Species richness of both native and invasive aquatic plants influenced by environmental conditions and human activity

Robert S. Capers, Roslyn Selsky, Gregory J. Bugbee, and Jason C. White

Abstract: Invasive plants alter community structure, threatening ecosystem function and biodiversity, but little information is available on whether invasive species richness responds to environmental conditions in the same way that richness of native plants does. We surveyed submerged and floating-leaved plants in 99 Connecticut (northeast USA) lakes and ponds, collecting quantitative data on abundance and frequency. We used multiple linear and logistic regression to determine which environmental conditions were correlated with species richness of invasive and native plants. Independent variables included lake area, maximum depth, pH, alkalinity, conductivity, phosphorus concentration, productivity, and dominance (the proportional abundance of the most abundant and frequently found species), plus two estimates of human activity. Species richness of both native and invasive richness was correlated with alkalinity and human activity. Native richness also increased with water clarity, lake area, and productivity; invasive species richness also rose with pH. We found no evidence that richness of one group affected richness of the other. We also investigated patterns of dominance and found that native plants were as likely to become dominant as invasive species. Dominance occurred overwhelmingly in shallow lakes with high productivity.

Key words: abiotic conditions, biodiversity, community structure, dominance, lakes, macrophyte.

Résumé : Les plantes envahissantes modifient la structure des communautés en menaçant les fonctions des écosystèmes et leur biodiversité, mais on connaît peu de chose à savoir si la richesse en espèces envahissantes réagit aux conditions du milieu de la même façon que la richesse en plantes indigènes. Les auteurs ont suivi les plantes submergées et à feuilles flottantes dans 99 lacs et étang du nord-est des États-Unis, en réunissant les données d'abondance et de fréquence. Ils ont utilisé la régression linéaire multiple et logistique pour déterminer quelles conditions environnementales montrent une corrélation avec les richesses en espèces des plantes envahissantes et indigènes. Les variables indépendantes comprennent la surface des lacs, la profondeur maximum, le pH, l'alcalinité, la conductivité, la teneur en phosphore, la productivité et la dominance (l'abondance proportionnelle des espèces les plus fréquentes et les plus abondantes), ainsi que deux valeurs estimées pour l'activité humaine. La richesse en espèces indigènes aussi bien qu'en espèces envahissantes montre une corrélation avec l'alcalinité et l'activité humaine. La richesse en espèces indigènes augmente également avec la clarté de l'eau, la surface du lac et la productivité; la richesse en espèces adventices augmente aussi avec le pH. On ne perçoit aucune preuve que la richesse d'un groupe affecte la richesse de l'autre. Les auteurs ont également examiné le patron de la dominance pour constater que les plantes indigènes ont autant de chance de devenir dominantes que les espèces envahissantes. On retrouve la dominance surtout dans les lacs peu profonds à forte productivité.

Mots-clés : conditions abiotiques, biodiversité, structure des communautés, dominance, lacs, macrophytes.

[Traduit par la Rédaction]

Introduction

Invasive plants are an economic and ecological problem in many aquatic systems (Pimentel et al. 2005). They can dominate lakes, interfering with recreation and reducing real estate values (Bergstrom et al. 1993; Pimentel et al. 2000; Rockwell 2003). Like terrestrial invasive plants, invasive aquatics are thought to exclude native vegetation, threaten rare species, and alter ecosystem processes (Vitousek et al. 1996; Mack et al. 2000). However, the exact relationship between native and invasive species remains elusive. Elton (1958) suggested that communities with many native species are less likely to be invaded, but the mechanism behind this community resistance hypothesis is not clear. Do native and invasive species compete with each other? Or is community composition determined primarily by abiotic environmental conditions and, if so, do native and invasive species respond similarly or differently to conditions?

Empirical evidence has been equivocal. Native species richness has been found to be inversely related to invasive species richness in small-scale manipulative experiments (Naeem et al. 2000; Engelhardt and Ritchie 2002), suggesting an antagonistic, probably competitive relationship. However, observational studies of plant communities under

R.S. Capers,[1,2] **R. Selsky, G.J. Bugbee, and J.C. White.** Department of Soil and Water, The Connecticut Agricultural Experiment Station, New Haven, CT 06504, USA.

[1]Corresponding author (e-mail: robert.capers@uconn.edu).
[2]Present address: George Safford Torrey Herbarium, Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269-3043, USA.

natural conditions typically have found that native and invasive species richness are positively correlated (Levine and D'Antonio 1999; Lonsdale 1999; Stohlgren et al. 1999; Houlahan and Findlay 2004), suggesting that both native and invasive species are responding to the same conditions and that communities are open, providing colonization opportunities for additional species.

Also uncertain is the role that dominance plays in invaded communities. Dominant species can control the occurrence of other species (McNaughton and Wolf 1970), leading to exclusion of those that are presumably less competitive, but questions have been raised (Houlahan and Findlay 2004) about whether invasive species are more likely to become dominant than native species.

We investigated patterns of species richness and dominance among native and invasive aquatic plants in 99 temperate lakes. We used multivariate analysis to determine which environmental conditions were associated with species richness of native and invasive plants. Because human activity such as recreational boating can affect aquatic plants (Johnstone et al. 1985; Newroth 1985; Warrington 1985), we included two measures of human activity among the variables to be tested for possible influence on species richness. We also asked whether invasive species were more likely than native plants to become dominant and whether lakes were more likely to be dominated by invasives than by native species.

Materials and methods

We conducted surveys of submerged and floating-leaved aquatic plants in 99 lakes and ponds in Connecticut (between 41°07′ and 42°03′N and 71°47′ and 73°30′W) during the period from late June to late September in 2004 and 2005. Lakes selected for surveys included water bodies in all areas of the state and across a wide range of sizes (0.07–181 ha) and trophic status (oligotrophic to hypertrophic). Surveyed lakes were disproportionately large compared with the more than 3400 named ponds and lakes in Connecticut, so the results may apply somewhat less generally to small ponds.

