Concordance of taxonomic richness patterns across multiple assemblages in lakes of the northeastern United States

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Abstract: We investigated the concordance of taxonomic richness patterns and their environmental correlates for assemblages of benthic macroinvertebrates, riparian birds, sedimentary diatoms, fish, planktonic crustaceans, and planktonic rotifers in 186 northeastern U.S. lakes. Taxon counts were standardized with respect to sampling effort using rarefaction. The degree of concordance among assemblage richness measures was low, but this was at least partly attributable to measurement precision. Aspects of lake morphology (area, depth) superseded other environmental features (climate, human development, water chemistry, nearshore physical habitat) as correlates of assemblage richness and were the strongest source of concordance. The benthic macroinvertebrates, birds, fish, and zooplankton all showed positive associations between richness and lake area. The diatoms showed negligible associations between richness and area and negative associations between richness and depth. Associations with human development were much weaker than with lake morphology and varied from positive (fish, planktonic crustaceans) to negative (diatoms). We conclude that taxonomic richness alone may be of ambiguous value as an indicator of biological integrity in lakes and that its natural drivers must be controlled for prior to assessing anthropogenic effects.

Résumé : Nous avons étudié la concordance de profils de diversité taxonomique avec leurs corrélats environnementaux chez des groupements de macroinvertébrés benthiques, d'oiseaux de rivage, de diatomées sédimentaires, de poissons et de crustacés et de rotifères planctoniques dans 186 lacs du nord-est des États-Unis. Nous avons normalisé les dénombrements des taxons en fonction de l'effort d'échantillonnage en appliquant le principe de raréfaction. Le degré de concordance entre les mesures de diversité des groupements était faible, mais cela était au moins en partie attribuable à la précision des mesures. Certains aspects de la morphologie des lacs (superficie, profondeur) étaient mieux corrélés à la diversité des groupements que d'autres caractéristiques environnementales (climat, développements anthropiques, chimie de l'eau, habitat riverain) et étaient les plus fortes sources de concordance. Nous avons observé des corrélations positives entre la diversité et la superficie des lacs chez les macroinvertébrés benthiques, les oiseaux, les poissons et le zooplankton. Il y avait des corrélations négligeables entre la diversité et la superficie et des corrélations négatives entre la diversité et la profondeur chez les diatomées. Les corrélations avec les développements anthropiques étaient beaucoup plus faibles qu'avec la morphologie des lacs et variaient de positives (poissons, crustacés planctoniques) à négatives (diatomées). Nous concluons que la seule diversité taxonomique peut constituer un indicateur ambigu de l'intégrité biologique des lacs et que les facteurs naturels qui la déterminent doivent être connus avant que soient évalués les effets anthropiques.

[Traduit par la Rédaction]

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Introduction

Most community studies focus on one taxonomically restricted assemblage of organisms (e.g., birds, fish, diatoms). This approach reduces the complexity of the problem, but also limits the scope of interpretation. The concordance or lack of it among different assemblages at the same locations helps us to assess the generality of our ecological understanding and may yield new insights by highlighting similarities and differences in how different assemblages respond to the environment (e.g., Jackson and Harvey 1993). The consideration of disparate assemblages also provides a more complete view of human effects on ecosystems because human activities alter multiple facets of the environment (Karr 1991).

Taxonomic richness is a simple biodiversity measure that allows for comparisons among taxonomically disparate assemblages of organisms (Prendergast et al. 1993*a*, 1993*b*). Perhaps because of its simplicity, richness is among the most commonly used diversity measures, but richness is sensitive to sampling effort, and protection of high-richness sites does not guarantee the effective conservation of rare or spatially restricted organisms (Prendergast et al. 1993*a*, 1993*b*; Dunn 1994). Despite these shortcomings, taxonomic richness is useful because it reflects processes affecting multiple species populations (MacArthur and Wilson 1967). For this study, we investigated the concordance of taxonomic richness patterns and their environmental correlates for six disparate assemblages (benthic macroinvertebrates, riparian birds, sedimentary diatoms, fish, planktonic crustaceans, planktonic rotifers) using data collected from 186 northeastern U.S. lakes.

Methods

Sampling design and field methods

The data were collected between 1991 and 1995 from 186 northeastern U.S. lakes (Fig. 1) by the U.S. Environmental Protection Agency's Environmental Monitoring and Assessment Program (EMAP) (Baker et al. 1997). The EMAP lakes were selected using a probability design to be representative of regional conditions (Larsen et al. 1994). Bird data were collected during the breeding season (late May through early July) when birds were most vocal. Data for the other assemblages and most habitat data were collected in July and August. The habitat data characterized each lake's temperature and dissolved oxygen (DO) profile, water chemistry, and lakeshore riparian and littoral zone structure (Baker et al. 1997). The assemblage and habitat data analyzed here are available at the EMAP website (http://www.epa.gov/emap/html/dataI/surfwatr/data/nelakes).

