The relative importance of local conditions and regional processes in structuring aquatic plant communities

ROBERT S. CAPERS*, ROSLYN SELSKY† AND GREGORY J. BUGBEE†
*Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, U.S.A.
†Department of Soil and Water, The Connecticut Agricultural Experiment Station, New Haven, CT, U.S.A.

SUMMARY

1. The structure of biological communities reflects the influence of both local environmental conditions and processes such as dispersal that create patterns in species' distribution across a region.
2. We extend explicit tests of the relative importance of local environmental conditions and regional spatial processes to aquatic plants, a group traditionally thought to be little limited by dispersal. We used partial canonical correspondence analysis and partial Mantel tests to analyse data from 98 lakes and ponds across Connecticut (northeastern United States).
3. We found that aquatic plant community structure reflects the influence of local conditions (pH, conductivity, water clarity, lake area, maximum depth) as well as regional processes.
4. Only 27% of variation in a presence/absence matrix was explained by environmental conditions and spatial processes such as dispersal. Of the total explained, 45% was related to environmental conditions and 40% to spatial processes.
5. Jaccard similarity declined with Euclidean distance between lakes, even after accounting for the increasing difference in environmental conditions, suggesting that dispersal limitation may influence community composition in the region.
6. The distribution of distances among lakes where species occurred was associated with dispersal-related functional traits, providing additional evidence that dispersal ability varies among species in ways that affect community composition.
7. Although environmental and spatial variables explained a significant amount of variation in community structure, a substantial amount of stochasticity also affects these communities, probably associated with unpredictable colonisation and persistence of the plants.

Keywords: dispersal, macrophytes, metacommunities, spatial structure, variance partitioning

Introduction

Most organisms are distributed non-randomly in space. They can show such spatial pattern if essential components of the environment are, themselves, patterned (Legendre & Fortin, 1989; Briers & Biggs,

2005; Cottenie, 2005; Beisner *et al.*, 2006). In other cases, spatial structure may result from dispersal, interspecific interactions such as competition or predation, or geological, climatic or historical processes such as continental drift, glaciation and human land use patterns (Borcard, Legendre & Drapeau, 1992; Hughes Martiny *et al.*, 2006; Thum & Stemberger, 2006; Fierer *et al.*, 2007; Mykra, Heino & Muotka, 2007). Some of these factors act locally and others regionally. The metacommunity concept (Leibold

Correspondence: Robert S. Capers, Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs CT 06269-3043, U.S.A. E-mail: robert.capers@uconn.edu

et al., 2004) explicitly recognises that both regional and local factors influence the composition of isolated communities that are linked by dispersal. The effect of competition and predation is assumed to have importance primarily at the local community level. Regional variation in environmental conditions influences community composition as species sort themselves along environmental gradients, but this is regulated by dispersal rates: high dispersal rates allow species to reach all localities with suitable conditions, producing a close relationship between the regional distribution of species and the regional distribution of environmental conditions (Vanormelingen *et al.*, 2008). With low dispersal rates, species are constrained to fewer localities, and the relationship with regional environmental variation is less strong. Thus, techniques that isolate the effect of regional variation in the environment permit inferences to be drawn about the relative importance of dispersal.

The proportion of variation in community composition that is related to environmental conditions is expected to be higher among organisms that are not limited by dispersal, with the extreme case in which all variation is explained by environmental conditions. At the opposite end of the spectrum are species for which environmental variation is unnecessary to explain distribution and for whom neutral community models are appropriate (Bell, 2001; HubBell, 2001). Thus, the variation that is not explainable by environmental conditions can be used to compare the relative importance of dispersal limitation and niche-determining processes across taxa (Cottenie, 2005; Beisner *et al.*, 2006). For example, Beisner *et al.* (2006) found that fish communities were structured only by dispersal and not at all by environmental conditions, whereas only environmental conditions (primarily dissolved carbon) affected community composition of bacteria. The evidence in some cases has been conflicting, however, and assumptions about dispersal limitation have not always been supported by evidence. Dispersal limitation has been found even in bacteria (Papke *et al.*, 2003), which had been thought to disperse widely and to have geographical distributions limited only by environmental conditions – ''everything is everywhere, but the environment selects'' (Baas-Becking, 1934; Finlay, 2002).

Aquatic plants traditionally have been thought to be limited very little by dispersal, based on the observa-

tion that many species are widely distributed (Darwin, 1859; Sculthorpe, 1967). Many species produce vegetative propagules that readily colonise newly available habitat (Barrat-Segretain & Amoros, 1996; Capers, 2003a). Seeds and fruits can be carried thousands of kilometres by waterfowl (Figuerola & Green, 2002), and at least occasional long-distance dispersal of these propagules appears to account for the cosmopolitan distribution of many (Les *et al.*, 2003). Genetic analyses, however, have found evidence of differentiation related to gene flow both among and within populations (Hollingsworth, Preston & Gornall, 1996; Gornall, Hollingsworth & Preston, 1998). Research at the regional scale has shown that connectivity in floodplain lakes increases species richness and community similarity (Bornette, Amoros & Lamouroux, 1998; Coops *et al.*, 1999), but among lakes and ponds, the relative influence of environmental conditions and dispersal limitation on community structure has not been tested explicitly, and the ability of aquatic plants to disperse long distances occasionally may be only weakly related to the distribution of plants on a smaller geographical scale.

The organisation of aquatic plant communities has broad ecological implications, because aquatic plants have been used as indicator species that integrate many measures of environmental health (Grasmück *et al.*, 1995; Thiébaut & Muller, 1998); thus, the plant community affects light (Ray, Rebertus & Ray, 2001), temperature (Unmuth *et al.*, 2000), turbulence (Petticrew & Kalff, 1992), water and sediment chemistry (Wigand, Stevenson & Cornwell, 1997) and the abundance and composition of other organisms, including phytoplankton (Mjelde & Faafeng, 1997), invertebrates (Dvorak & Best, 1982) and fish (Chick & McIvor, 1994). Here, we assess the relative importance of environmental conditions and of dispersal for structuring aquatic plant communities in lakes and ponds across a region of 12 500 km^2. We use ordination to examine whether the regional distribution of submerged and floating-leaved plants can be explained entirely in terms of the distribution of environmental variables, as would be the case if the plants are unlimited by dispersal, or whether there is spatial pattern in the plants' distribution after accounting for the effect of environmental conditions. This finding would suggest that the distribution of the plants is limited to some degree by their inability to reach all available lakes. We also evaluated whether

community similarity declines with distance among lakes, after accounting for differences in environmental conditions, as it would if dispersal limits distribution. Finally, we tested whether dispersal-related functional traits can explain the geographical distribution of species.

Methods

Sampling methodology

We conducted surveys of 98 lakes and ponds in the state of Connecticut in the northeastern United States between late June and late September of both 2004 and 2005. We selected lakes non-randomly but included water bodies in all areas of the state, of varying perturbation by humans and across a range of environmental conditions. We conducted surveys from small boats, slowly paddling or motoring through all areas shallow enough to support aquatic plants, recording all submerged and floating-leaved species (emergent species were recorded only if they were growing submerged), 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. Although samples with a grapple may underestimate true richness (Capers, 2000), this is unlikely to affect the results presented here because these 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 was 1.8 m). We also established line transects (80 m long) perpendicular to the shoreline in each lake (full details in Capers *et al.*, 2007), and combined species recorded in transects with those identified in surveys to compile the full species list for each lake. Taxonomy followed Crow & Hellquist (2000*a,b*). Both *Myriophyllum heterophyllum* Michx. and a hybrid (*Myriophyllum heterophyllum* X *laxum*) occur in the region, and they can be distinguished only with molecular analysis (Moody & Les, 2002); we treated both as *M. heterophyllum*. We removed plants in the Lemnaceae from the analysis because their occurrence was recorded inconsistently during the 2 years of the surveys. We deposited voucher specimens at the University of Connecticut (CONN) and the Connecticut Agricultural Experiment Station (NHES).