We conducted surveys by slowly paddling or motoring small boats through 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 deeper water. While samples taken with a grapple may underestimate true richness (Westlake 1969; Capers 2000) this is unlikely to affect the results presented here because grapple samples primarily confirmed the absence of plants from water more than 4 m deep in the studied lakes, presumably because of light limitation (median Secchi depth = 2.0 m). We obtained quantitative information on abundance in 80 m transects perpendicular to the shoreline, running from the shore into deep water. Samples were obtained 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. Each sample consisted of the plants within a circle with a 2 m diameter, centered on the point. We selected transect locations nonrandomly to represent the variety of habitat types in each lake such as sandy substrate, silty substrate, and steeply sloping littoral, while being careful to avoid bias that could result from selecting sites that were more or less likely to support aquatic vegetation. At least one transect (10 sampling points) was established in each lake or pond, and one transect was established for each 24 ha of surface area. The abundance of each species in a sample was ranked on a scale of 1–5 (1, present but rare, a single stem; 2, present but uncommon, few stems; 3, common; 4, abundant; 5, extremely abundant or dominant). Total species richness in each lake was the cumulative total of species observed during the boat surveys and in the transects and is thought to be an unbiased estimate of the total number of species present.

In the deepest part of each lake, we recorded Secchi depth and obtained water samples at a depth of 50 cm (surface) and 50 cm above the bottom (bottom). Water samples were analyzed for pH, alkalinity, conductivity, and total phosphorus. Conductivity and pH were measured with a Fisher-Accumet AR20 m (Fisher Scientific International Inc., Hampton, N.H.). Alkalinity was quantified by titration and expressed as mg/L $CaCO_3$. The titrant was 0.16 N 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 (Andrew et al. 1995). Aquatic plants generally are limited by nitrogen (Hutchinson 1975), but nitrogen and phosphorus concentrations are positively correlated ($r = 0.75$, $p < 0.0001$ for Total N and Total P in a study of 70 Connecticut lakes; Frink and Norvell 1984), so we interpret Total P as a general measure of nutrient status in the lakes selected.

To estimate human activity at each lake, we assigned categorical values to each lake based separately on accessibility for boats and restrictions on boat motors, using data from the Connecticut Department of Environmental Protection Boating Division, land owners, and observations by survey personnel. Access scores were as follows: 1, lakes with state boat ramps; 2, lakes with municipal or private ramps; 3, lakes with access only for car-top boats; 4, lakes with access only for boats that can be carried in; 5, no practical access. Motor restrictions are presumed to make lakes less attractive to people with power boats, so the restrictions provide a second assessment of boating and other human activities. Motor restrictions were scored as: 1, all motors allowed; 2, only electric motors allowed; 3, no motors allowed.

We determined dominance in each lake by calculating the mean abundance of each species in all sampling locations, based on the 5-point abundance scale and including locations where a species was absent (assigning a 0 abundance value to those locations): $D = \text{Max}(\Sigma A_i/n)$ where A_i is the abundance of species i in all locations and n is the number of samples obtained in a lake. Each lake, thus, had a single species with the highest mean abundance. We declared that a species was dominant in a lake if it achieved a mean abundance value that was 50% or greater of the 5.0 maximum: the score a species would receive if present in every sample with the maximum abundance score of 5 in every sample. A score of 50% indicates that a species was both widespread in a lake and abundant. In practice, no species was declared dominant that occurred in fewer than 60% of a lake's samples. To assess the importance of productivity on species richness, we estimated total abundance of all species as the

Table 1. In surveys of 99 lakes in Connecticut, USA, 90 aquatic plant taxa were recorded.

Species	N	Weight
Alisma sp.	1	3
Brasenia schreberi J. F. Gmel.	52	4
Cabomba caroliniana Gray	10	3
Callitriche heterophylla Pursh	4	2
Callitriche sp.	7	2
Cardamine sp.	1	2
Ceratophyllum demersum L.	40	3
Ceratophyllum echinatum Gray	14	3
Eichhornia crassipes (Mart.) Solms	1	5
Elatine americana (Pursh) Arn.	1	1
Elatine minima (Nutt.) Fisch. & Mey.	19	1
Elatine sp.	1	1
Elatine triandra Schkuhr	3	1
Eleocharis acicularis (L.) Roemer & J. A. Schultes	31	1
Eleocharis parvula (R. & S.) Link	1	1
Eleocharis sp.	21	1
Elodea canadensis Michx.	9	2
Elodea nuttallii (Planch.) St. John	46	2
Eriocaulon aquaticum (Hill) Druce	25	2
Glossostigma cleistanthum W. R. Barker	3	2
Gratiola aurea Pursh	20	2
Isoëtes acadiensis Kott.	1	2
Isoëtes echinospora Dur.	10	2
Isoëtes engelmannii A. Braun	3	2
Isoëtes lacustris L.	1	2
Isoëtes riparia Engelm.	1	2
Isoëtes sp.	6	2
Isoëtes tuckermanii A. Br.	5	2
Isoëtes × *eatonii* R. Dodge	1	2
Juncus pelocarpus E. Mey.	5	3
Lobelia dortmanna L.	3	2
Ludwigia palustris (L.) Ell.	12	3
Marsilia quadrifolia L.	1	3
Megalodonta beckii (Torr. ex Spreng.) Greene	3	2
Myriophyllum alterniflorum DC	1	2
Myriophyllum heterophyllum Michx.	21	4
Myriophyllum humile (Raf.) Morong	13	2
Myriophyllum sibiricum Komarov	2	4
Myriophyllum spicatum L.	28	3
Myriophyllum tenellum Bigel.	5	1
Najas flexilis (Willd.) Rostk. & Schmidt	43	2
Najas gracillima (A. Br.) Magnus	6	2
Najas guadalupensis (Spreng.) Magnus	20	2
Najas minor All.	21	2
Nuphar variegata Engelm. ex Durand	56	5
Nymphaea odorata Ait.	64	5
Nymphaea odorata subsp. *tuberosa* (Paine) Wiersema & Hellquist	2	5
Nymphoides cordata (Ell.) Fern.	9	3
Polygonum amphibium L.	9	4
Pontederia cordata L.	21	3
Potamogeton amplifolius Tuckerm.	26	4
Potamogeton bicupulatus Fern.	41	3
Potamogeton confervoides Reichenb.	1	2
Potamogeton crispus L.	20	3
Potamogeton epihydrus Raf.	40	3

Table 1 (*concluded*).