Benthic macroinvertebrates

Sediment samples were collected using a modified KB corer at 10 evenly spaced locations along the lake perimeter. The top 13 cm of the sediment core was retained for processing (Baker et al. 1997). Because distributions of benthic macroinvertebrates are often limited by available oxygen (Brinkhurst 1974), thermally stratified lakes were sampled in well-oxygenated areas (≥ 5 mg·L^{-1}) of the sublittoral zone at or near the upper limit of the metalimnion (a depth generally between 3 and 5 m). In shallow basins without thermal stratification, samples were obtained in weedless areas >1 m deep. Samples were sieved (No. 60, 250-µm mesh), combined, and preserved. In the laboratory, an attempt was made to identify at least 150 individuals randomly chosen from each pooled

Fig. 1. Locations of the 186 northeastern U.S. lakes sampled for biological assemblages by EMAP between 1991 and 1995. The locations of some lakes have been adjusted slightly to minimize overlap.
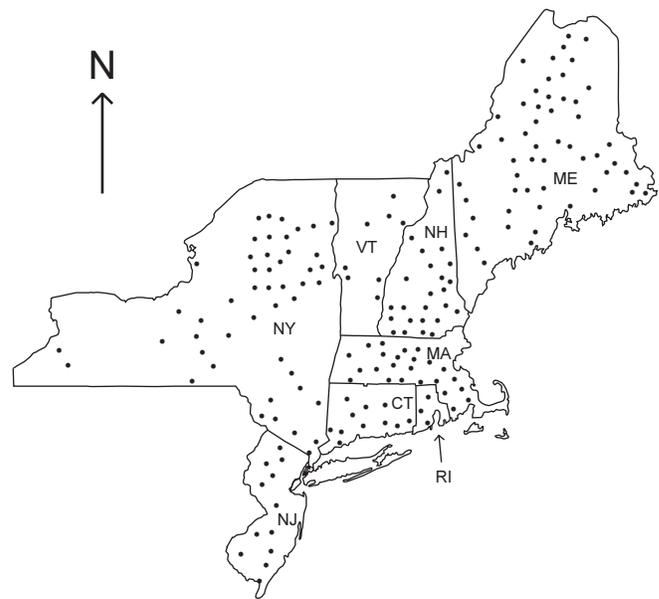
sample, but many samples contained <150 individuals total. Annelids (phylum Annelida, segmented worms) and chironomids (family Chironomidae, nonbiting midges) were identified to genus. The two groups were combined to compute benthic macroinvertebrate richness because sample sizes were insufficient to analyze the two groups separately. Other benthic taxa were not analyzed here because they were collected infrequently and identified to a coarser and more variable taxonomic resolution.

Riparian birds

Riparian birds were surveyed by canoe along a transect 10 m from and parallel to the lakeshore between 0.5 h before sunrise and 4 h after sunrise on days with minimal wind and precipitation (Baker et al. 1997). Data were collected every 200 m along the lake perimeter. All individuals seen or heard within a 100-m radius during a 5-min period were recorded to species at each stop. For lakes with perimeters >4.8 km, 24 point counts were stratified with respect to the relative occurrence of habitats along the lakeshore. Both terrestrial and aquatic species were used to calculate richness, but most individuals surveyed were terrestrial passerines (~80%).

Sedimentary diatoms

A single sediment diatom sample was obtained from the deepest portion of each lake using a modified KB corer (Baker et al. 1997). The top 1 cm of the core was retained. In the laboratory, the diatoms were separated from the sediments using standard techniques and mounted on glass slides (Dixit and Smol 1994). About 500 diatoms were counted and identified along transects at 1250× magnification under oil immersion. Identifications were made to the lowest taxonomic level using standardized taxonomic procedures (Dixit and Smol 1994).

Fish

Fish were sampled using gill nets, trap nets, minnow traps, and beach seines (Baker et al. 1997). Data for all gear were combined. The level of sampling effort was determined by lake size and ranged from one to 10 sets of each passive gear and up to six seining sites (Whittier et al. 1997). We excluded nonbreeding

Table 1. Mean number of taxa per lake, the number of repeat visits used to estimate variance parameters, estimates of richness variance associated with between-lake differences (σ^2_{lake}) and measurement variability (σ^2_{rep}), and the signal-to-noise ratio ($\sigma^2_{\text{lake}} / \sigma^2_{\text{rep}}$).

