly paddling or motoring through all areas shallow enough to support aquatic plants, recording all species present, based on visual observation and collections with a long-handled (3.7 m) rake. A grapple was used to sample in water too deep to be reached with the rake. While samples with a grapple may underestimate true richness (Westlake 1969, Sheldon and Boylen 1978, Capers 2000), this is unlikely to affect the results presented here because grapple samples primarily confirmed the absence of plants from water >4 m deep in the studied lakes, presumably because of light limitation (median Secchi depth = 2.0 m). Quantitative information on abundance was obtained in transects perpendicular to the shoreline, running for a distance of 80 m from the shore into deep water. Sampling locations were established along each transect at points 0, 5, 10, 20, 30, 40, 50, 60, 70, and 80 m from the shore, a total of 10 samples on each transect. Transect locations were selected to represent the variety of habitat types that were apparent in each lake, while being careful to avoid bias that could result from, for instance, selecting sites that were more or less likely to support aquatic vegetation. A minimum of one transect (10 sampling points) was established in each lake. To equalize sampling effort in lakes of different area, one transect was established for each 24 ha of surface area. Each sample on a transect consisted of the plants within a circle with a 2 m diameter, centered on the sampling location. Abundance of each species present in each sample was ranked on a scale of 1–5 (1 = rare, a single stem; 2 = uncommon, few stems; 3 = common; 4 = abundant; 5 = extremely abundant or dominant). Two specimens of every species collected in each lake were dried, mounted, and deposited in the herbaria of the University of Connecticut (CONN) and the Connecticut Agricultural Experiment Station (NHES).

Water temperature and dissolved oxygen were measured at a depth of 0.5 m and 0.5 m above the bottom in the deepest part of the lake, using a YSI 58 meter (YSI Incorporated, Yellow Springs, Ohio, USA). We ob-

tained water samples at the same depths, and Secchi depth was measured. Water samples were stored at 3°C until analyzed for pH, alkalinity, conductivity, and total phosphorus. Conductivity and pH were measured with a Fisher-Accumet AR20 meter (Fisher Scientific International Incorporated, Hampton, New Hampshire, USA). Alkalinity was quantified by titration and expressed as milligrams of $CaCO_3$ per liter. The titrant was 0.08 mol/L H_2SO_4 with an end point of pH 4.5. Total phosphorus analysis on samples acidified with three drops of concentrated H_2SO_4 was done using the ascorbic acid method and potassium persulfate digestion (American Public Health Association 1995).

Analysis

We used three procedures to analyze the relationship between native and invasive aquatic plant species richness. First, we used Pearson correlation coefficients of native and invasive species richness (using the Bonferroni adjustment in determining significance) at three spatial scales: in sampling plots within lakes where invasive species were recorded in samples, in whole-lake communities, and in lakes aggregated into counties ($n = 8$). Many samples had no plants at all in them, which can produce spurious positive correlation between nonnatives and natives, but indicates only that many locations support neither native nor invasive plants. To avoid this, we removed from the within-lake analysis all samples in which no plants were recorded so that the correlation analysis more correctly reflects whether native species richness and invasive species richness vary in the same way.

We also used linear regression to determine whether native species richness increased with lake area at the same rate in lakes with invasive plants as in lakes without them, limiting the analysis to lakes with an area of no more than 380 ha, the area of the largest lake that lacked invasive species. If invasive plants affected native species richness in Connecticut lakes through competition or by altering their ability to colonize, the slope of the regression line describing the rise of native richness with area should be different in lakes with invasives and those without.

Finally, we used logistic regression in separate analyses to test whether the presence or density of native plants affected the probability of occurrence of invasive species in samples. In analyzing whether native species' presence was related to presence of invasives, a total of 5644 samples were combined from all lakes where invasive species were recorded in samples. Samples were assigned a value of 0 or 1, depending on whether native plants were absent or present. To analyze whether the abundance of native plants was related to the probability of invasives' occurrence, we included only samples where native plants occurred ($n = 2980$). As a conservative estimate of native abundance, each sample was assigned the value of the most abundant native species (using the 1–5 scores).