Species	N	Weight
Potamogeton foliosus Raf.	16	2
Potamogeton friesii Rupr.	1	2
Potamogeton gramineus L.	19	3
Potamogeton hybrid	1	3
Potamogeton illinoensis Morong	5	3
Potamogeton natans L.	20	3
Potamogeton nodosus Poir.	1	3
Potamogeton oakesianus Robbins	4	3
Potamogeton obtusifolius Mert. & Koch	2	2
Potamogeton perfoliatus L.	12	3
Potamogeton praelongus Wulfen	3	3
Potamogeton pulcher Tuckerm.	19	3
Potamogeton pusillus L.	37	2
Potamogeton pusillus subsp. *gemmiparus* (Robbins) Haynes & Hellquist	5	2
Potamogeton robbinsii Oakes	19	3
Potamogeton spirillus Tuckerm.	6	3
Potamogeton vaseyi Robbins	3	2
Potamogeton zosteriformis Fern.	12	3
Proserpinaca palustris L.	3	3
Ranunculus longirostris Godr.	4	1
Sagittaria sp.	23	3
Sparganium sp.	12	3
Stuckenia pectinata (L.) Börner	8	3
Unidentified sedge	5	1
Utricularia geminiscapa Benj.	11	1
Utricularia gibba L.	37	1
Utricularia intermedia Hayne	7	1
Utricularia minor L.	1	1
Utricularia purpurea Walt.	34	2
Utricularia radiata Small	24	1
Utricularia subulata L.	1	1
Utricularia vulgaris L.	28	2
Vallisneria americana Michx.	26	3
Zannichellia palustris L.	3	1
Zosterella dubia (Jacq.) Small	5	3

Note: Those in boldface are invasive species. Also shown are the number of lakes in which each species occurred (*N*) and weights assigned to each species in estimating productivity; weights ranging from 1–5 were used to adjust for differences in the biomass produced by the species (see Materials and methods).

sum of the weighted mean abundance of each species across all samples. Mean abundance of each species was weighted (multiplied by a value ranging from 1 for very small plants to 5 for very robust, floating-leaved plants; Table 1) to adjust for variation in the biomass of the plants. Basing productivity on abundance is common with plants (Tilman et al. 1996) and is valid with aquatic plants because they largely die back each winter, so vegetation appearing in a lake each year is almost entirely the product of that year's growth.

We used linear regression to determine which variables (including pH, conductivity, alkalinity, and phosphorus in surface and bottom samples, lake area, maximum depth, Secchi depth, boat access, motor restrictions, productivity, dominance) had the greatest influence on species richness. Separate analyses were conducted with native and invasive species, limiting analyses of invasives to lakes where they

occurred. Species richness of native species was included in the invasive species regression (and invasives in the regression for natives) to determine whether each group affected the other. We also used logistic regression with the full data set to determine which environmental conditions affected the probability of invasive species' occurrence. Because dominance appeared to be influential in some analyses, we used linear regression to examine which environmental conditions contributed most to the development of dominance.

In linear regression, all variables were entered, and both backward stepwise and forward stepwise procedures were used ($p < 0.15$ to enter a model and $p < 0.05$ to remain) to determine which variables had a significant effect. When results of the two procedures were not the same, the most parsimonious model was chosen based on the Akaike Information Criteria (Zar 1984). In logistic regression, each variable was tested individually for significance, and those that were significant then were entered together, and the reverse stepwise procedure was used. Variables were transformed to satisfy regression assumptions, using natural log transformations in most cases. Productivity and dominance estimates were arcsine square-root transformed. Access and boat motor restriction data were entered as dummy variables. We used Systat (Version 7, SPSS Inc., San Jose, Calif.) to perform all analyses.

Invasive species were those identified as invasive or potentially invasive by the Connecticut Invasive Plants Council. One recently identified species, mud-mat (*Glossostigma cleistanthum* W.R. Barker), was included because it is spreading rapidly through the northeast United States (Les et al. 2006). Taxonomy follows Crow and Hellquist (2000*a*, 2000*b*). Variable-leaf water-milfoil (*Myriophyllum heterophyllum* Michx.) and a hybrid (*Myriophyllum heterophyllum* ×*laxum*) both occur in the northeastern United States, and they cannot be distinguished without molecular analysis (Moody and Les 2002; D.H. Les, personal communication, 2006); both are treated here as *M. heterophyllum*. Two subspecies (*Nymphaea odorata* subsp. *tuberosa* and *Potamogeton pusillus* subsp. *gemmiparus*) are treated as separate species in the analyses. Duckweeds were eliminated from all analyses because of inconsistency in the way they were recorded in the 2 years of the surveys. We prevented the possible double-counting of species (and inflating species richness values) by assuming that a plant identified only to genus in a lake was the same species as another plant of the same genus that was identified to the species level. 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).

Results

We recorded a total of 90 taxa in 99 lakes, including 8 invasive species (Table 1). Invasive species occurred in 63 of the lakes; of lakes with invasives, 33 had a single species, 19 had two, 10 had three, and one had four invasive species. Species richness of native plants ranged from 1–27 species (mean ± SE = 11.3 ± 0.64 species; Table 2), and richness of invasives ranged from 0–4 species (1.7 ± 0.10 species in lakes where invasive species occurred).

Table 2. Mean, standard error, and the range of values for measured and calculated variables in 99 lakes.