Richness measure	Mean no. of taxa	No. of repeat visits	σ^2_{lake}	σ^2_{rep}	$\sigma^2_{\text{lake}}/\sigma^2_{\text{rep}}$
Benthos	13.54	46	3.28	8.25	0.40
Birds	16.54	26	1.95	3.33	0.59
Diatoms	53.00	5	271.43	26.21	10.36
Fish	6.45	37	3.80	1.00	3.80
Planktonic crustaceans	8.42	33	5.32	1.35	3.94
Planktonic rotifers	11.60	34	7.97	6.32	1.26

stocked fish but included native and nonnative species thought to breed in the lake as part of fish richness.

Zooplankton

Zooplankton were sampled using a single vertical net tow taken in the deepest portion of the lake from 0.5 m off the bottom to the surface (Baker et al. 1997). Two nets were fitted to a single harness for sampling: a cone net (30 cm in diameter, 202-μm mesh) for the macrozooplankton and a Wisconsin net (15 cm in diameter, 48-μm mesh) with a 25-cm-long reducing collar for the microzooplankton. Subsamples of individuals (generally >100) were chosen at random from each net and identified to species (Stemberger and Lazorchak 1994). Two zooplankton richness measures were computed, one for cone-netted crustaceans and the other for Wisconsin-netted rotifers.

Statistical approach

Standardizing richness measures

Taxonomic richness showed a significant positive association with the number of individuals counted in the samples for all assemblages other than the diatoms ($P < 0.01$), indicating that richness variation was partly a function of individual counts. To control for this source of variation, we used rarefaction to determine the number of taxa that would be encountered in random draws (without replacement) of 50, 30, 50, 90, and 90 individuals from the benthic macroinvertebrate, bird, fish, planktonic crustacean, and planktonic rotifer samples, respectively (Benson and Magnuson 1992). These cutoff values were chosen as a compromise between the number of lakes that could be analyzed (only lakes whose samples were greater than or equal to the cutoff could be analyzed) and the number of individuals used to estimate richness. While arbitrary, the rarefaction measures used were highly correlated with others determined using quadruple the numbers of individuals ($r > 0.88$). For consistency, we used rarefaction estimates of richness for the diatoms based on fixed counts of 400 individuals. The number of lakes analyzed ranged from 115 for the benthic macroinvertebrates to a 175 for the birds; 84 of these lakes had samples of adequate size to determine rarefaction measures for all six assemblages.

Precision of rarefaction richness measures

Some lakes were visited multiple times during the same year to estimate precision. We subjected the assemblage data (including repeat visit data) to one-way analysis of variance (ANOVA) to estimate richness variance attributable to between-lake differences (σ^2_{lake}) and measurement variability (σ^2_{rep}). The lakes were coded as random categorical variables in the ANOVA model (model II of Snedecor and Cochran 1967) because they were chosen at random from throughout the region (Larsen et al. 1994). The F statistic for this model estimates $(k\sigma^2_{\text{lake}} + \sigma^2_{\text{rep}}) / \sigma^2_{\text{rep}}$, where $k = 1$ when all lakes are visited only once and increases with replication. The signal-to-noise ratio ($\sigma^2_{\text{lake}}/\sigma^2_{\text{rep}}$) served as our precision measure because only that portion of the richness variance associated with between-lake differences (σ^2_{lake}) could be modeled effectively us-

ing our lake comparative approach. Precision was relatively good for diatom richness and relatively poor for bird and benthic macroinvertebrate richness (Table 1). The relatively high signal-to-noise ratio for diatom richness may partly reflect the fact that diatom assemblages had, on average, considerably more taxa per lake than the other assemblages (Table 1), and therefore more potential for richness variation between lakes (i.e., signal, σ^2_{lake}).