We recorded the latitude and longitude of the deepest point in each lake with Trimble GeoXT and Garmin 76 GPS units (Trimble Navigation Ltd, Sunnyvale, CA, U.S.A.; Garmin Ltd, Olathe, KS, U.S.A.). We measured water clarity (Secchi depth) at that location and recorded water temperature and dissolved oxygen 0.5 m below the surface and 0.5 m above the bottom, using a YSI 58 meter (YSI Inc., Yellow Springs, OH, U.S.A). We obtained water samples at the same depths, and these were stored at 3 °C until analysed for pH, alkalinity, conductivity and total phosphorus. Conductivity and pH were measured with a Fisher-Accumet AR20 m (Fisher Scientific International Inc., Hampton, NH, U.S.A.). Alkalinity was quantified by titration and expressed as milligram per litre $CaCO_3$. 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 performed using the ascorbic acid method and potassium persulphate digestion (Eaton, Clescenti & Greenberg, 1995).

Statistical analyses

We constructed a presence/absence matrix of all species present in the 98 lakes, and this was reduced to species present in five or more lakes ($n = 57$ species). We used canonical correspondence analysis (CCA; Ter Braak, 1986; Legendre & Legendre, 1998) executed with Canoco (Version 4.5, Ter Braak & Šmilauer, 2002) to estimate the proportion of variation in community composition that was associated with local environmental variables and regional spatial structure. We began the analysis with 15 environmental variables (dissolved oxygen, water temperature, alkalinity, pH, conductivity and phosphorus content at both the surface and just above the bottom of each lake, plus lake area, Secchi depth and maximum depth). All variables except pH were Ln-transformed to improve normality, and all variables then were transformed to their standard normal deviate equivalents ([x – mean] divided by the standard deviation) to accommodate the different units used to measure the variables. We used correlation and a preliminary CCA to identify variables that were uninformative or strongly correlated with other variables, and these were removed. Because all seven of the remaining environmental variables entered the model in at least some of the analyses,

we included all as potential explanatory variables and covariates in the analyses. These seven variables were as follows: lake area (Area), Secchi depth (Secchi), maximum depth (Depth), pH of bottom water (pH), conductivity of bottom water (Conductivity), phosphorus content of bottom water (P) and dissolved oxygen of surface water (DO). Spatial structure in the data was determined by including nine variables needed to compose a cubic trend surface (Borcard *et al.*, 1992), which ensures that not only linear patterns in the species data were identified but also complex features such as gaps and patches were identified. The nine spatial variables were the latitude (Lat) and longitude (Lon) of each lake, plus LatLon, Lat^2, Lon^2, Lat^2Lon, $LatLon^2$, Lat^3 and Lon^3. All analyses were run with forward selection ($\alpha = 0.05$), using a Monte Carlo test with 999 permutations under the reduced model to test the significance of variables.

We used partial CCA (Borcard *et al.*, 1992; Legendre & Legendre, 1998) to estimate the proportion of variation that could be attributed separately to environmental variables and spatial components. To partition variation in this way, separate analyses were conducted, first using environmental and spatial variables alone as independent variables and then conducting analyses in which one set of variables was used as independent variables and the other variables were included as covariates (Borcard *et al.*, 1992; Legendre & Legendre, 1998). The proportion of variation explained was calculated as the sum of all constrained eigenvalues divided by the total inertia. Variation components are given as follows: total environmental variation, including any spatial component [E]; total spatial variation, including any environmental component [S]; environmental variation with no spatial component [E|S] and spatial variation with no environmental component [S|E]. We calculated variation resulting from correlation of environmental variables with spatial structure as [E]–[E|S] and the total proportion of variation explained as [E + S|E] (Borcard *et al.*, 1992; Legendre & Legendre, 1998).

Partial CCA isolates the respective effects of space and environmental conditions, but spatial structure can take several shapes and may not be related exclusively to distance and dispersal. To examine more specifically whether dispersal affects aquatic plant communities, we used Mantel tests to determine whether distance between lakes was correlated with community similarity (Legendre & Fortin, 1989). We first conducted Mantel tests using only distance and similarity matrices. The distance matrix contained the pairwise Euclidean distances between all lakes, calculated from the latitude and longitude, then centred and standardised. The similarity matrix contained the pairwise Jaccard similarity of aquatic plant communities between lakes, calculated using EstimateS (Colwell, 2006). Because a relationship between similarity and distance may be affected by environmental conditions, we also conducted Mantel tests to determine whether distance among lakes was correlated with pairwise differences between values of the environmental variables. We then used partial Mantel tests (Legendre & Fortin, 1989; Hughes Martiny *et al.*, 2006) to determine whether distance and community similarity were correlated after removing the potentially confounding effects of the significant environmental variables. This was carried out with Mantel tests of matrices assembled from the residuals of linear regression analyses involving the similarity, distance and environment matrices. We also tested the residuals of multiple regressions including all significant environmental variables, thus simultaneously removing the effect of all the environmental variables from the partial Mantel analysis. The significance of correlations was tested with 999 permutations (one-tailed test with $\alpha = 0.05$), using PopTools (Hood, 2006).

To investigate more explicitly the role of dispersal, we assessed the effect that functional traits linked to dispersal had on the geographical distribution of plant species. To do this, we first analysed the distribution of distances among lakes where a species occurred, calculating the proportion of interlake distances that were between 0 and 20 km, the proportion that were 20 and 40 km apart, etc. We assumed that species having better-than-average dispersal abilities should have a higher proportion of short interlake distances than species with poor dispersal abilities because of the importance of streams connecting nearby lakes. The interlake distances for all species are inevitably influenced by the distances among the lakes themselves, so we compared the interlake distance distribution for each species to that for the lakes themselves to establish whether species dispersed more or less well than expected. To determine the statistical significance of each species' departure from the all-lakes distribution, we calculated the interlake distances for a random draw of lakes (n = the number of lakes in which each

species occurred) and then repeated the procedure 1000 times to determine the probability that a departure as great as observed in each 20-km distance class occurred by chance. We limited this analysis to the 26 species occurring in 20 or more lakes because they should provide the strongest signal if dispersal ability influences distribution of aquatic plants. We also limited the analysis to interlake distances of 100 km or less, where any dispersal limitation would be most likely to appear. Next, we assembled information on functional traits linked to dispersal, based on Willby, Abernethy & Demars (2000) and other sources from the aquatic plant literature (Barrat-Segretain, 1996; Crow & Hellquist, 2000a,b) among others. We divided species into categories based on the number of traits likely to increase their dispersal: reproducing sexually, producing large numbers of reproductive structures, dispersing readily with vegetative fragments, spreading on stolons or rhizomes, producing other kinds of propagules such as winter buds or turions, growing unrooted and remaining viable while being distributed by birds and/or boats. We used Fisher's exact test to assess the independence of the interlake distance distribution of species and their dispersal-related functional traits.

Results

Plant communities

We recorded 91 species in the 98 surveyed lakes, species richness ranging from 0 to 28 (mean ± standard error, 12.4 ± 0.68 species). After species present in fewer than five lakes were removed from the dataset, 57 remained (Table 1) and richness ranged from 0 to 27, with a mean of 11.7 ± 0.64 species. The most frequent species were floating-leaved plants *Nymphaea odorata* (in 63 lakes), *Nuphar variegata* (55) and *Brasenia schreberi* (52) and the submerged *Elodea nuttallii* (46), *Najas flexilis* (43) and *Potamogeton bicupulatus* (41). The range of environmental variables is listed in Table 2, and correlation among them is summarised in Table 3.

Relative contribution of local and regional factors

The fraction of variation explained by the local (environmental) and regional (spatial) variables, alone and together, was always highly significant ($P = 0.001$; Monte Carlo test of first constrained axis).