Variable	Mean	SE	Range
N	11.3	0.64	0.0–27
I	1.7	0.10	0.0–4
Area (ha)	28.2	3.53	0.1–181.4
Depth (m)	4.8	0.42	1.0–30.0
Secchi (m)	2.4	0.17	0.4–10.2
Conductivity1 (μS/cm)	126.5	7.28	19.4–375.0
pH1	6.6	0.08	4.8–9.3
Alkalinity1 (mg/L)	29.4	2.57	0.7–100.5
Phosphorus1 (ppb)	35	5.3	0.0–334
Conductivity2	143.0	9.10	20.7–600.0
pH2	6.2	0.06	4.8–8.1
Alkalinity2	39.0	3.88	0.8–261.0
Phosphorus2	70	8.2	0.0–369
Dominance	40.0	2.5	2.0–96.0
Productivity	14.6	1.02	0.7–50.0

Note: N, native species richness; I, invasive species richness; Area, surface area of surveyed lakes; Depth, maximum depth of the lakes. Variables with the number 1 are based on surface water samples, and those with the number 2 are based on water samples drawn from just above the bottom. Dominance is a measure, expressed as a percent of maximum possible cover, of the most abundant species' abundance. Productivity is a measure of each lakes' productivity, based on abundance and frequency of the species occurring there.

Many of the independent variables were correlated with each other (Table 3). Linear regression showed that native species richness was significantly correlated with water clarity, productivity, alkalinity, human activity (declining in lakes where motors were prohibited), and lake area ($F_{[5,93]} = 30.30$, $p < 0.0001$; Table 4; Fig. 1A). The best-fit model explained 60% of variability in richness. Linear regression limited to the 63 lakes with invasive species found that alkalinity, pH, and human activity (motor restrictions), were significantly correlated with invasive species richness ($p = 0.0001$; $R^2 = 27\%$; Table 4, Fig. 1B). Logistic regression indicated that the probability of invasive species' occurrence increased with human activity (motor restrictions) and surface water alkalinity but not with other environmental variables (Table 4).

Of the 99 lakes, 29 had high dominance. The dominant species was a native plant in 22 lakes and an invasive in 7. Invasive species were dominant in 11% of the lakes where they occurred, compared with native plants, which were dominant in 22% of the lakes where they occurred ($\chi^2 = 1.71$, $p = 0.19$). The species most frequently found as a dominant are native to Connecticut, coontail (*Ceratophyllum demersum* L.), in six lakes, and Robbins pondweed (*Potamogeton robbinsii* Oakes) in four (Table 5). Among nonnative species, *Myriophyllum heterophyllum* was dominant in three lakes, fanwort (*Cabomba caroliniana* Gray) was dominant in two, and *Najas minor* All. was dominant in one. Eurasian water-milfoil (*Myriophyllum spicatum* L.), which was the most frequently found invasive plant, did not occur as a dominant in any of the surveyed lakes. Of the 82 native plants recorded in the 99 lakes, 10 became dominant in at least one lake, compared with eight invasive species, of which four were dominant in at least one lake ($\chi^2 = 2.87$, $p = 0.09$).

Table 3. Correlation among variables tested for influence on species richness of native and invasive aquatic plant species in 99 Connecticut (northeast USA) ponds and lakes.

	I	*N*	Access	Motors	Area	Depth	Secchi	Cond1
I	1							
N	0.0834	1						
Access	**−0.3727**	**−0.3950**	1					
Motors	−0.3246	**−0.5308**	**0.5277**	1				
Area	**0.4516**	**0.3541**	**−0.4185**	**−0.3828**	1			
Depth	0.2054	0.3503	−0.3271	−0.2013	**0.4962**	1		
Secchi	−0.0923	**0.4457**	−0.2293	−0.2031	0.3224	**0.5562**	1	
Cond1	0.2180	**−0.3760**	0.1244	0.1007	0.0246	0.0155	−0.2803	1
pH1	**0.5080**	−0.2321	−0.0967	0.0275	0.1683	0.1295	−0.1682	**0.4790**
Alk1	0.3160	**−0.3854**	0.0747	0.0932	0.0192	−0.0230	−0.2492	**0.7853**
Phos1	−0.0530	**−0.4235**	0.2107	0.1364	−0.2142	−0.2611	−0.4190	0.1351
Cond2	0.1880	**−0.3987**	0.1400	0.1385	−0.0322	0.0069	−0.2770	**0.9264**
pH2	**0.4727**	−0.3148	0.0726	0.0474	0.1341	0.0636	−0.2435	**0.5862**
Alk2	**0.4213**	−0.2109	0.0183	0.0294	−0.0078	0.1102	−0.2095	**0.5397**
Phos2	−0.0729	**−0.3581**	0.1416	0.2644	−0.3034	−0.0065	−0.2152	0.2966
Dom	0.0909	−0.1170	0.2137	0.0075	−0.2865	−0.3071	−0.2745	−0.1020
Prod	0.1995	0.2599	0.0118	−0.1613	−0.1396	−0.1665	−0.2000	−0.1761

	pH1	Alk1	Phos1	Cond2	pH2	Alk2	Phos2	Dom	Prod
pH1	1								
Alk1	**0.6174**	1							
Phos1	0.0566	0.2058	1						
Cond2	0.4332	**0.7590**	0.1472	1					
pH2	**0.8083**	**0.6954**	0.1913	**0.5618**	1				
Alk2	**0.5062**	**0.7390**	0.1398	**0.6175**	**0.5604**	1			
Phos2	0.1284	**0.4062**	**0.5586**	0.3487	0.1440	0.3203	1		
Dom	−0.0183	−0.0325	0.1120	−0.0990	−0.0469	0.0665	0.0391	1	
Prod	−0.0960	−0.0770	−0.0567	−0.1452	−0.0966	0.0170	−0.0592	**0.7013**	1

Note: Pearson's correlation coefficients significant at the $p = 0.05$ level after Bonferroni correction for multiple comparisons are in boldface. Variable names are as in Table 2.

The variables that were significantly correlated with dominance in multiple linear regression were productivity, lake area, and maximum depth. We analyzed the effect of depth further by dividing lakes into two groups: those with a maximum depth of > 3 m and those with maximum depth < 3 m; within each group, depth had no effect on dominance. Of the 29 lakes with a dominant species, 19 (66%) had a maximum depth of less than 3 m, compared with 20 of the 70 lakes that did not have dominant plants (29%; $\chi^2 = 10.23$, $p = 0.001$), indicating that dominance developed disproportionately in shallow lakes. Because the effect of depth was not linear over the range of the variable, it was removed from the analysis, and the best-fit linear regression model, including productivity and lake area, explained 52% of variation in dominance ($F_{[2, 96]} = 52.80$, $p < 0.0001$; Fig. 2).