Measurement error is a nonecological factor that will reduce the correlation among richness measures and therefore the perceived concordance among assemblages. We estimated the maximum potential correlations among richness measures using the variance parameters σ^2_{lake} and σ^2_{rep}. The product-moment correlation between two variables can be expressed as $\sigma_{12}/(\sigma_1\sigma_2)$, where σ_{12} is the covariance for the variable pair and σ_1 and σ_2 are their standard deviations (Snedecor and Cochran 1967). The standard deviation of each richness measure is $(\sigma^2_{\text{lake}} + \sigma^2_{\text{rep}})^{1/2}$ when repeat data are excluded (i.e., $k = 1$ from above). The covariance of two measures that are perfectly correlated is equal to the product of their standard deviations, so we estimated the maximum potential covariance for each assemblage pair as the product of their estimates for σ_{lake}, assuming perfect correlation in variance attributable to between-lake differences (σ^2_{lake}) and no correlation in variance attributable to measurement variability (σ^2_{rep}). The formula for the maximum potential correlation (r) between two assemblage richness measures is then $\{\sigma^2_{\text{lake}(1)}\sigma^2_{\text{lake}(2)}(\sigma^2_{\text{lake}(1)} +\sigma^2_{\text{rep}(1)})^{-1}(\sigma^2_{\text{lake}(2)} + \sigma^2_{\text{rep}(2)})^{-1}\}^{1/2}$, where $\sigma^2_{\text{lake}(1)}$ and $\sigma^2_{\text{lake}(2)}$ are the two measures' variances attributable to between-lake differences, and $\sigma^2_{\text{rep}(1)}$ and $\sigma^2_{\text{rep}(2)}$ are their variances attributable to measurement variability. Methods described by Snedecor and Cochran (1967) were used to test the null hypothesis that the observed correlation was equal to its potential maximum (i.e., that the assemblage pair demonstrated perfect positive covariation in richness variance attributable to between-lake differences).

Multiple linear regression

Taxonomic richness for each assemblage was modeled using multiple linear regression. We performed a principal components analysis (PCA) on the correlations among the six richness measures to isolate concordant richness patterns. Scores on PCA axes with eigenvalues >1 were also modeled using multiple linear regression. We analyzed data collected during a single visit to each lake for regression analysis.

In selecting candidate predictors, our goal was to consider factors that might influence multiple assemblages concordantly. The environmental variables analyzed (Table 2) were obtained from a variety of sources (Anderson et al. 1976; U.S. Bureau of Census 1990; O'Connor et al. 1996; Baker et al. 1997). Variables were transformed as necessary to normalize their distributions (Snedecor and Cochran 1967). We used forward variable selection in multiple linear regression to select the best subset of predictors for each richness measure. Variable additions continued until the F statistic for the change at the step dropped below the significance threshold ($P > 0.05$).

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Table 2. Explanatory variables analyzed, their minimums, medians, and maximums in their original units, and their means and standard deviations (after transformation where applicable) for the 186 lakes.

| Explanatory variable | Original units | | | Transformation | Values analyzed | |
	Minimum	Median	Maximum		Mean	σ
Lake morphology						
Lake area (ha)	1	29	3306	$\log_{10}(x)$	1.61	0.82
Maximum lake depth (m)	1.0	6.4	47.2	$\log_{10}(x)$	0.83	0.40
Littoral zone structure						
Macrophyte cover (types present per stop)	0.0	1.3	3.0	None	1.40	0.83
Climate						
Seasonality (July–Jan. mean temperature, °C)	23.3	27.7	30.4	None	27.17	1.69
Water chemistry						
pH*	4.38	7.08	9.05	pH − 7	0.02	0.79
Minimum DO (mg·L^{-1})	0.0	3.5	8.6	None	3.75	3.16
Minimum temperature (°C)	0.0	16.1	29.0	None	15.40	6.64
Total phosphorus (µg·L^{-1})*	0	10	176	$\log_{10}(x + 1)$, centered	0.00	0.34
Human development						
Watershed (humans·km^{-2})*	0	9.5	1760	$\log_{10}(x + 1)$, centered	0.00	0.88
Shoreline (proportion of shore where present)*	0	0.38	1	$\arcsin(x^{1/2})$, centered	0.00	0.52

*Quadratic terms were also analyzed for these variables.

Among the environmental variables analyzed were (Table 2) (*i*) two aspects of lake morphology (area, depth) because of their influence on population processes (MacArthur and Wilson 1967), habitat diversity (Williams 1964), and other biotic and abiotic factors (e.g., Robinson and Tonn 1989); (*ii*) the average number of macrophyte types present in 15-m-wide sections of the nearshore littoral zone (emergent, submergent, floating) because macrophytes provide food for birds (Hoyer and Canfield 1994), substrates for zooplankton and diatoms (Dixit and Smol 1994), and predation refuges for benthic macroinvertebrates and fish (Turner and Mittelbach 1990); (*iii*) seasonality (the difference between average July and January mean temperature); and (*iv*) four measures of water condition (minimum temperature, minimum DO, pH, total phosphorus). Our expectation was that richness would peak in circumneutral waters, so pH was expressed as deviations from 7.0 (observed pH − 7) and both linear and quadratic terms were analyzed. Results of previous EMAP studies indicate that humans have altered northeastern U.S. lakes and their biological assemblages at broad spatial scales (Dixit and Smol 1994; Whittier et al. 1997). Human density in the watershed and the proportion of the lake's perimeter with human development present within 100 m of the shore served as regional and local assays of land use. Because taxonomic richness may peak at sites of intermediate productivity or disturbance intensity where spatiotemporal heterogeneity is maximized (Huston 1979), we analyzed linear and quadratic terms for phosphorus, human density in the watershed, and the proportion of the lakeshore with human development (all centered by their respective means).