We calculated beta diversity among lakes in each county both as $\beta = \gamma/\alpha$ where γ was the combined species richness for the county and α was the richness of each lake, and as $\beta = \gamma - \alpha$. The results were qualitatively the same, and only those based on the multiplicative beta are reported here. We used the mean beta for each county in correlation analysis to determine if turnover, i.e., spatial variation, among lake communities was related to variability in abiotic conditions or to mean values of those conditions. Separate correlation analyses were conducted for native and invasive species, using the total species list for all lakes ($n = 103$ lakes for native species and $n = 63$ for invasives). Abiotic variables were transformed before the analyses to eliminate colinearity between means and variance, using either natural logs or a Box-Cox transformation. We used Systat Version 11 (Systat 2004) to perform all analyses.

Taxonomy follows Crow and Hellquist (2000*a*, *b*). *Myriophyllum heterophyllum* and a hybrid (*Myriophyllum heterophyllum* × *laxum*) both occur in Connecticut, and they cannot be distinguished without molecular analysis (Moody and Les 2002; D. H. Les, *personal communication*); both are treated here as *M. heterophyllum*. Invasive species are those identified as invasive or potentially invasive by the Connecticut Invasive Plants Council. One additional, recently identified species, mud-mat (*Glossostigma cleistanthum* W. R. Barker), was included because it is spreading rapidly through the Northeast (Les et al. 2006).

RESULTS

A total of 87 native aquatic plant taxa and 8 invasive species were recorded in the 103 lakes. Invasive species were recorded in samples in 60 lakes and were recorded during surveys in 3 additional lakes, so invasives occurred in a total of 63 lakes (61%). Of lakes with invasive plants, 33 had a single species, 19 had two, 10 had three, and 1 had four. Native species richness in the lakes ranged from 1 to 27 species (Fig. 1).

Native–invasive correlation across spatial scales

Native and invasive species richness in samples were significantly correlated in 23 of the 60 lakes (38%) where invasives occurred in samples. Correlation was negative in 16 lakes ($r = -0.19$ to -0.90). Correlation was positive in seven lakes ($r = 0.28–0.61$), demonstrating that invasive species were more likely to occur where native species did in 12% of the lakes. Lakes where significant correlation was found were not significantly larger than other lakes (106.2 ± 21.9 ha [mean ± SE] compared with 93.2 ± 15.9 ha, $t = -0.48$, $P = 0.63$), providing reassurance that significant correlation did not result simply from the higher number of samples in larger lakes.

When all samples were combined for the 60 lakes, significant positive correlation in species richness was detected ($n = 5644$ samples, $r = 0.19$, $P < 0.0001$), but this result was greatly influenced by the number of
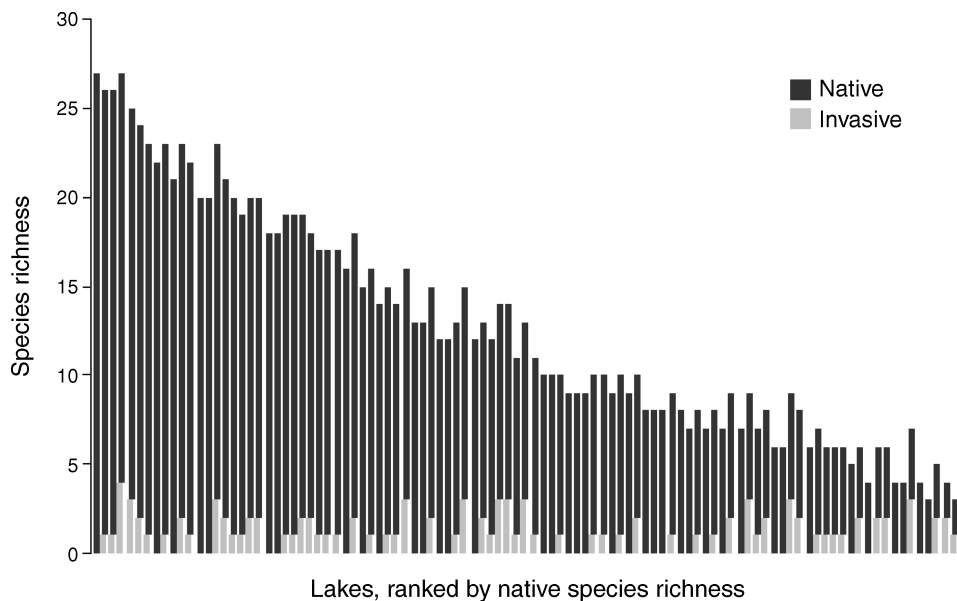
Fɪɢ. 1. Species richness of native and invasive aquatic plants are shown for 103 surveyed lakes, ranked by native richness. Invasive species were recorded in 63 of the lakes.

samples in which no plants were recorded. The relationship disappeared when the analysis was limited to locations where invasives were recorded ($n = 1654$ samples, $r = 0.02$, $P = 0.40$; Fig. 2A). Mean richness of native and invasive plants in samples were not correlated ($r = 0.010$, $P = 0.45$, Fig. 2B). Total richness of native species was not correlated with invasive species richness when all lakes with invasive species were included ($n = 63$, $r = 0.006$, $P = 0.96$; Fig. 2C).