Discussion

Our results indicate that abiotic variables and human activities affected both native and invasive species richness. While environmental variables (Secchi depth, alkalinity, and area for native species; alkalinity and pH for invasives) differed somewhat in their effects on the two groups of species, the groups responded identically to human activity: more activity was associated with higher species richness for both native and invasive species. We discuss first the effect of

abiotic variables on richness and dominance, then address the influence of human activities.

The variables that affected species richness have been found to be influential in previous studies of aquatic plants. High transparency allows plants to grow deeper than they could in more turbid water (Squires et al. 2002). The positive effect of area, which was significant only for native species, is believed to be related to the species-area effect (MacArthur and Wilson 1967). Species richness of both native and invasive plants was correlated with alkalinity (Table 2), and its importance (or that of pH) has long been recognized in the northeast United States and eastern Canada (Hellquist 1980; Roberts et al. 1985; Catling et al. 1986; Jackson and Charles 1988; Weiher and Boylen 1994; Srivastava et al. 1995). The effect of alkalinity relates to physiological differences among plants, some of which can use bicarbonate as a carbon source and some of which require carbon dioxide, which is unavailable in waters with even moderately high pH (Madsen and Sand-Jensen 1991). Elodeids, for instance, are most commonly found in nonacidic hardwater lakes (Moyle 1945; Seddon 1972). It is significant that native and invasive plants in Connecticut lakes responded differently to alkalinity. Native species richness declined, while both the richness of invasives and the probability of their occurrence increased. This may reflect differences in the ecological affinities of the native and non-native regional species pools: Among all the potential colonizing

Table 4. Results of linear and logistic regression analyses to determine which variables had the greatest influence on occurrence and species richness of native and invasive aquatic plants in Connecticut lakes.

A. Linear regression for species richness				
Effect	Coefficient	SE	t	p
For native species				
Constant	10.0305	2.0843	4.8125	<0.0001
Secchi	3.5121	0.7701	4.5607	<0.0001
Productivity	0.1728	0.0423	4.0815	0.0001
Motors	−2.0754	0.5671	−3.6597	0.0004
Alk1	−0.0612	0.0166	−3.6924	0.0004
Area	0.9434	0.3562	2.6488	0.0095
For invasive species				
Constant	−1.5795	1.0824	−1.4592	0.1498
Alk2	0.0065	0.0024	2.6867	0.0094
pH2	0.4322	0.1733	2.4935	0.0155
Motors	0.4417	0.1839	2.4018	0.0195

B. Analysis of variance					
Source	Sum-of-Squares	df	Mean-Square	F-ratio	p
For native species[a]					
Regression	2491.0142	5	498.2028	30.3014	<0.0001
Residual	1529.0666	93	16.4416		
For invasive species[b]					
Regression	12.3922	3	4.1307	8.7274	0.0001
Residual	27.9252	59	0.4733		

C. Logistic regression for invasive species occurrence			
Effect	Wald statistic	df	χ^2 significance
Constant	9.3934	4	0.0520
Alk1	12.9119	4	0.0117
Motors	10.5929	4	0.0315

Note: log likelihood, −114.9519; log likelihood of constants only model = LL(0) = −130.9614; 2[LL(N)–LL(0)] = 32.0190 with 12 df; χ^2 p-value = 0.0014; McFadden's ρ^2 = 0.1222.

[a]Adjusted R^2 = 0.5992.
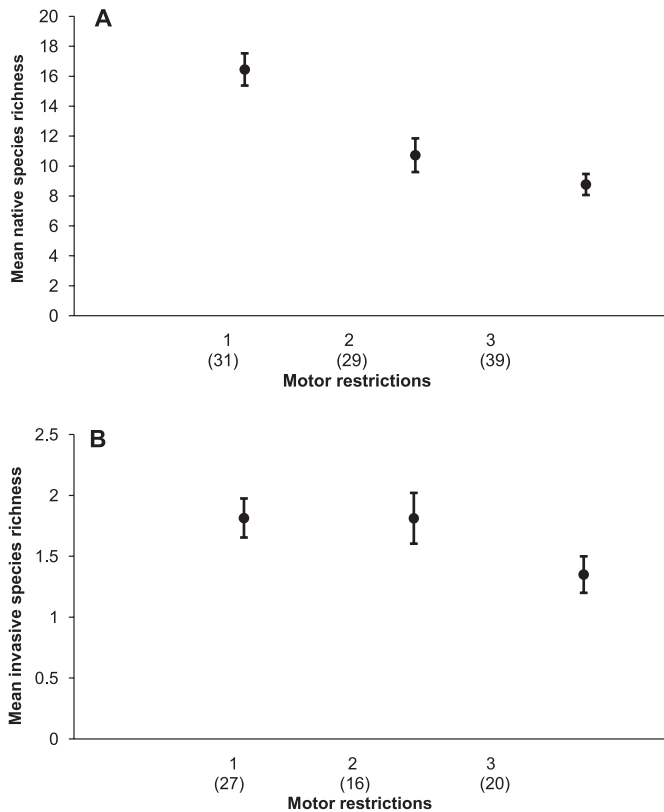
[b]Adjusted R^2 = 0.2721.

species, invasive species may have stronger affinities for alkaline waters. The number of native species with broad ecological tolerance is much higher than the number specializing on the more geographically limited hardwater areas. The affinities of many species have not been determined, but at least two of Connecticut's most frequently found invasives (*Myriophyllum spicatum* and *Potamogeton crispus*) are known to have affinities for alkaline waters (Hellquist 1980; Nichols and Shaw 1986). As a result, invasion probability may be particularly high in areas with alkaline waters, which are largely confined in Connecticut to the coastal plain and limestone hills in the western part of the state.