Table 1 In surveys of 98 lakes in Connecticut, U.S.A., 91 submerged and floating-leaved aquatic plant taxa were recorded, of which 57 were present in five or more lakes. Shown are those species and the number of lakes in which each occurred

Species	N
Brasenia schreberi J. F. Gmel.	52
Cabomba caroliniana Gray	10
Callitriche sp.	7
Ceratophyllum demersum L.	39
Ceratophyllum echinatum Gray	14
Elatine minima (Nutt.) Fisch. & Mey.	19
Eleocharis acicularis (L.) Roemer & J. A. Schultes	31
Eleocharis sp.	21
Elodea canadensis Michx.	8
Elodea nuttallii (Planch.) St. John	46
Eriocaulon aquaticum (Hill) Druce	25
Gratiola aurea Pursh	20
Isoëtes echinospora Dur.	10
Isoëtes sp.	6
Isoëtes tuckermanii A. Br.	5
Juncus pelocarpus E. Mey.	5
Ludwigia palustris (L.) Ell.	12
Myriophyllum heterophyllum Michx.	17
Myriophyllum humile (Raf.) Morong	13
Myriophyllum spicatum L.	27
Myriophyllum tenellum Bigel.	5
Najas flexilis (Willd.) Rostk. & Schmidt	43
Najas gracillima (A. Br.) Magnus	6
Najas guadalupensis (Spreng.) Magnus	19
Najas minor All.	21
Nuphar variegata Engelm. ex Durand	55
Nymphaea odorata Ait.	63
Nymphoides cordata (Ell.) Fern.	9
Polygonum amphibium L.	9
Pontederia cordata L.	21
Potamogeton amplifolius Tuckerm.	25
Potamogeton bicupulatus Fern.	41
Potamogeton crispus L.	20
Potamogeton epihydrus Raf.	40
Potamogeton foliosus Raf.	16
Potamogeton gramineus L.	18
Potamogeton gemmiparus (Robbins) Haynes & Hellquist	5
Potamogeton illinoensis Morong	5
Potamogeton natans L.	20
Potamogeton perfoliatus L.	12
Potamogeton pulcher Tuckerm.	19
Potamogeton pusillus L.	37
Potamogeton robbinsii Oakes	18
Potamogeton spirillus Tuckerm.	6
Potamogeton zosteriformis Fern.	11
Sagittaria sp.	22
Sparganium sp.	12
Stuckenia pectinata (L.) Börner	8
Unidentified sedge	5
Utricularia geminiscapa Benj.	11
Utricularia gibba L.	37
Utricularia intermedia Hayne	7
Utricularia purpurea Walt.	34

Table 1 (*Continued*)

Species	N
Utricularia radiata Small	24
Utricularia vulgaris L.	28
Vallisneria americana Michx.	26
Zosterella dubia (Jacq.) Small	5

Table 2 The lake and water variables used in the ordination and similarity analyses of aquatic plant communities in 98 lakes and ponds in Connecticut, U.S.A.

	Mean	SE	Median	Minimum	Maximum
Area (ha)	28.2	3.6	15.2	0.1	181.4
Secchi (m)	2.4	0.2	2.0	0.4	10.2
DO	7.2	0.3	7.2	0.3	24.5
Maximum depth (m)	4.9	0.4	3.8	1	30
Conductivity (uS cm^{-1})	143	9	123	21	600
pH	6.2	0.1	6.2	4.8	8.1
P (ppb)	70	8	49	n.d.	369

Note: (n.d. = not detected.) Measurements of surface water were used for dissolved oxygen, and measurements of water taken from the bottom of the studied lakes were used for pH, conductivity and phosphorus.

Table 3 Correlation among the seven environmental variables that were included in the canonical correspondence analysis of aquatic plants

	Area	Depth	Secchi	DO	Cond	pH	P
Area	1						
Depth	0.4965	1					
Secchi	0.3228	0.5587	1				
DO	0.2234	0.2835	0.2007	1			
Cond	−0.0321	0.0074	−0.2775	−0.0246	1		
pH	0.1343	0.0652	−0.2449	0.2748	0.5618	1	
P	−0.3031	−0.0060	−0.2157	−0.1097	0.3485	0.1436	1

With all environmental and spatial variables entered together, the first four canonical axes accounted for 17% of variation in species data and 62% of variation in the species–environment relationship. Overall, environmental and spatial variables together explained 27.5% of variation in species occurrences, leaving 72.5% unexplained (S1). Of the total variation, 16.7% was associated with environmental variables, and 15.0% was associated with spatial structure. Of

the variation explained by environmental variables, 25% was correlated with spatial variables.

Forward selection identified five environmental variables that entered the CCA: pH, Conductivity, Area, Depth and Secchi. Among environmental variables, Axis 1 was most strongly related with pH and Conductivity (interset correlation of 0.74 and 0.61, respectively) after accounting for spatial structure in the environment (Fig. 1a). Axis 2 was most strongly associated with Area, DO and P (interset correlations of 0.51, 0.44 and −0.43, respectively). Among the spatial variables, three were significant in explaining species' distributions: Lon, LatLon and LatLon^2. In a CCA including only spatial variables, Axis 1 was most strongly related with longitude; the interset correlation was −0.65, becoming −0.51 when environmental covariates were entered, indicating that the measured abiotic conditions varied from east to west across the region (Fig 1b). Entering covariates also affected the proportion of variation explained (Table 4). Both pH and Conductivity had large spatial components but retained significant explanatory power after spatial covariates were entered (Fig. 1a). Secchi, however, no longer entered the model when spatial covariates were entered, indicating that it was highly correlated with spatial pattern. All three spatial variables remained significant when environmental variables were entered as covariates (Fig. 1b).

Among the species, most closely associated species with high pH and conductivity were *Potamogeton illinoensis*, *Stuckenia pectinata* and *Potamogeton crispus*, whereas *Myriophyllum humile* was associated most closely with acidic water (Fig. 1a). Species separating along Axis 2 included *Najas gracillima*, *P. perfoliatus* and *Myriophyllum tenellum*, all associated with larger lakes and low phosphorus concentration, whereas *Potamogeton foliosus* was associated with smaller, eutrophic lakes at the other end of Axis 2. The results also suggest that high nutrient concentrations are associated with small ponds and that larger lakes tend to have higher clarity and higher DO (Fig. 1a).

Community similarity

Mean Jaccard similarity between plant communities was 0.17 (range 0–0.75), indicating that communities shared fewer than 20% of species on average; < 1% of all similarity values were > 0.50. Mantel tests indi-