Cumulative richness of native species in the eight Connecticut counties ranged from 41 to 61 species, and cumulative richness of invasive species ranged from one to five. Native and invasive richness in counties were not correlated ($n = 8$, $r = 0.51$, $P = 0.20$; Fig. 2D), nor were mean native and invasive richness of lakes, aggregated by counties, correlated ($n = 8$, $r = -0.48$, $P = 0.22$, Fig. 2E).

Beta diversity

Beta diversity was calculated among lakes within counties. The number of surveyed lakes varied within counties from 4 to 22; analysis of beta diversity among invasive species communities was limited to lakes where invasives actually occurred ($n = 3$ in one county and 5 in another, ranging from 6 to 13 in others), but removing the two counties with the fewest lakes from the analysis did not change the results. Beta diversity of native plants and invasive plants were not correlated ($r = 0.54$, $P = 0.17$, Fig. 2F).

Beta diversity of native and invasive plants was uncorrelated with variation in environmental variables, providing no evidence that species richness increased with spatial scale because of greater environmental heterogeneity in larger areas or that turnover among communities was related to this heterogeneity. Native

plant turnover was marginally correlated with mean pH ($r = 0.90$, $P = 0.06$) and mean alkalinity of water taken from lake bottoms ($r = 0.92$, $P = 0.04$), indicating that beta diversity among lakes in a county rose as alkalinity and pH increased, but not as the conditions became more variable. Invasive plant turnover was correlated with none of the mean values.

Invasive species response to native presence, abundance

Logistic regression indicated that the probability of occurrence of five of six invasive species (*Myriophyllum spicatum*, *M. heterophyllum*, *Potamogeton crispus*, *Cabomba caroliniana*, and *Glossostigma cleistanthum*) commonly recorded in samples ($n = 5644$) was higher where native plants occurred, and there was no relationship with the sixth species, *Najas minor* (Table 1). The results provide no evidence that, by their presence, native plants reduced the ability of invasive species to establish within lakes. In fact, the presence of native plants increased the likelihood of invasive plants' occurrence, suggesting the species have similar affinities for abiotic conditions. However, the probability of occurrence of three invasives (*Myriophyllum heterophyllum*, *Najas minor*, and *Glossostigma cleistanthum*) declined as native plants' abundance increased ($n = 2980$ samples). This indicates that density may provide some resistance against invasion (Fig. 3). The probability of occurrence of three other invasives (*Myriophyllum spicatum*, *Potamogeton crispus* and *Cabomba caroliniana*) was unaffected by native plants abundance.