Boating activity has been widely reported to result in the introduction of invasive aquatic plants because vegetative fragments are carried on boats, especially power boats, and their trailers (Warrington 1985). Johnstone et al. (1985) found invasive aquatic plants in 39 of 47 (83%) of lakes with boating and fishing and none of the 27 lakes without these activities. Boat inspectors in British Columbia found that 4.3% of trailered boats carried fragments of invasive *Myriophyllum spicatum* (213 of 4948 boats), compared with 0.06% of untrailered boats (5 of 7731; Dove and Taylor 1982). Although boating activity may contribute to the

spread of invasive plants in lakes sampled in this study as well, we measured boating only indirectly and cannot isolate its effects from those of many other anthropogenic factors such as increased residential and commercial development and eutrophication that could influence aquatic plant communities. What is significant, however, is that human activity affected not only invasive but also native species. Presumably, the same factors that favour invasives favour natives as well. While this may not be surprising, this effect apparently has not been documented previously. The fact that motors entered the model for native richness even after area was in the model indicates that human activity's positive effect on native richness is not related strictly to the fact that larger lakes are more likely to have boat launches that accommodate power boats and to have extensive residential development of their shorelines. The mechanism by which human activity affects species richness is unclear but could be related to increased propagule pressure (Lockwood et al. 2005) and (or) disturbance (Shea and Chesson 2002).

Nutrient levels appear to have no effect on species richness in the lakes sampled. In waters with low to moderate nutrient levels, plant communities are generally most influenced by sediment texture and water chemistry, usually

Fig. 1. Effect of human activity on (A) native and (B) invasive aquatic plant species richness in 99 Connecticut lakes, in northeastern United States. Human activity was estimated based on the kinds of boat motors allowed in lakes; lakes having power boats were assumed to get more boat traffic (and have more human activity in general) than lakes where motors were banned. Shown are the mean (±1 SE) species richness values in lakes with different rules on use of outboard motors. Motor restrictions were defined as follows: 1, all motors allowed; 2, gas motors banned; 3, no motors allowed. The number of lakes in each category is shown in parentheses. In multiple regression models, species richness of both native and invasive species was significantly lower in lakes where motors were banned.

Table 5. The dominant aquatic plant species recorded in a survey of 99 Connecticut lakes are shown.

Species	N
Ceratophyllum demersum	6
Potamogeton robbinsii	4
Myriophyllum heterophyllum	3
Utricularia purpurea	3
Cabomba caroliniana	2
Elodea nuttallii	2
Nymphaea odorata	2
Brasenia schreberi	1
Najas flexilis	1
Najas gracillima	1
Najas minor	1
Potamogeton crispus	1
Potamogeton pusillus	1
Potamogeton perfoliatus	1

Note: Of the total, 29 lakes had dominant species, defined as species with mean abundance and frequency values of at least 50% of the maximum possible in a lake. Invasive species are in boldface.

Fig. 2. What produces dominance? In surveys of submerged and floating-leaved plant communities in 99 northeastern United States lakes, dominance developed primarily in shallow water bodies with high productivity. Maximum depth was natural log-transformed, and productivity, based on total plant abundance, was arcsine square-root transformed.

measured by pH or alkalinity, and these are determined, in turn, largely by geology (Frink and Norvell 1984). In highly eutrophic lakes, nutrient levels assume greater importance (Srivastava et al. 1995), often as productivity reaches such high levels that biodiversity declines, presumably because of interspecific competition. Although nutrient levels in Connecticut lakes have risen in the past 100 years (Frink and Norvell 1984), their effect appears to be relatively minor at present. One of the few studies to find that trophic level was strongly associated with aquatic plant community composition included lakes with a much higher range of Total P (3000–6000 µg/L; Srivastava et al. 1995). Still, the Connecticut lakes included 20 with Total $P > 100$ µg/L, placing them in the hypertrophic range at which declines in richness have been reported among northern European lakes (Rørslett 1991). That we found no association between species richness and trophic status indicates that nutrient-enriched lakes in Connecticut may have features such as increased habitat diversity that compensates for the loss of

sensitive species, as Rørslett (1991) suggested for European lakes. However, it also is possible that species are declining in abundance in our eutrophic lakes and that they could be locally extirpated by more eutrophic conditions in the future. We measured only species richness, which is an imperfect measure of biological diversity, and the evenness of the abundance distribution of species may be affected by eutrophication before species richness is. We found no evidence that rare species, which would be lost first with increasingly skewed abundance distributions, were less likely to be found in lakes with dominant species than other lakes. Of lakes with high dominance, 72% had at least one species listed as endangered, threatened, or of special concern in Connecticut, compared with 59% of lakes where no species was dominant. Still, eutrophication could be affecting abundance distributions and dominance levels without having any present effect on rare species or on species richness.

Dominance developed primarily in shallow lakes, but all shallow lakes did not have dominant plants. What separated shallow lakes with high dominance from those with low dominance was productivity: most of the shallow lakes with moderate to high productivity had high dominance, and shallow lakes with very low productivity did not (Fig. 2). High levels of dominance often are associated with eutrophication and declining biodiversity, especially in shallow lakes, which Scheffer (2004) defines as those less than 3 m deep. We found that dominance developed in the majority of lakes less than 2.8 m deep, compared with only 16% of deeper lakes. It is significant that non-native plants were no more likely than native species to become dominant, either comparing across species or comparing performance in the lakes where they occurred. The dominant species was a native plant in 76% of the 29 lakes with high dominance. Houlahan and Findlay (2004) found similar results in studying plant diversity in Ontario wetlands. They concluded that the key to conserving biodiversity is to discourage species from becoming community dominants, regardless of their geographic origin.

Neither native nor invasive species richness was significantly affected by richness of the other group. These results suggest that environmental conditions, not biotic interactions, determine community membership among aquatic plants. They suggest that the number of native species does not provide resistance against invasion in aquatic plant communities, as predicted by the community resistance hypothesis. And, as Rørslett (1991) reported for northern European lakes, communities appear open and easily accommodate additional species. The relationship between native and invasive species richness is scale-dependent. Negative correlation is most likely to be observed at the smallest spatial scales, at which neighboring plants interact, and evidence has been found in the studied lakes that high plant density (but not species richness) provides resistance against invasion by some species in individual sampling locations (Capers et al. 2007). At larger scales, correlation between native and invasive richness often is positive (native and invasive richness is uncorrelated at the whole-lake level in this study system; Capers et al. 2007), which can result either from a uniform response to environmental conditions or because of increasing heterogeneity of environmental factors in larger areas (Levine and D'Antonio 1999). Species richness rises with area in the studied lakes, but this increase is not correlated with increases in resource heterogeneity (Capers et al. 2007).