Results

Individual assemblages

Benthic macroinvertebrate richness was positively associated with lake area, accounting for 15% of the variance (Table 3; Fig. 2*a*). Addition of macrophyte cover, minimum temperature, and minimum DO increased the total variance accounted for by the model to 34%, with benthos richness positively associated with macrophyte cover and DO and negatively associated with temperature.

Riparian bird richness increased with lake area, account-

ing for 25% of the variance (Table 3; Fig. 2*b*). Addition of seasonality (accounting for an additional 4% of the variance) indicated that bird species richness was higher to the north where climatic variation was more pronounced.

Linear and quadratic terms for pH were first to enter into the diatom model, together accounting for 27% of the variance (Table 3). There were also negative associations with lake depth (accounting for an additional 10% of the variance) and lakeshore human development (accounting for an additional 2%).

Fish richness was positively associated with lake area, accounting for 30% of the variance (Table 3; Fig. 2*d*). A positive association with human density in the watershed accounted for an additional 9% of the variance. Addition of linear and quadratic terms for lakeshore human development together accounted for an additional 3% of the variance, with signs for the terms implying a richness peak with intermediate levels of human development along the lakeshore. Note that this model includes native and nonnative species as part of fish richness.

The number of planktonic crustacean species increased with lake area, accounting for 28% of the variance (Table 3; Fig. 2*e*). Addition of the quadratic term for pH and minimum DO (both negative associations) increased the total variance accounted for by the model to 37%. There was also a positive association with lakeshore human development, accounting for an additional 2% of the variance.

The number of planktonic rotifer species increased with lake area, accounting for 10% of the variance (Table 3; Fig. 2*f*). There was also a negative association with minimum temperature and a positive association with macrophyte cover, together accounting for an additional 7% of the variance.

Concordance of richness patterns

Correlations among richness measures were consistently low for the 84 lakes with richness measures for all assem-

**Table 3.** Explanatory variables and their coefficients in the multiple linear regression models.

Model	Variable	Coefficient	R^2	F statistic
Benthos ($n = 115$)	Intercept	11.89		
	Lake area	1.17	0.15	19.84
	Macrophytes	1.12	0.21	8.18
	Minimum temperature	–0.20	0.25	7.11
	Minimum DO	0.35	0.34	14.36
Birds ($n = 175$)	Intercept	6.95		
	Lake area	1.30	0.25	58.27
	Seasonality	0.27	0.29	8.88
Diatoms ($n = 171$)	Intercept	68.61		
	pH	–8.11	0.16	31.79
	pH^2	–5.87	0.27	26.11
	Lake depth	–14.43	0.37	27.21
	Shoreline human development	–4.82	0.39	5.51
Fish ($n = 169$)	Intercept	4.07		
	Lake area	1.58	0.30	72.17
	Human density in watershed	0.52	0.39	24.10
	Shoreline human development^2	–1.31	0.40	4.02
	Shoreline human development	0.76	0.42	5.15
Planktonic crustaceans ($n = 169$)	Intercept	6.59		
	Lake area	1.69	0.28	65.23
	pH^2	–0.61	0.32	10.52
	Minimum DO	–0.17	0.37	13.00
	Shoreline human development	0.68	0.39	4.72
Planktonic rotifers ($n = 177$)	Intercept	10.56		
	Lake area	1.19	0.10	18.46
	Minimum temperature	–0.14	0.14	8.56
	Macrophytes	0.90	0.17	7.64
Richness PC1 ($n = 84$)	Intercept	–1.77		
	Lake area	1.10	0.41	57.40
	Macrophytes	0.48	0.47	9.61
	pH^2	–0.47	0.54	11.26
	Minimum temperature	–0.05	0.58	7.89
Richness PC2 ($n = 84$)	Intercept	2.39		
	Lake depth	1.24	0.23	24.48
	pH	0.58	0.36	15.94
	Seasonality	–0.13	0.39	4.57

Note: The order of entry into the model proceeds from top to bottom as determined by forward variable selection. The multiple coefficient of determination (R^2) represents the proportion of the variance explained by the model with the inclusion of that explanatory variable and all variables preceding it in the model.

blages (Table 4), but 13 of the 15 correlations were positive and two of those were significant ($P < 0.05$, Bonferroni-adjusted α level to control for multiple comparisons, Zar 1984). As expected, the correlations were consistently lower than their potential maxima (Table 4). However, despite the low correlations observed, we failed to reject the null hypothesis of perfect richness correlation among assemblages (after accounting for measurement variability) for the five comparisons involving the benthic macroinvertebrates ($P > 0.05$, Bonferroni adjusted), suggesting that measurement variability contributed to the weak associations observed.