Effect of invasive species on diversity/area relationship

Linear regression analysis showed that native plant species richness (S) increased with lake area at the same
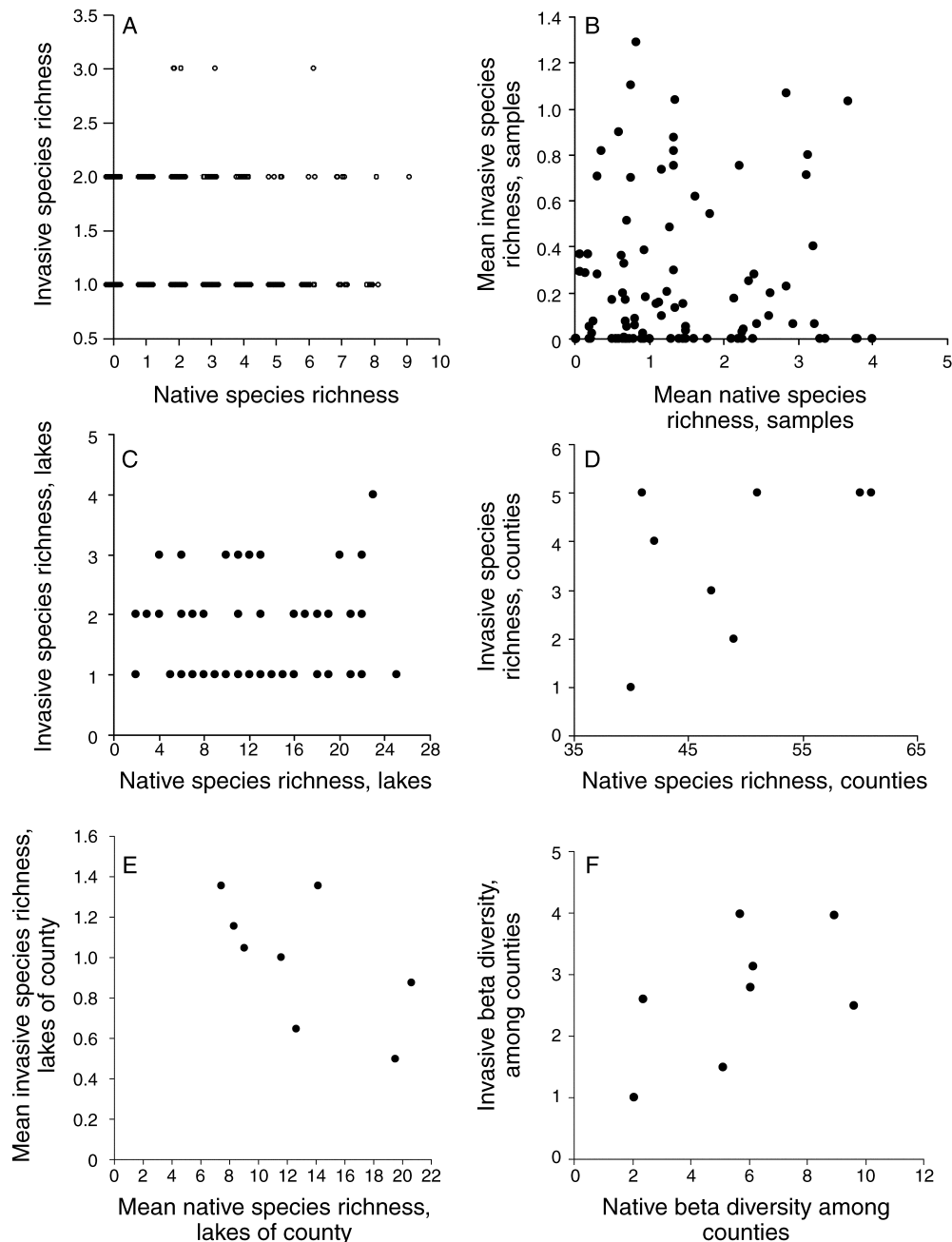
FIG. 2. The relationship between total and mean richness of native and invasive aquatic plants is shown for three spatial scales. Richness was not significantly correlated at any spatial scale. (A) Species richness in samples where invasive species occurred ($n = 1654$ samples, $r = 0.02$, $P = 0.40$). Data points were jittered in the graph so the high number of samples at many of the points could be seen. (B) Mean richness in samples within lakes ($r = 0.10$, $P = 0.46$). (C) Total richness in lakes where invasive species occurred ($n = 63$ lakes, $r = 0.01$, $P = 0.96$). (D) Total richness in the lakes of Connecticut's eight counties ($r = 0.51$, $P = 0.20$). (E) Mean richness in lakes of the counties ($r = -0.44$, $P = 0.22$). (F) Beta diversity of native and invasive plants was not significantly correlated ($r = 0.54$, $P = 0.17$). Beta diversity measured turnover among the plant communities of lakes, aggregated by county.

rate whether invasive plants were present or not ($\ln[S] = 1.93 + 0.015 \times$ [area in lakes with invasives] and $\ln[S] = 1.93 + 0.025 \times$ [area in lakes without invasives]; difference in slopes $F_{1,90} = 1.38$, $P > 0.05$, Fig. 4). Thus, we found no evidence that invasive species

depressed native species richness in the surveyed lakes. However, because of their presence, invasive species increased total richness of aquatic plants. Mean richness in lakes was higher in lakes with invasives than those without when the analysis was limited to lakes of

TABLE 1. Results of logistic regression testing whether (A) the probability of occurrence of six invasive aquatic plant species was affected by the presence or absence of native plants in samples (coded 1 or 0, $n = 5644$ samples) and (B) whether the probability of invasive species' occurrence was affected by density of native plants (coded 1–5, $n = 2980$ sites where native plants occurred).