The effects of rising species richness on biotic communities with the addition of non-native species have been little studied (Sax et al. 2002), and it cannot be assumed that they are negative. Introduction of new species does not always lead to local extirpation (Mooney and Cleland 2001); in many cases, newly arrived species are accommodated through altered niche occupancy as a result of competitive interactions (Mooney and Cleland 2001). Furthermore, greater species richness can increase ecosystem stability (Tilman 1996). What is clear is that the studied communities are not saturated and colonization opportunities exist for additional species, native as well as invasive. We need next to identify the mechanisms by which human activities lead to higher species richness (Crowl et al. 2008) and to study the effects of this increase on community dynamics and ecosystem function.

Acknowledgements

References

Andrew, D.E., Clescenti, L.S., and Greenberg, A.E. 1995. Standard methods for the examination of water and wastewater. 19th ed. American Public Health Association, Washington, D.C.

Bergstrom, J.C., Cordell, H.K., Teasley, J.J., Souter, R., Messonier, M.L., Betz, C.J., Smith, M.M., and Barber, L.R. 1993. Aquatic plant coverage and outdoor recreation at Lake Guntersville, Alabama: a study of user preferences, economic values and economic impacts. Joint report of Tennessee Valley Authority, Muscle Shoals, Ala., and U.S. Army Corps of Engineers, Vicksburg, Miss.

Capers, R.S. 2000. A comparison of two sampling techniques in the study of submerged macrophyte richness and abundance. Aquat. Bot. **68**: 87–92. doi:10.1016/S0304-3770(00)00102-9.

Capers, R.S., Selsky, R., Bugbee, G.J., and White, J. 2007. Aquatic plant community invasibility and scale-dependent patterns in native and invasive species richness. Ecology, **88**: 3135–3143. doi:10.1890/06-1911.1. PMID:18229847.

Catling, P.M., Freedman, B., Stewart, C., Kerekes, J.J., and Lefkovitch, L.P. 1986. Aquatic plants of acid lakes in Kejimkujik National Park, Nova Scotia: floristic composition and relation to water chemistry. Can. J. Bot. **64**: 724–729. doi:10.1139/b86-092.

Crow, G.E., and Hellquist, C.B. 2000a. Aquatic and wetland plants of northeastern North America. Vol. 1. Pteridophytes, gymnosperms and angiosperms: dicotyledons. University of Wisconsin Press, Madison, Wisc.

Crow, G.E., and Hellquist, C.B. 2000b. Aquatic and wetland plants of Northeastern North America. Vol. 2. Angiosperms: monocotyledons. University of Wisconsin Press, Madison, Wisc.

Crowl, T.A., Crist, T.O., Parmenter, R.R., Belovsky, G., and Lugo, A.E. 2008. The spread of invasive species and infectious disease as drivers of ecosystem change. Frontiers in Ecology and Environmental Management, **6**(5): 238–246. Published by the Ecological Society of America, Washington, D.C. doi:10.1890/070151.

Dove, R., and Taylor, B. 1982. Studies on Aquatic Macrophytes, Part 34: The 1981 Aquatic plant quarantine project. Ministry of Environment, Province of British Columbia, Victoria, B.C.

Elton, C.S. 1958. The ecology of invasions by animals and plants. Methuen, London, UK.

Engelhardt, K.A.M., and Ritchie, M.E. 2002. The effect of aquatic plant species richness on wetland ecosystem processes. Ecology, **83**: 2911–2924.

Frink, C.R., and Norvell, W.A. 1984. Chemical and physical properties of Connecticut Lakes. Connecticut Agricultural Experiment Station Bulletin No. 817, New Haven, Conn.

Hellquist, C.B. 1980. Correlation of alkalinity and the distribution of *Potamogeton* in New England. Rhodora, **82**: 331–344.

Houlahan, J.E., and Findlay, C.S. 2004. Effect of invasive plant species on temperate wetland plant diversity. Conserv. Biol. **18**: 1132–1138. doi:10.1111/j.1523-1739.2004.00391.x.

Hutchinson, G.E. 1975. A treatise on limnology. Vol. 3. John Wiley, New York, N.Y.

Jackson, S.T., and Charles, D.F. 1988. Aquatic macrophytes in Adirondack (New York) lakes: patterns of species composition in relation to environment. Can. J. Bot. **66**: 1449–1460. doi:10.1139/b88-199.

Johnstone, I.M., Coffey, B.T., and Howard-Williams, C. 1985. The role of recreational boat traffic interlake dispersal of macrophytes: a New Zealand case study. J. Environ. Manag. **20**: 263–279.

Les, D.H., Capers, R.S., and Tippery, N.P. 2006. Introduction of *Glossostigma* (Phrymaceae) to North America: a taxonomic and ecological overview. Am. J. Bot. **93**: 927–939. doi:10.3732/ajb.93.6.927.

Levine, J.M., and D'Antonio, C.M. 1999. Elton revisited: a review of evidence linking diversity and invasibility. Oikos, **87**: 15–26. doi:10.2307/3546992.

Lockwood, J.L., Cassey, P., and Blackburn, T. 2005. The role of propagule pressure in explaining species invasions. Trends Ecol. Evol. **20**: 223–227. doi:10.1016/j.tree.2005.02.004. PMID:16701373.

Lonsdale, W.M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology, **80**: 1522–1536.

MacArthur, R.H., and Wilson, E.O. 1967. Theory of island biogeography. Princeton University Press, Princeton, N.J.

Mack, R., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., and Bazzaz, F.A. 2000. Biotic invasions: causes, epidemiology, global consequences and control. Ecol. Appl. **10**: 689–710. doi:10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2.