PCA of the six richness measures identified two axes of variation with eigenvalues >1 for the 84 lakes (Table 5). The first principal component (richness PC1) had positive loadings for all assemblages and represented the dominant trend in concordant richness patterns. The diatoms had a markedly lower correlation with this axis ($r^2 = 0.10$) than the other assemblages ($r^2 \geq 0.26$), indicating that they were relatively less affected by those factors inducing concordant patterns on richness PC1. This axis' strong positive association with lake area (accounting for 41% of the variance, Table 3) thus indicated that richness showed a strong positive association

Fig. 2. Relationship between taxonomic richness and lake area for the six assemblages.
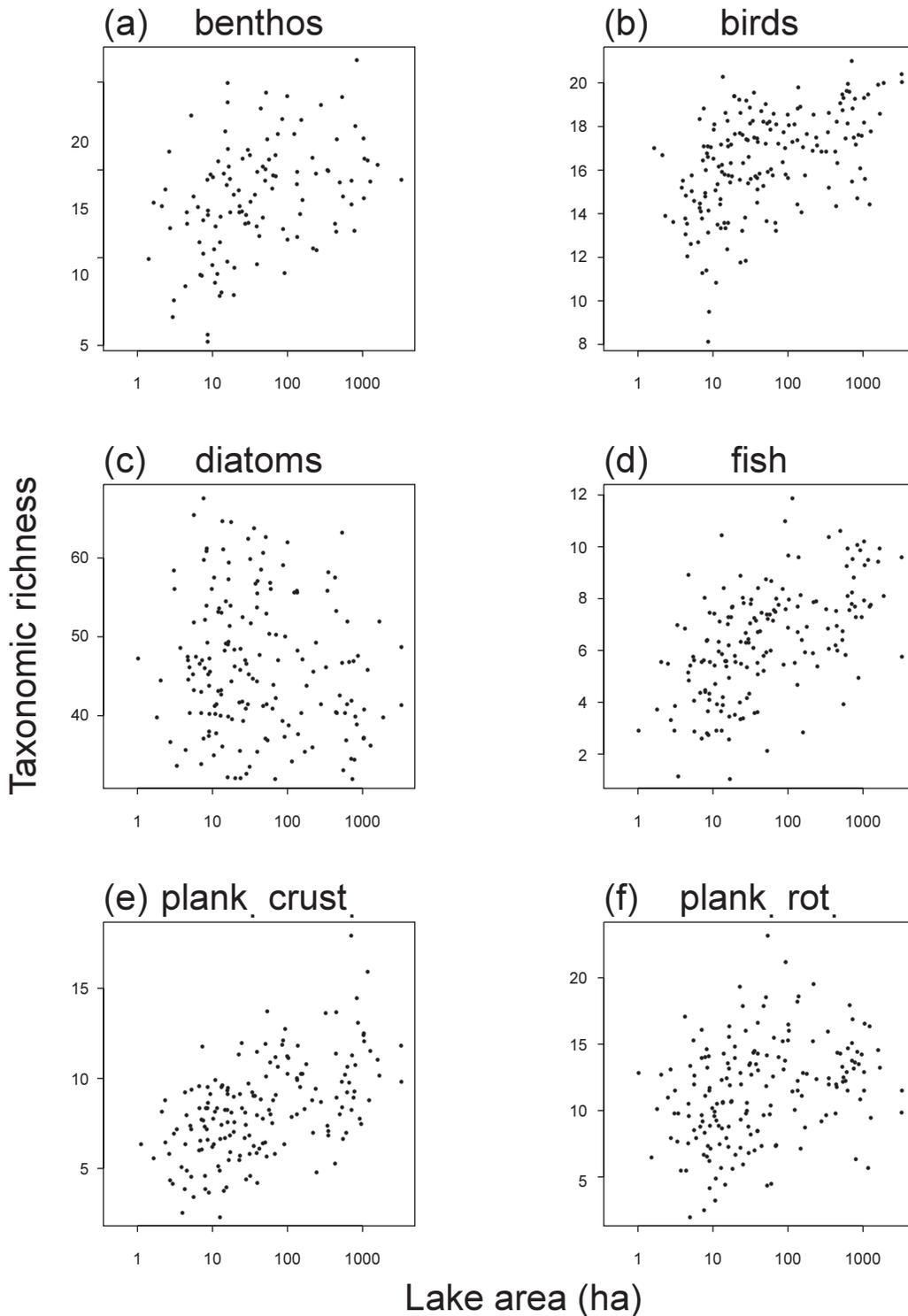
with lake area for all assemblages other than the diatoms (Fig. 2), as was true for the assemblage-specific richness models (Table 3). There were also weaker negative associations with macrophyte cover, the quadratic term for pH, and minimum temperature, collectively accounting for an additional 17% of the variance. The signs for the terms implied associations with richness similar to those observed in the diatom and planktonic crustacean models (pH) and the benthos and planktonic rotifer models (minimum temperature, macrophyte cover).