Fig. 1 Biplot of CCA of 57 aquatic plant species in 98 lakes, showing the first two axes and the most strongly correlated environmental variables (a) and spatial variables (b). Only variables with $r > 0.40$ are shown ($r > 0.25$ in b). Spatial variables were entered as covariates in a, and environmental covariates were entered in b. Species abbreviations are: Brashr, *Brasenia schreberi*; Cabcar, *Cabomba caroliniana*; Callsp, *Callitriche* sp.; Cerdem, *Ceratophyllum demersum*; Cerech, *Ceratophyllum echinatum*; Elamin, *Elatine minima*; Elecic, *Eleocharis acicularis*; Elesp, *Eleocharis* sp.; Elocan, *Elodea canadensis*; Elonut, *Elodea nuttallii*; Eriaqu, *Eriocaulon aquaticum*; Graaur, *Gratiola aurea*; Isoech, *Isoetes echinospora*; Isosp, *Isoetes* sp.; Isotuc, *Isoetes tuckermanii*; Junpel, *Juncus pelocarpus*; Ludpal, *Ludwigia palustris*; Myrhet, *Myriophyllum heterophyllum*; Myrhum, *Myriophyllum humile*; Myrspi, *Myriophyllum spicatum*; Myrten, *Myriophyllum tenellum*; Najflx, *Najas flexilis*; Najgra, *Najas gracillima*; Najgua, *Najas guadalupensis*; Najmin, *Najas minor*; Nupvar, *Nuphar variegata*; Nymcor, *Nymphoides cordata*; Nymodo, *Nymphaea odorata*; Polamp, *Polygonum amphibium*; Poncor, *Pontederia cordata*; Potamp, *Potamogeton amplifolius*; Potbic, *Potamogeton bicupulatus*; Potcri, *Potamogeton crispus*; Potepi, *Potamogeton epihydrus*; Potfol, *Potamogeton foliosus*; Potgem, *Potamogeton gemmiparus*; Potgra, *Potamogeton gramineus*; Potill, *Potamogeton illinoensis*; Potnat, *Potamogeton natans*; Potper, *Potamogeton perfoliatus*; Potpul, *Potamogeton pulcher*; Potpus, *Potamogeton pusillus*; Potrob, *Potamogeton robbinsii*; Potspi, *Potamogeton spirillus*; Potzos, *Potamogeton zosteriformis*; Sagsp, *Sagittaria* sp.; Spasp, *Sparganium* sp.; Stupec, *Stuckenia pectinatus*; Unised, Unidentified sedge; Utrgem, *Utricularia geminiscapa*; Utrgib, *Utricularia gibba*; Utrint, *Utricularia intermedia*; Utrpur, *Utricularia purpurea*; Utrrad, *Utricularia radiata*; Utrvul, *Utricularia vulgaris*; Valame, *Vallisneria americana*; Zosdub, *Zosterella dubia*.
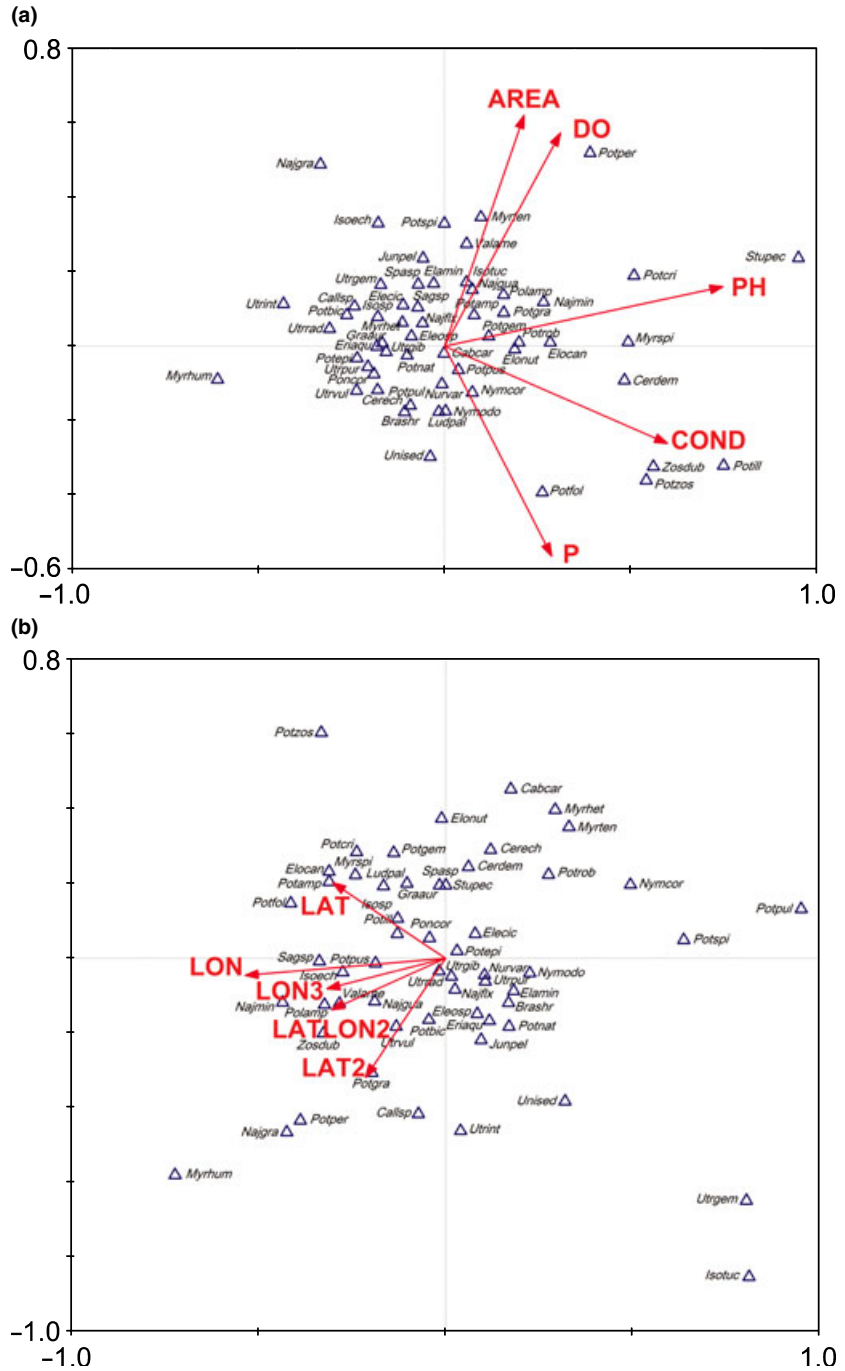
cated that the Euclidean distance between lakes was significantly and negatively correlated with similarity ($r = -0.17$, $P < 0.001$; i.e. as distance between lakes increased, the plant communities became less similar; Fig. 2). Mantel tests also indicated that distance was correlated with differences among lakes in three environmental variables – all positively, indicating that differences among environmental conditions increased with distance: pH ($r = 0.14$, $P < 0.005$), Conductivity ($r = 0.26$, $P < 0.001$) and P ($r = 0.11$, $P = 0.031$). Distance was not correlated with differences among lakes in DO ($r = -0.03$, $P = 0.74$), Secchi ($r = 0.05$, $P = 0.15$), Area ($r = 0$, $P = 0.44$) or Depth ($r = 0.05$, $P = 0.17$).

Table 4 Comparison of marginal and conditional λ values for CCA analyses

Variable	Marginal λ	Conditional λ		
		E	E+S	S
pH	0.25	0.16	0.25	–
Cond	0.19	0.06	0.07	–
DO	0.09	0.04	0.05	–
Area	0.08	0.06	0.07	–
Depth	0.08	0.06	0.07	–
Secchi	0.08	0.03	0.05	–
P	0.08	0.04	0.04	–
Lon	0.16	–	0.16	0.06
Lon^3	0.12	–	0.05	0.04
Lat^{2}Lon	0.10	–	0.05	0.03
LatLon^2	0.06	–	0.07	0.05
LatLon	0.06	–	0.06	0.05
Lat	0.06	–	0.04	0.04
Lat^3	0.05	–	0.05	0.04
Lat^2	0.05	–	0.03	0.04
Lon^2	0.03	–	0.03	0.04

Note: Marginal λ refers to the variance in species occurrences explained by the variable alone. Conditional λ refers to the additional variation in species occurrences explained after inclusion of other variables in the forward selection procedure.

Partial Mantel tests indicated that the significant correlation between similarity and distance remained after removing the effects of the three environmental variables correlated with distance: pH ($r = -0.14$, $P < 0.001$), Conductivity ($r = -0.13$, $P < 0.001$) and P ($r = -0.16$, $P < 0.001$). Distance and similarity were less strongly correlated after simultaneously removing the effect of the three environmental variables, but the correlation was still highly significant ($r = -0.10$, $P = 0.004$). This correlation indicates that differences in environmental variables related to distance cannot entirely explain the difference in community similarity. Communities become increasingly dissimilar with distance even after accounting for distance-related differences in environmental conditions. Similarity was significantly correlated with differences in pH ($r = -0.25$, $P < 0.001$), Conductivity ($r = -0.20$, $P < 0.001$), P ($r = -0.16$, $P = 0.007$), DO ($r = -0.13$, $P = 0.004$) and Secchi ($r = -0.08$, $P = 0.05$) but not Area ($r = -0.04$, $P = 0.25$) or Depth ($r = 0$, $P = 0.49$). Partial Mantel tests indicated that, after the effect of distance was removed, the correlation remained between similarity and differences in all five environmental variables (pH: $r = -0.14$, $P < 0.007$; Conductivity: $r = -0.12$, $P < 0.01$; P: $r = -0.15$, $P = 0.006$; DO: $r = -0.17$, $P = 0.006$ and Secchi: $r = -0.16$, $P = 0.01$).
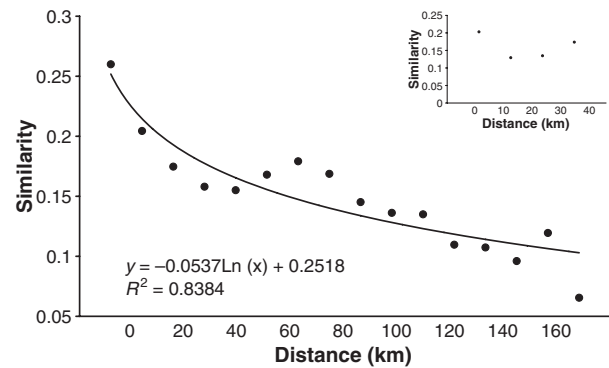
Fig. 2 The similarity of aquatic plant communities declined with the pairwise distance between lakes. The mean Jaccard similarity value in 10-km distance classes is plotted here against distance. A logarithmic trend line best characterised the decline in similarity with distance. The inset shows the non-significant correlation between similarity and distance in lakes in a smaller geographical area, New Haven County (see text).