Madsen, T.V., and Sand-Jensen, K. 1991. Photosynthetic carbon assimilation in aquatic macrophytes. Aquat. Bot. **41**: 5–40. doi:10.1016/0304-3770(91)90037-6.

McNaughton, S.J., and Wolf, L.L. 1970. Dominance and the niche in ecological systems. Science, **167**: 131–139. doi:10.1126/science.167.3915.131. PMID:5409637.

Moody, M.L., and Les, D.H. 2002. Evidence of hybridity in invasive watermilfoil (*Myriophyllum*) populations. Proc. Natl. Acad. Sci. U.S.A. **99**: 14867–14871. doi:10.1073/pnas.172391499. PMID:12407174.

Mooney, H.A., and Cleland, E.E. 2001. The evolutionary impact of invasive species. Proc. Natl. Acad. Sci. U.S.A. **98**: 5446–5451. doi:10.1073/pnas.091093398. PMID:11344292.

Moyle, J.B. 1945. Some chemical factors influencing the distribution of aquatic plants in Minnesota. Am. Midl. Nat. **34**: 402–420. doi:10.2307/2421128.

Naeem, S., Knops, J.M.H., Tilman, D., Howe, K.M., Kennedy, T., and Gale, S. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos, **91**: 97–108. doi:10.1034/j.1600-0706.2000.910108.x.

Newroth, P.R. 1985. A review of Eurasian water milfoil impacts and management in British Columbia. *In* Proceedings of the 1st International Symposium on Watermilfoil (*Myriophyllum spicatum*) and Related Haloragaceae Species. 23–24 July 1985, Washington, D.C. Aquatic Plant Management Society, Vicksburg, Miss. pp. 139–153.

Nichols, S.A., and Shaw, B.H. 1986. Ecological life histories of the three aquatic nuisance plants, *Myriophyllum spicatum*, *Potamogeton crispus* and *Elodea canadensis*. Hydrobiologia, **131**: 3–21. doi:10.1007/BF00008319.

Pimentel, D., Lach, L., Zuniga, R., and Morrison, D. 2000. Environmental and economic costs of nonindigenous species in the United States. Bioscience, **50**: 53–65. doi:10.1641/0006-3568(2000)050[0053:EAECON]2.3.CO;2.

Pimentel, D., Zuniga, R., and Morrison, D. 2005. Update on the en-

vironmental and economic costs associated with alien-invasive species in the United States. Ecol. Econ. **52**: 273–288. doi:10.1016/j.ecolecon.2004.07.013.

Roberts, D.A., Singer, R., and Boylen, C.W. 1985. Three submersed macrophyte communities of Adirondack lakes (New York, U.S.A.) of varying degrees of acidity. Aquat. Bot. **21**: 219–235. doi:10.1016/0304-3770(85)90050-6.

Rockwell, H.W. 2003. Summary of a survey of the literature on the economic impact of aquatic weeds. [Online]. Report for the Aquatic Ecosystem Restoration Foundation, Marietta, Ga. Available from www.aquatics.org/pubs/economic_impact.pdf [accessed 24 May 2006].

Rørslett, B. 1991. Principal determinants of aquatic macrophyte richness in northern European lakes. Aquat. Bot. **39**: 173–193. doi:10.1016/0304-3770(91)90031-Y.

Sax, D.F., Gaines, S.D., and Brown, J.H. 2002. Species invasions exceed extinctions on islands worldwide: a comparative study of plants and bees. Am. Nat. **160**: 766–783. doi:10.1086/343877. PMID:18707464.

Scheffer, M. 2004. Ecology of shallow lakes. Kluwer Academic Publishers, Dordrecht, the Netherlands.

Seddon, B. 1972. Aquatic macrophytes as limnological indicators. Freshw. Biol. **2**: 107–130. doi:10.1111/j.1365-2427.1972.tb00365.x.

Shea, K., and Chesson, P. 2002. Community ecology theory as a framework for biological invasions. Trends Ecol. Evol. **17**: 170–176. doi:10.1016/S0169-5347(02)02495-3.

Squires, M.M., Lesack, L.F.W., and Huebert, D. 2002. The influence of water transparency on the distribution and abundance of macrophytes among lakes of the Mackenzie Delta, Western Canadian Arctic. Freshw. Biol. **47**: 2123–2135. doi:10.1046/j.1365-2427.2002.00959.x.

Srivastava, D.S., Staicer, C.A., and Freedman, B. 1995. Aquatic vegetation of Nova Scotian lakes different in acidity and trophic status. Aquat. Bot. **51**: 181–196. doi:10.1016/0304-3770(95)00457-B.

Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkhan, M.A., Schell, L.D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M., and Son, Y. 1999. Exotic plant species invade hot spots of native plant diversity. Ecol. Monogr. **69**: 25–46.

Tilman, D. 1996. Biodiversity: population versus ecosystem stability. Ecology, **77**: 350–363. doi:10.2307/2265614.

Tilman, D., Wedin, D., and Knops, J. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature (London), **379**: 718–719. doi:10.1038/379718a0.

Vitousek, P.M., D'Antonio, C.M., Loope, L.I., and Westerbrooks, R. 1996. Biological invasions as global environmental change. Am. Sci. **84**: 468–478.

Warrington, P.D. 1985. Factors associated with the distribution of *Myriophyllum* in British Columbia. *In* Proceedings of the 1st International Symposium on Watermilfoil (*Myriophyllum spicatum*) and Related Haloragaceae Species, 23–24 July 1985, Vancouver, British Columbia. Aquatic Plant Management Society, Vicksburg, Miss. pp. 79–94.

Weiher, E.R., and Boylen, C.W. 1994. Alterations in aquatic plant community structure following liming of an acidic Adirondack lake. Can. J. Fish. Aquat. Sci. **51**: 20–24. doi:10.1139/f94-004.

Westlake, D.F. 1969. Macrophytes. *In* A manual on methods for measuring primary production in aquatic environments. *Edited by* R.A Vollenweider. IBP Handbook No. 12. Blackwell Scientific Publications, Oxford, UK. pp. 25–32.

Zar, J.H. 1984. Biostatistical analysis. 2nd ed. Prentice Hall, Englewood Cliffs, N.J.