Invasive species	Estimate	SE	t	P	Odds ratio†	df	P	McFadden's rho²‡
A) Presence or absence of native plants								
Cabomba caroliniana	1.0881	0.1362	7.9881	<0.0001	73.4109	1	0.0001	0.0308
Glossostigma cleistanthum	1.5118	0.3314	4.5623	<0.0001	27.5885	1	0.0001	0.0384
Myriophyllum heterophyllum	1.2094	0.1215	9.9515	<0.0001	116.4964	1	0.0001	0.0396
Myriophyllum spicatum	0.6642	0.0764	8.6920	<0.0001	78.7874	1	0.0001	0.0160
Najas minor	0.1465	0.1713	0.8548	0.3927	0.7344	1	0.3915	0.0006
Potamogeton crispus	0.8498	0.2010	4.2275	<0.0001	19.6944	1	0.0001	0.0164
B) Density of native plants								
Cabomba caroliniana	0.0858	0.0628	1.3669	0.1716	1.8956	1	0.1686	0.0012
Glossostigma cleistanthum	−0.3482	0.1165	−2.9891	0.0028	8.7403	1	0.0031	0.0159
Myriophyllum heterophyllum	−0.1797	0.0520	−3.4542	0.0006	11.7643	1	0.0006	0.0058
Myriophyllum spicatum	−0.0082	0.0413	−0.1985	0.8426	0.0394	1	0.8427	0
Najas minor	−0.4315	0.0972	−4.4417	<0.0001	19.4564	1	0.0001	0.0264
Potamogeton crispus	−0.0913	0.0946	−0.9650	0.3345	0.9198	1	0.3375	0.0011

Note: The coded values for presence/absence and native plant density were used in the regression analyses.

† The odds ratio tests the odds of a species' occurrence with native plants against the odds of its occurrence where there are no native plants.

‡ McFaddens' rho² estimates the proportion of variation explained by a logistic regression model.

comparable areas (13.6 ± 0.87 species with invasives, 10.6 ± 0.96 species without invasives, $t_{59,39} = 2.31$, $P = 0.02$).

DISCUSSION

In light of the lack of a correlation between native and nonnative plant diversity, it appears that resistance to nonnative invasion is not caused by native species richness in Connecticut lakes. However, high density of native plants may be able to limit the spread of at least some invasive species within lakes. Negative correlation between native and invasive species richness often has been found at small spatial scales in grasslands (Naeem et al. 2000, Davies et al. 2005) and forests (Wiser et al. 1998, Brown and Peet 2003, Gilbert and Lechowicz 2005). If competition between close neighbors accounts for the relationship, as seems likely (Huston 1999), it should occur in communities where disturbance and stresses resulting from resource limitation are minimal (Grime 1979). Such conditions are uncommon among the aquatic plant communities we surveyed. Native plant richness and invasive plant richness were correlated at the smallest spatial scale in a minority of lakes (38%), and the correlation was positive in one-third of those.

The logistic regression analysis suggests that occurrence and species richness of native plants provide no resistance against invasion. To the contrary, the presence of native plants in samples increased the likelihood that five invasive species would occur there as well. This positive relationship between native and invasive species likely indicates that locations favorable for native plants also were favorable for invasives. However, we cannot rule out the possibility that facilitation occurs, possibly because established plants can trap propagules of other plants.

While the presence of native species increases the probability of occurrence of invasives within lakes, the density of native plants had a negative effect on three invasive species, limiting the frequency of *Myriophyllum heterophyllum*, *Najas minor,* and *Glossostigma cleistanthum*. Presumably, densely growing native plants prevented establishment of the invasives or outcompeted them. In the case of *Glossostigma*, the pattern results from the species' ecological affinities. *Glossostigma* occurs disproportionately on sandy sediment and in water with high clarity and low pH, alkalinity, and conductivity (Les et al. 2006), where few other species become abundant.