Dispersal-related traits analysis

Twenty-six species were sufficiently widespread to analyse their interlake distance distributions, being present in 20 or more lakes. Of these, four were significantly under-dispersed (Table 5), occurring in significantly fewer nearby lakes than expected (*Nymphaea odorata*, *Nuphar variegata*, *Brasenia schreberi* and *Pontederia cordata*; Fig. 3). Thirteen were significantly over-dispersed (*Ceratophyllum demersum*, *Utricularia purpurea*, *U. radiata*, *Myriophyllum heterophyllum*, *Najas minor*, *Elodea nuttallii*, *Potamogeton epihydrus*, *P. amplifolius*, *P. natans*, *P. crispus*, *Elatine minima*, *Gratiola aurea* and *Sagittaria* sp.). Six species did not depart from the expected distribution of interlake distances, and three (*Myriophyllum spicatum*, *Eleocharis acicularis* and *Eriocaulon aquaticum*) were significantly under-dispersed at some distances and over-dispersed at others.

Based on functional traits, the species were divided into two classes – those most likely to disperse readily and those unlikely to disperse readily (Table 5). Four of the 11 species with the fewest dispersal-related traits were under-dispersed in nearby lakes, and nine of the 15 species with the most dispersal-related traits occurred in a disproportionately high number of nearby lakes. The null hypothesis of independence among the dispersal traits and actual dispersal, based on the interlake distance distributions, was rejected whether we treated species

Table 5 Functional traits used to divide species into two groups based on their dispersal ability. A trait scored with a 1 indicates a species has that dispersal-related trait (based on Willby *et al.*, 2000; and other sources). Species in bold occurred in disproportionately few of nearby lakes, and those that are underlined were over-represented in nearby lakes. Those in normal typeface did not depart from the expected distribution of interlake distances, and those in bold and underlined were under-represented at some distances and over-represented at others. The dispersal ability of species was significantly associated with their distribution among lakes in a Fisher's exact test

	Reproduces sexually	Reproduces by fragmentation	Reproduces vegetatively (on stolons, rhizomes)	Produces winter buds/ turions	Likely to be moved by birds and/or boats	Unrooted growth form	Number of reproductive structures per year
Poorly dispersing species							
<u>*Potamogeton amplifolius*</u>	1	0	1	0	0	0	Low
<u>*Gratiola aurea*</u>	1	0	0	0	0	0	Moderate-High
Vallisneria americana	1	0	1	0	0	0	Moderate
Nymphaea odorata	1	0	1	0	0	0	Moderate
Brasenia schreberi	1	0	1	0	0	0	Moderate
<u>*Sagittaria* sp.</u>	1	0	1	0	0	0	High
<u>**Eriocaulon aquaticum**</u>	1	0	1	0	0	0	Moderate-High
Pontederia cordata	1	0	1	0	0	0	Moderate-High
<u>**Eleocharis acicularis**</u>	1	0	1	0	1	0	Moderate
<u>*Nuphar variegata*</u>	1	0	1	0	0	0	High
<u>*Potamogeton epihydrus*</u>	1	1	1	0	1	0	Low
Strongly-dispersing species							
<u>*Elatine minima*</u>	1	0	1	0	1	0	High
<u>*Elodea nuttallii*</u>	1	1	1	1	1	0	Low
Najas flexilis	1	1	1	0	1	0	Moderate
Potamogeton pusillus	1	1	0	1	1	0	High
Potamogeton bicupularis	1	1	1	1	1	0	Moderate
<u>**Myriophyllum spicatum**</u>	1	1	1	1	1	0	Moderate
Potamogeton natans	1	1	1	0	1	0	High
Ceratophyllum demersum	1	1	0	1	1	1	Moderate
<u>*Potamogeton crispus*</u>	1	1	1	1	1	0	High
<u>*Utricularia radiata*</u>	1	1	0	1	1	1	Moderate
Najas minor	1	1	1	0	1	0	High
<u>*Myriophyllum heterophyllum*</u>	1	1	1	1	1	0	Moderate-High
Utricularia gibba	1	1	1	1	1	1	Moderate
Utricularia vulgaris	1	1	1	1	1	1	Moderate-High
<u>*Utricularia purpurea*</u>	1	1	1	1	1	1	Moderate-High

with ambiguous results like those with no deviation from the expected distribution (Fisher's exact test, $P = 0.008$ for the observed distribution and $P = 0.046$ for that and all less likely distributions) or removed them from the analysis ($P = 0.003$ and $P = 0.027$). However, overall frequency of these species was not correlated with dispersal traits; instead, frequency was highly correlated with the proportion of space each species occupied on the first two axes of a principal components analysis (PCA; $r = 0.75$, $P < 0.0001$), indicating that species' environmental tolerance regulates their overall frequency while dispersal influences where they occur within the range of suitable conditions.

Discussion

Our results indicate that environmental conditions strongly influence the composition of aquatic plant communities, as many others have found previously. However, our results also show spatial patterning in the geographical distribution of species that is unrelated to the distribution of the environmental conditions and thus is probably related to species' dispersal abilities. The CCA found that explicable variation in aquatic plant community composition could be divided almost equally between environmental conditions and spatial structure; of the explained variation, 45% related to the measured environmental
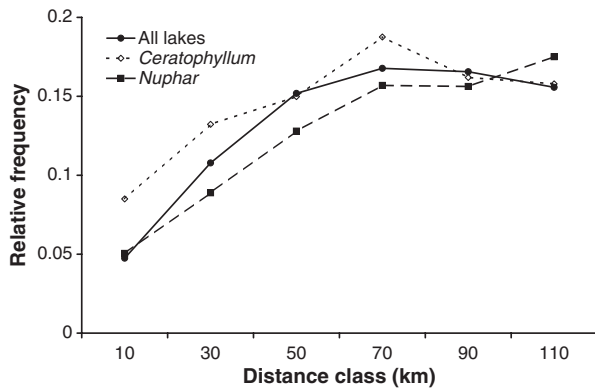
Fig. 3 This plot illustrates the way in which the distribution of species' interlake distances was compared with the distribution of interlake distances among all the lakes themselves (bold line). *Ceratophyllum demersum* (short dashes) occurred in a disproportionately high number of nearby lakes, and *Nuphar variegata* (long dashes) occurred in fewer nearby lakes than would be expected. Functional traits (unrooted habit, reproduction both by sexual means and vegetative fragmentation) make *Ceratophyllum* a species that disperses readily, but *Nuphar* disperses only via seeds, suggesting that geographical distributions are related to dispersal ability. The deviation was statistically significant for *Ceratophyllum* at 0–20 km and 20–40 km, and it was significant for *Nuphar* at 20–40 km and marginally ($P = 0.056$) at 40–60 km.

variables after removing correlation with spatial structure, and 40% was purely spatial. Production of abundant vegetative fragments allows many aquatic plants to disperse and colonise locally, and birds bearing seeds ensure dispersal across and among continents. In our study area, however, aquatic plant communities, like those of other passive dispersers, appear to be structured in part by their failure to reach all lakes with suitable environmental conditions. The spatial patterning among plants also affected community similarity, which declined with distance among lakes, even after accounting for distance-related environmental effects. The farther apart lakes were, the less likely they were to have the same complement of species. The association of dispersal-related functional traits with the geographical distribution of species provides evidence that this spatial patterning is produced at least in part by dispersal limitation. Given that dispersal limitation has been found among other organisms that rely on passive dispersal, such as microbes, the finding should not be surprising, yet it runs counter to traditional thinking about aquatic plant communities (but see Cook, 1987).