The second principal component (richness PC2) captured that assemblage covariation remaining after controlling for area-induced concordant patterns on richness PC1 (Table 5). The diatoms were by far the most influential assemblage on the axis ($r^2 = 0.76$). Lake depth accounted for the most variance in richness PC2 (23%), with the sign for the term im-

Table 4. Pearson product-moment correlations among richness measures for the six taxonomic assemblages are given below the matrix diagonal ($n = 84$); above the matrix diagonal (in parentheses) are estimates of the maximum potential correlations among richness measures, computed by assuming no correlation in variance attributable to measurement variability (σ^2_{rep}) and perfect correlation in variance attributable to between-lake differences (σ^2_{lake}) (see Table 1).

	Benthos	Birds	Diatoms	Fish	Planktonic crustaceans	Planktonic rotifers
Benthos		(0.32)	(0.51)	(0.47)	(0.48)	(0.40)
Birds	0.18		(0.58)*	(0.54)*	(0.54)*	(0.45)*
Diatoms	0.37†	0.11		(0.85)*	(0.85)*	(0.71)*
Fish	0.26	0.13	–0.01		(0.79)*	(0.66)*
Planktonic crustaceans	0.31†	0.27	–0.07	0.27		(0.67)*
Planktonic rotifers	0.22	0.12	0.04	0.15	0.24	

Note: Significance levels below the matrix diagonal pertain to the null hypothesis that the observed correlations = 0, while those above pertain to the null hypothesis that the correlations observed (below matrix diagonal) are equal to their potential maxima (above the matrix diagonal).

*$P < 0.05$, Bonferroni correction applied to α level to control for multiple tests; null hypothesis: observed correlation (below diagonal) equals the potential maximum (above diagonal) (one-tailed test).

†$P < 0.05$, Bonferroni correction applied to α level to control for multiple tests; null hypothesis: correlation = 0 (two-tailed test).

Table 5. Eigenvalues and the percent variance captured by the principal components (eigenvalues >1) derived from correlations among the six assemblage richness measures ($n = 84$), along with each assemblage's loadings and the proportion of its variance (r^2) shared with the PCA axes.

	Richness PC1		Richness PC2	
	Loading	r^2	Loading	r^2
Benthos	0.53	0.54	–0.35	0.14
Birds	0.38	0.27	0.04	0.00
Diatoms	0.23	0.10	–0.80	0.76
Fish	0.40	0.30	0.27	0.09
Planktonic crustaceans	0.48	0.45	0.38	0.17
Planktonic rotifers	0.37	0.26	0.17	0.03
Eigenvalue		1.93		1.18
% variance		32		20

plying that diatom richness declined with increasing depth, as in the diatom model (Table 3). The subsequent addition of pH accounted for an additional 13% of the variance, with seasonality then contributing an additional 3%.

Discussion

Measurement precision

Our results indicate that the low correlations among the six assemblage richness measures were at least partly attributable to measurement variability, demonstrating that precision is an important consideration when assessing the concordance of assemblages. Errors in diversity measurement will also make the identification of species-rich "hot spots" (Prendergast et al. 1993*a*) for conservation purposes problematic, even if variation in recording effort is controlled (Prendergast et al. 1993*b*), as was done for this study. Measurement uncertainty should therefore also be considered as part of biodiversity assessment.