Three species that are serious invasive nuisances in Connecticut, *Myriophyllum spicatum, Potamogeton crispus,* and *Cabomba caroliniana* (Les and Mehrhoff 1999), occurred as frequently where native plants grew densely as where they grew sparsely. This may reflect an affinity for similar environmental conditions (Levine and D'Antonio 1999), in which case it would indicate that native plants, no matter how dense, did not prevent colonization of these species. Another possibility is that native and nonnative species colonized these lakes at the same time, perhaps after severe disturbance. It also shows that native plants remain abundant in the presence of invasives, providing evidence that interspecific competition plays a limited role in determining community structure among these plants. *M. spicatum* has occurred in Connecticut since at least 1979 and the other two species since the 1930s, so it is unlikely that they have not yet fully established but could reduce native abundance in the future.

We found that the relationship between native and invasive plants overall was weak, even at the smallest spatial scale. Moreover, there was little evidence for a change to a positive relationship between native and
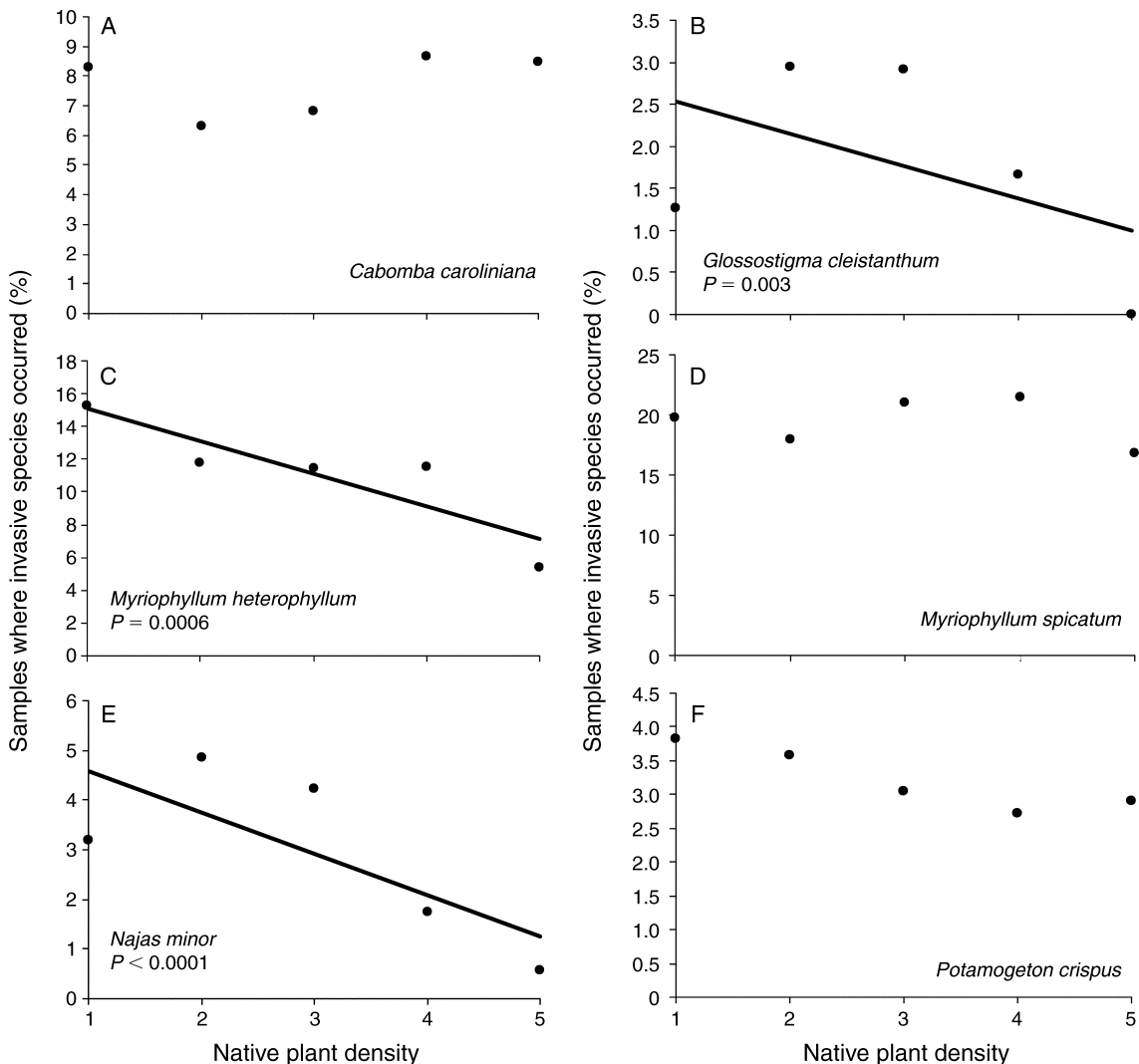
FIG. 3. Increasing density of native plants resulted in a significant reduction in the probability of occurrence of three invasive species in sampling locations ($n = 2980$) in Connecticut lakes: (B) *Glossostigma cleistanthum*, (C) *Myriophyllum heterophyllum,* and (E) *Najas minor*. Three other invasives were unaffected by native plants, even when growing at high density: (A) *Cabomba caroliniana*, (D) *Myriophyllum spicatum*, and (F) *Potamogeton crispus*. Native plant density in sampling locations was ranked as 1–5 (rare to dominant; see *Methods*). Probabilities were calculated by logistic regression analysis.