The influence of dispersal limitation would be expected to be less in areas smaller we studied. In

fact, this is what we observed within New Haven County, which has an area of 2233 km^2 and was the most thoroughly surveyed of the State's eight counties ($n = 21$ lakes). Community similarity was not significantly correlated with distance in this area (Mantel test, $r = -0.10$, $P = 0.10$; Fig. 2). Mean distance between lakes in the county was 29.8 km, compared with a statewide average of 56.2 km.

The relative importance of dispersal and environmental conditions varies not just with spatial scale but also among organisms. The evidence to date indicates that dispersal is more limiting among organisms that are vulnerable in transit (like fish out of water) than among organisms with resistant resting stages such as phytoplankton (Beisner *et al.*, 2006). Both environmental conditions and dispersal influence zooplankton (Havel, Shurin & Jones, 2002; Cottenie *et al.*, 2003; Beisner *et al.*, 2006; Thum & Stemberger, 2006), macroinvertebrates (Mykra *et al.*, 2007) and macrophytes (this study). For these organisms, neutral models (Bell, 2001; Hubbell, 2001) may not adequately explain the observed patterns because they do not take into consideration the response of species to environmental heterogeneity. While we did find evidence for dispersal limitation, we also found unequivocal evidence for environmental determinism. Metacommunity models are a better conceptual fit than neutral models for aquatic plants because they can accommodate fitness differences among species and differences in habitat quality across a landscape (Leibold *et al.*, 2004; Beisner *et al.*, 2006).

The environmental conditions found to have the most influence on community composition in our lakes are among those found almost universally to influence aquatic plant community composition: pH (or alkalinity), lake area, depth (or other measure of topography) and water clarity. The importance of pH has been well documented in northeast North America (Hellquist, 1980; Roberts, Singer & Boylen, 1985; Catling *et al.*, 1986; Capers *et al.*, 2009) and elsewhere (Spence, 1967; Heegaard *et al.*, 2001) and 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 & Sand-Jensen, 1991). Elodeids, for instance, are most commonly found in non-acidic hardwater lakes (Moyle, 1945; Seddon, 1972; Lacoul & Freedman, 2006). High transparency allows plants to grow

deeper than they could in more turbid water (Squires, Lesack & Huebert, 2002) and often is associated with oligotrophic conditions (Scheffer, 2004). A positive relationship between lake area and species richness is believed to be related to the greater habitat variability in large lakes, and the reduced probability of extirpation associated with larger population size (the species–area relationship; Jones, Li & Maberly, 2003). As often is the case in lake surveys (Downing *et al.*, 2006; Wagner *et al.*, 2008), the surveyed lakes were disproportionately large compared with the more than 3400 named ponds and lakes in Connecticut (89% of water bodies in a state database are < 10 ha in area, compared with 38% of surveyed lakes); so our results may apply somewhat less generally to particularly small ponds. The CCA identified strong east–west environmental gradients known to occur in the region. Among spatial variables, longitude was most strongly correlated with Axis 1 of the CCA, and it was most strongly correlated with conductivity and pH (S2). The western part of the region has hard water lakes on calcareous geology, and lakes with more acidic water occur in the east (Hellquist,1980); this gradient is known to affect the distribution of aquatic plants across the region (S3).

The proportion of variation explained by all variables was relatively low, which is not unusual for analyses using CCA. Cottenie (2005) found in a meta-analysis of 158 data sets that the mean amount of variation explained by environmental and spatial variables was < 50% and sometimes much lower. At least some of the unexplained variation in the Connecticut lakes is likely to relate to environmental conditions that we did not measure. Sediment texture was not measured, for instance, and it can affect aquatic plants (Anderson & Kalff, 1988; Barko, Gunnison & Carpenter, 1991). Furthermore, we did not measure nitrogen, although phosphorus is strongly correlated with nitrogen in Connecticut lakes ($r = 0.75$, $P < 0.0001$ in a study of 70 Connecticut lakes; Frink & Norvell, 1984), and total Kjeldahl nitrogen was not significant in a CCA of a subset of our lakes ($n = 70$). The environmental variables in this analysis included those that consistently explain the occurrence of aquatic plants, so it is unlikely that unmeasured variables are related to more than a small proportion of the unexplained variation in our communities.

We suspect that the large amount of unexplained variation indicates a high degree of stochasticity in community organisation, resulting from chance establishment and extinction. Aquatic plant communities are highly dynamic, recovering quickly from frequent small-scale disturbance caused by ice, fish, waterfowl, boats and other agents (Barrat-Segretain & Amoros, 1996; Capers, 2003b). Although many aquatic plants produce abundant vegetative fragments, so few of them may reach new lakes via birds or boats that the chances of establishing and persisting are very low or non-existent, as is suspected of being the case with microbes (Hughes Martiny *et al.*, 2006). The very low floral similarity among our lakes (76% of similarity values <0.25 and <1% of similarity values >0.50) lends support to this conclusion. Edvardsen & Økland (2006) found that community composition of plants in 64 Norwegian ponds was weakly associated with 56 environmental and land use variables, and they concluded that their ponds were colonised individualistically as a result of stochastic germination, establishment and dispersal. A large amount of stochasticity in the organisation of bacterial communities also has been suggested recently (Sloan *et al.*, 2006; Langenheder & Ragnarsson, 2007). Because it makes dispersal through the water possible, connectivity influences plant community composition along rivers (Bornette *et al.*, 1998; Demars & Harper, 2005), but Boschilia, Oliveira & Thomaz (2008) inferred that community assembly was in part a random process even in such lotic systems. Our lakes were largely isolated from each other, but connections among them certainly affect community composition and contribute to the unexplained variation in our analysis, and the effect of connectivity on dispersal-related variation needs to be quantified. Predation, herbivory and competition are much less likely than dispersal limitation to be responsible for the regional pattern. Aquatic plants are grazed by many vertebrate and invertebrate animals, which can dramatically reduce plant abundance and distribution within a community (Lodge, 1991), but there is little evidence that grazing can be so extensive as to remove a species from natural communities (this can occur in mesocosms; Elger, Willby & Caballo-Martinez, 2009). Therefore, herbivory is less likely to affect regional analyses of species presence, such as ours, than those involving abundance. Competition also may affect abundance (McCreary, 1991), and it can prevent individual species from colonising at small scales (Capers *et al.*, 2007), but it rarely has been shown to

reduce species richness at the community level. In fact, invasive plant richness usually rises with native plant richness (Levine & D'Antonio, 1999; Lonsdale, 1999), suggesting that communities are open to additional colonists and that new or existing species are not competitively excluded.

Spatial pattern could result from the recent arrival and incomplete distribution of non-native species, but this is unlikely to affect our analyses. Most of the region's invasive aquatic plants arrived decades ago and have spread thoroughly across the region. Even recent arrivals have spread quickly, and no dispersal-related aggregation is apparent in their distributions. *Najas minor*, for instance, arrived in the region sometime after 1990, but it occurred in 21% of surveyed lake. Historical processes/events and human activity also can cause spatial patterning in species distribution, and we cannot rule out these agents. However, the association of dispersal-related functional traits with species distribution in space suggests that dispersal limitation contributes. While habitat specialisation also could cause the patterns we saw among species with lower occurrence rates among the nearest lakes, the species showing the most evidence of dispersal limitation were the species with the highest frequency in our dataset – *Nymphaea odorata* and *Nuphar variegata*. Both show wide tolerance across the range of conditions that exist in the lakes analysed, occurring in more than 60% of ordination space defined by the first two axes of the PCA in which all the environmental conditions were entered, indicating that they are generalists, not specialists within the region. Among the species that occurred in disproportionately high numbers of nearby lakes were *Ceratophyllum demersum* and *Utricularia purpurea*, species that are un-rooted and that disperse with both seeds and vegetative propagules.