invasive species richness at larger spatial scales, unlike studies in terrestrial systems (Lonsdale 1999, Stohlgren et al. 2003, Davies et al. 2005). Lakes with three invasive species (none had more than four) had as few as four native plants and as many as 22. Species richness in counties was higher than in lakes for both native and invasive plants, but there was no evidence that the increases were correlated or that the higher richness in counties was related to environmental heterogeneity. Richness appears to rise in the surveyed region because of areal effects.

The inability of aquatic plant communities to resist invasion except at the very highest plant density levels indicates that niche space is available for colonizers, unlike grassland systems, where competition is an important structuring force and where resistance has more usually been found. The openness of aquatic plant communities, like those on islands, may be related to their depauperate nature. We believe disturbance is even more important in providing niche opportunities, as has been found in other systems (Davis et al. 2000, Lockwood et al. 2005, Von Holle and Simberloff 2005). Brown and Peet (2003) proposed that invasibility depends on the degree to which community composition is driven by immigration processes, mediated by "low-intensity disturbance" and propagule pressure. Although a direct connection between invasibility of aquatic plant communities and disturbance has not been demonstrated, freshwater systems are known to be particularly vulnerable to invasion (Shea and Chesson
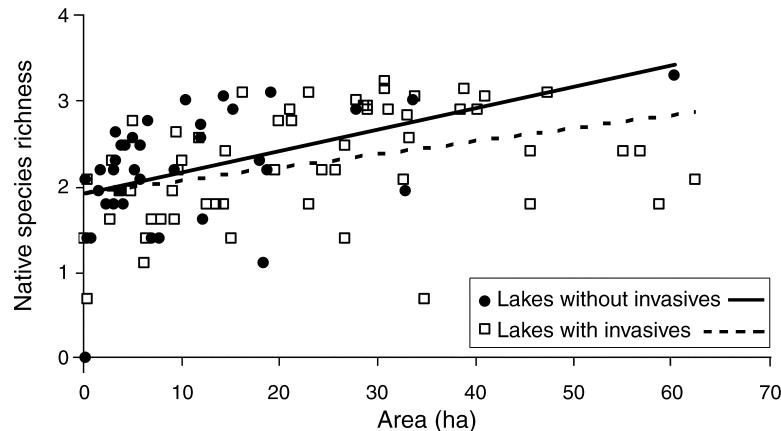
FIG. 4. Native species richness (natural log-transformed) increased significantly with area, both in lakes that had invasive aquatic plants and in those that did not. The slopes of the lines describing the relationship were not significantly different. The analysis was limited to lakes no more than 380 ha in size so the sizes of the lakes in the two groups were comparable.

2002), and submerged plant communities often are highly disturbed by boats, grazing waterfowl, waves, lowered water levels, and ice scour (Jupp and Spence 1977, Murphy and Eaton 1983), persisting through recolonization, usually by vegetative propagules (Barrat-Segretain 1996, Combroux et al. 2001, Capers 2003).

Our results provide further evidence that negative correlation between native and invasive species richness does not occur universally, and that resistance may be limited to communities in which high density leads to competitive exclusion. Earlier work supports this suggestion. Cleland et al. (2004) found that invasibility increased with native richness but decreased with native plant productivity. Experiments manipulating density through seed addition or plant removal also have shown that dominance may be more important than species richness in determining invasibility (Smith et al. 2004), and modeling has shown that invasibility increases in communities with weakly interacting species (Case 1990). In the absence of evidence that invasive aquatic plants affect the relationship between native species richness and lake area, it appears that invasive species increase total species richness of many aquatic plant communities in Connecticut lakes, potentially increasing community stability (Holling 1973, Tilman 1996).

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