Our analysis of functional traits may be vulnerable to a certain amount of subjectivity; it is difficult to know how to rank overall dispersal ability (is an annual habit and a large production of seeds more important than an unrooted growth form and production of many vegetative fragments?). There also may be other ways to explain species deviation from the expected distribution of interlake distances, so the distributions may not be explicable entirely in terms of dispersal ability. Nevertheless, the grouping of species by functional traits does correspond in general to expectations about dispersal ability, and many of the best dispersing species do, in fact, occur in disproportionately high numbers of nearby lakes. Our finding that even several species with presumably poor dispersal ability occurred in disproportionately high numbers of nearby lakes suggests that there is much to learn about the dispersal of aquatic plants.

Despite numerous adaptations for local dispersal, evidence that the plants disperse well at the landscape scale in systems with high connectivity such as along rivers and the fact that many aquatic plants have cosmopolitan distributions that suggest high dispersal abilities globally, strong spatial structure unrelated to environmental conditions is evident in their distribution among lakes regionally. This does not mean that all of the species we studied are dispersal-limited; in fact, our analysis of functional traits suggests that species vary in dispersal limitation. They are likely to vary in colonisation abilities as well (Linton & Goulder, 2000). Neither does dispersal limitation mean the species never disperse across the region. Many clearly do. As a group, however, community structure is affected by limits preventing every species from occurring in every lake. For macrophytes, the questions of importance relate to how species vary in dispersal and colonisation abilities, and how these differences affect the spatial pattern in species' occurrence and community composition.

Acknowledgments

References

Anderson M.R. & Kalff J. (1988) Submerged aquatic macrophyte biomass in relation to sediment character-

istics in ten temperate lakes. *Freshwater Biology*, **19**, 115–121.

Baas-Becking L.G.M. (1934) *Geobiologie of Inleiding tot de Milieukunde*. Van Stockum and Zon, The Hague.

Barko J.W., Gunnison D. & Carpenter S.R. (1991) Sediment interactions with submerged macrophyte growth and community dynamics. *Aquatic Botany*, **41**, 41–65.

Barrat-Segretain M.H. (1996) Strategies of reproduction, dispersion and competition in river plants: a review. *Vegetatio*, **123**, 13–37.

Barrat-Segretain M.H. & Amoros C. (1996) Recovery of riverine vegetation after experimental disturbance. A field test of the patch dynamics concept. *Hydrobiologia*, **321**, 53–68.

Beisner B.E., Peres-Neto P.R., Lindstrom E.S., Barnett A. & Longhi M.L. (2006) The role of environmental and spatial processes in structuring lake communities from bacteria to fish. *Ecology*, **87**, 2985–2991.

Bell G. (2001) Neutral macroecology. *Science*, **293**, 2413–2418.

Borcard D., Legendre P. & Drapeau P. (1992) Partialling out the spatial component of ecological variation. *Ecology*, **73**, 1045–1055.

Bornette G., Amoros C. & Lamouroux N. (1998) Aquatic plant diversity in riverine wetlands: the role of connectivity. *Freshwater Biology*, **39**, 267–283.

Boschilia S.M., Oliveira E.F. & Thomaz S.M. (2008) Do aquatic macrophytes co-occur randomly? An analysis of null models in a tropical floodplain. *Oecologia*, **156**, 203–214.

Briers R.A. & Biggs J. (2005) Spatial patterns in pond invertebrate communities: separating environmental and distance effects. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **15**, 549–557.

Capers R.S. (2000) A comparison of two sampling techniques in the study of submerged macrophyte richness and abundance. *Aquatic Botany*, **68**, 87–92.

Capers R.S. (2003a) Macrophyte colonization in a freshwater tidal wetland (Lyme, CT, USA). *Aquatic Botany*, **77**, 325–338.

Capers R.S. (2003b) Six years of submerged plant community dynamics in a freshwater tidal wetland. *Freshwater Biology*, **48**, 1640–1651.

Capers R.S., Selsky R., Bugbee G.J. & White J. (2007) Aquatic plant community invasibility and scale-dependent patterns in native and invasive species richness. *Ecology*, **88**, 3135–3143.

Capers R.S., Selsky R., Bugbee G.J. & White J. (2009) Species richness of both native and invasive aquatic plants influenced by environmental conditions and human activity. *Botany*, **87**, 306–314.

Catling P.M., Freedman B., Stewart C., Kerekes J.J. & Lefkovitch L.P. (1986) Aquatic plants of acid lakes in Kejimkujik National Park, Nova Scotia; floristic composition and relation to water chemistry. *Canadian Journal of Botany*, **64**, 724–729.

Chick J.H. & McIvor C.C. (1994) Patterns in the abundance and composition of fishes among beds of different macrophytes: viewing a littoral zone as a landscape. *Canadian Journal of Fisheries and Aquatic Science*, **51**, 2873–2882.

Colwell R.K. (2006) EstimateS: statistical estimation of species richness and shared species from samples. Version 8. Persistent URL purl.oclc.org/estimates.

Cook C.D.K. (1987) Dispersion in aquatic and amphibious vascular plants. In: *Plant Life in Aquatic and Amphibious Habitats*. (Ed. R.M.M. Crawford), pp. 179–190. Blackwell Scientific Publications, Oxford.

Coops H., Hanganu J., Tudor M. & Oosterberg W. (1999) Classification of Danube Delta lakes based on aquatic vegetation and turbidity. *Hydrobiologia*, **415**, 187–191.

Cottenie K. (2005) Integrating environmental and spatial processes in ecological community dynamics. *Ecology Letters*, **8**, 1175–1182.

Cottenie K., Michels E., Nuytten N. & De Meester L. (2003) Zooplankton metacommunity structure: regional vs. local processes in highly interconnected ponds. *Ecology*, **88**, 991–1000.

Crow G.E. & Hellquist C.B. (2000a) *Aquatic and Wetland Plants of Northeastern North America. Vol. 1 Pteridophytes, Gymnosperms and Angiosperms: Dicotyledons*. University of Wisconsin Press, Madison, WI, USA.

Crow G.E. & Hellquist C.B. (2000b) *Aquatic and Wetland Plants of Northeastern North America. Vol. 2 Angiosperms: Monocotyledons*. University of Wisconsin Press, Madison, WI, USA.

Darwin C.R. (1859) *On the Origin of Species by Means of Natural Selection*. J. Murray, London.

Demars B.O.L. & Harper D.M. (2005) Distribution of aquatic vascular plants in lowland rivers: separating the effects of local environmental conditions, longitudinal connectivity and river basin isolation. *Freshwater Biology*, **50**, 418–437.

Downing J.A., Prairie Y.T., Cole J.J. *et al.* (2006) The global abundance and size distribution of lakes, ponds, and impoundments. *Limnology and Oceanography*, **51**, 2388–2397.

Dvorak J. & Best E.P.H. (1982) Macro-invertebrate communities associated with the macrophytes of Lake Vechten: structural and functional relationships. *Hydrobiologia*, **95**, 115–126.

Eaton A.D., Clescenti L.S. & Greenberg A.E. (1995) *Standard Methods for the Examination of Water and Wastewater*, 19th edn. American Public Health Association, Washington.

Edvardsen A. & Økland R.H. (2006) Variation in plant species richness in and adjacent to 64 ponds in SE Norwegian agricultural landscapes. *Aquatic Botany*, **85**, 79–91.

Elger A., Willby N.J. & Caballo-Martinez M. (2009) Invertebrate grazing during the regenerative phase affects the ultimate structure of macrophyte communities. *Freshwater Biology*, **54**, 1246–1255.

Fierer N., Morse J.L., Berthrong S.T., Bernhardt E.S. & Jackson R.B. (2007) Environmental controls on the landscape-scale beogeography of stream bacterial communities. *Ecology*, **88**, 2162–2173.

Figuerola J. & Green A.J. (2002) Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. *Freshwater Biology*, **47**, 483–494.

Finlay B.J. (2002) Global dispersal of free-living microbial eukaryote species. *Science*, **296**, 1061–1063.

Frink C.R. & Norvell W.A. (1984) *Chemical and Physical Properties of Connecticut lakes*. Connecticut Agricultural Experiment Station Bulletin No. 817, New Haven, CT.

Gornall R.J., Hollingsworth P.M. & Preston C.D. (1998) Evidence for spatial structure and directional gene flow in a population of an aquatic plant, *Potamogeton coloratus*. *Heredity*, **80**, 414–421.

Grasmück N., Haury J., Léglize L. & Muller S. (1995) Assessment of the bio-indicator capacity of aquatic macrophytes using multivariate analysis. *Hydrobiologia*, **300/301**, 115–122.

Havel J.E., Shurin J.B. & Jones J.R. (2002) Estimating dispersal from patterns of spread: spatial and local control of lake invasions. *Ecology*, **83**, 3306–3318.

Heegaard E., Birks H.H., Gibson C.E., Smith S.J. & Wolfe-Murphy S. (2001) Species-environmental relationships of aquatic macrophytes in Northern Ireland. *Aquatic Botany*, **70**, 175–223.

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

Hollingsworth P.M., Preston C.D. & Gornall R.J. (1996) Genetic variability in two hydrophilous species of *Potamogeton*, *P. pectinatus* and *P. filiformis* (Potamogetonaceae). *Plant Systematics and Evolution*, **202**, 233–254.

Hood G.M. (2006) PopTools version 2.7.5. Available at: http://www.cse.csiro.au/poptools.

Hubbell S. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.

Hughes Martiny J.B., Bohannan B.J.M., Brown J.H. *et al.* (2006) Microbial biogeography: putting microorganisms on the map. *Nature Reviews Microbiology*, **4**, 102–112.

Jones J.I., Li W. & Maberly S.C. (2003) Area, altitude and aquatic plant diversity. *Ecography*, **26**, 411–420.

Lacoul P. & Freedman B. (2006) Relationships between aquatic plants and environmental factors along a steep Himalayan altitudinal gradient. *Aquatic Botany*, **84**, 3–16.

Langenheder S. & Ragnarsson H. (2007) The role of environmental and spatial factors for the composition of aquatic bacterial communities. *Ecology*, **88**, 2154–2161.

Legendre P. & Fortin M.-J. (1989) Spatial pattern and ecological analysis. *Vegetatio*, **80**, 107–138.

Legendre P. & Legendre L. (1998) *Numerical Ecology*, 2nd edn. Elsevier, Amsterdam.

Leibold M.A., Holyoak M., Mouquet N. *et al.* (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, **7**, 601–613.

Les D.H., Crawford D.J., Kimball R.T., Moody M.L. & Landolt E. (2003) Biogeography of discontinuously distributed hydrophytes: a molecular appraisal of intercontinental disjunctions. *International Journal of Plant Science*, **164**, 917–932.

Levine J.M. & D'Antonio C.M. (1999) Elton revisited: A review of evidence linking diversity and invasibility. *Oikos*, **87**, 15–26.

Linton S. & Goulder R. (2000) Botanical conservation value related to origin and management of ponds. *Aquatic Conservation and Freshwater Ecosystems*, **10**, 77–91.

Lodge D.M. (1991) Herbivory on freshwater macrophytes. *Aquatic Botany*, **41**, 195–224.

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

Madsen T.V. & Sand-Jensen K. (1991) Photosynthetic carbon assimilation in aquatic macrophytes. *Aquatic Botany*, **41**, 5–40.

McCreary N.J. (1991) Competition as a mechanism of submerged macrophyte community structure. *Aquatic Botany*, **41**, 177–194.

Mjelde M. & Faafeng B.A. (1997) *Ceratophyllum demersum* hampers phytoplankton development in some small Norwegian lakes over a wide range of phosphorus concentrations and geographical latitude. *Freshwater Biology*, **37**, 355–365.

Moody M.L. & Les D.H. (2002) Evidence of hybridity in invasive watermilfoil (*Myriophyllum*) populations. *Proceedings of the National Academy of Science USA*, **99**, 14867–14871.

Moyle J.B. (1945) Some chemical factors influencing the distribution of aquatic plants in Minnesota. *American Midland Naturalist*, **34**, 402–420.

Mykra H., Heino J. & Muotka T. (2007) Scale-related patterns in the spatial and environmental components

of stream macroinvertebrate assemblage variation. *Global Ecology & Biogeography*, **16**, 149–159.

Papke R.T., Ramsing N.B., Bateson M.M. & Ward D.M. (2003) Geographical isolation in hot spring cyanobacteria. *Environmental Microbiology*, **5**, 650–659.

Petticrew E.L. & Kalff J. (1992) Water flow and clay retention in submerged macrophytes beds. *Canadian Journal of Fisheries and Aquatic Science*, **49**, 2483–2489.

Ray A.M., Rebertus A.J. & Ray H.L. (2001) Macrophyte succession in Minnesota beaver ponds. *Canadian Journal of Botany*, **79**, 487–499.

Roberts D.A., Singer R. & Boylen C.W. (1985) Three submersed macrophyte communities of Adirondack lakes (New York, USA) of varying degrees of acidity. *Aquatic Botany*, **21**, 219–235.

Scheffer M. (2004) *Ecology of Shallow Lakes*. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Sculthorpe C.D. (1967) *The Biology of Aquatic Vascular Plants*. Edward Arnold Publishers Ltd, London.

Seddon B. (1972) Aquatic macrophytes as limnological indicators. *Freshwater Biology*, **2**, 107–130.

Sloan W.T., Lunn M., Woodcock S., Head I.M., Nee S. & Curtis T.P. (2006) Quantifying the roles of immigration and chance in shaping prokaryote community structure. *Environmental Microbiology*, **8**, 732–740.

Spence D.H.N. (1967) Factors controlling the distribution of freshwater macrophytes with particular reference to the lochs of Scotland. *Journal of Ecology*, **55**, 147–170.

Squires M.M., Lesack L.F.W. & Huebert D. (2002) The influence of water transparency on the distribution and abundance of macrophytes among lakes of the Mackenzie Delta, Western Canadian Arctic. *Freshwater Biology*, **47**, 2123–2135.

Ter Braak C.J.F. (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, **67**, 1167–1179.

Ter Braak C.J.F. & Šmilauer P. (2002) *Canoco for Windows Version 4.5*. Biometris-Plant Research International, Wageningen, The Netherlands.

Thiébaut G. & Muller S. (1998) Les communautés de macrophyte aquatiques comme descripteurs de la qualité de l'eau: example de la rivière Moder. *Annals of Limnology*, **34**, 141–153.

Thum R.A. & Stemberger R.S. (2006) Pure spatial and spatially structured environmental variables explain *Skistodiaptomus* copepod range limits in northeastern USA. *Canadian Journal of Fisheries and Aquatic Science*, **63**, 1397–1404.

Unmuth J.M.L., Lillie R.A., Dreikosen D.S. & Marshall D.W. (2000) Influence of dense growth of Eurasian watermilfoil on lake water temperature and dissolved oxygen. *Journal of Freshwater Ecology*, **15**, 497–503.

Vanormelingen P., Cottenie K., Michels E., Muylaert K., Vyverman W. & de Meester L. (2008) The relative importance of dispersal and local processes in structuring phytoplankton communities in a set of highly interconnected ponds. *Freshwater Biology*, **53**, 2170–2183.

Wagner T., Soranno P.A., Cheruvilil K.A., Renwick W.H., Webster K.E., Vaux P. & Abbitt R.J.F. (2008) Quantifying sample biases of inland lake sampling programs in relation to lake surface area and land use/cover. *Environmental Monitoring and Assessment*, **141**, 131–147.

Wigand C., Stevenson J.C. & Cornwell J.C. (1997) Effects of different submersed macrophytes on sediment biogeochemistry. *Aquatic Botany*, **56**, 233–244.

Willby N.J., Abernethy V.J. & Demars B.O.L. (2000) Attribute-based classification of European hydrophytes and its relationship to habitat utilization. *Freshwater Biology*, **43**, 43–74.