Lake morphology

All assemblages, other than the diatoms, showed a positive association between richness and lake area, and lake area was most important in inducing concordant richness patterns. Our richness measures controlled for sampling effort using rarefaction; thus the number of taxa per unit lake area increased with lake area, implying that the patterns arose from ecological processes (Hill et al. 1994). The species–area relationship applies to both aquatic and terrestrial systems (Connor and McCoy 1979), but a variety of mechanisms have been invoked to explain the pattern (Hill et al. 1994). The habitat diversity hypothesis asserts that richness is greater for larger areas because they encompass a greater breadth of environmental conditions and so can accommodate more taxa (Williams 1964). The theory of island biogeography asserts that the richness of habitat islands represents an equilibrium between stochastic colonization and extinction events (MacArthur and Wilson 1967). Richness is thought to be greater on larger habitat islands because they support larger populations that are thus less prone to extinction. Both of these hypotheses have garnered extensive empirical support (Hill et al. 1994), but given that lake area is a two-dimensional measure of a three-dimensional environment, the pattern may also reflect lake area's influence on other factors including predation, temperature and DO stratification, pH, and productivity (e.g., Tonn and Magnuson 1982; Matuszek and Beggs 1988; Robinson and Tonn 1989). These hypotheses are not mutually exclusive. Rather, the consistency of the pattern across such disparate taxonomic groups suggests that multiple processes were at work simultaneously, although their relative influence likely varied among assemblages. For example, island biogeographic mechanisms related to population processes were probably less important to riparian birds than to fish given the more insular nature of lakes to the latter assemblage (Tonn and Magnuson 1982).

In contrast with the other assemblages, the diatoms showed little association between richness and lake area and a negative association between richness and depth. The deepwater sediment samples of diatoms integrate pelagic species and benthic species occupying diverse substrates (e.g., mud, rock, sand, macrophytes) throughout the lake (Dixit and Smol 1994). However, the benthic diatoms are far more speciose than the pelagic diatoms (Wetzel 1983), suggesting that shallower lakes were of higher richness because their samples contained proportionally greater numbers of benthic diatom species.

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Other nonanthropogenic factors

The associations of diatom richness with pH indicate that more diatom species were able to tolerate circumneutral waters than either acidic or alkaline conditions, a pattern consistent with their sensitivity to pH (Dixit and Smol 1994). Zooplankton richness was similarly constrained by pH here as in other studies (e.g., Locke and Sprules 1994). The zooplankton were also negatively associated with DO, perhaps because low-oxygen areas served as refuges from fish predation. In contrast, benthic macroinvertebrate richness increased with DO, a finding consistent with oxygen availability limiting distributions of benthic macroinvertebrates (Brinkhurst 1974). Benthic macroinvertebrates were sampled in well-oxygenated waters of the sublittoral zone in the thermally stratified lakes, but many of the lakes surveyed were shallow and had no thermal stratification. Some of these shallow lakes may have had DO that was sufficiently low near the sediment–water interface to limit the diversity of benthic macroinvertebrates throughout the sublittoral zone. The negative association between benthic macroinvertebrate richness and water temperature may have also been related to oxygen availability because cooler lakes were generally deeper ($r = -0.82$, $n = 115$, $P < 0.01$) and of lower productivity ($r = 0.57$, $P < 0.01$) and were thus more likely to have a well-established thermocline with relatively high oxygen concentrations at the bottom (Wetzel 1983). Rotifer richness was also higher in lakes with lower minimum temperatures, presumably because thermally stratified lakes were able to accommodate both warm- and cold-water rotifer species.

Littoral rotifers are far more speciose than pelagic rotifers (Wetzel 1983), so the positive association that we observed between rotifer richness and macrophyte cover may have occurred if littoral rotifers were incidentally sampled in the water column. Incidental capture of littoral organisms might also help to explain the positive association between benthic macroinvertebrate richness and macrophyte cover if "true" sublittoral samples could not be obtained in shallow lakes where macrophytes covered a large portion of the lake bottom.

Anthropogenic factors

Anthropogenic effects on taxon richness varied among assemblages and were weak compared with those of lake morphology and other factors. The positive association that we observed between fish richness and regional human development is likely attributable to human introductions of fish species because none of the anthropogenic variables were important predictors if we dropped nonnative species from the model. Instead, the quadratic term for pH became most important after lake area and no other terms entered the model. We observed this positive association with human development despite evidence indicating that introductions of nonnative littoral predators for sportfishing, particularly *Micropterus* spp., have reduced or eliminated cyprinid species from lakes throughout much of this region (Whittier et al. 1997). Apparently, introduced fish species have more than offset any concomitant losses of native species. Chapleau et al. (1997) similarly observed that while introductions of piscivores to small Quebec lakes (<61 ha) have brought about marked declines in cyprinid species over the last 85 years, overall fish species richness has remained relatively unchanged. Associations with land use varied from negative to positive for the diatoms and planktonic crustaceans, but both associations may have reflected the sensitivity of these two assemblages to phosphorus, chloride, and other chemicals introduced into lakes through human activities (Dixit and Smol 1994; Stemberger and Lazorchak 1994).

Conclusions

Our results indicate that lake morphology was important in inducing concordant richness patterns among taxonomically disparate assemblages, but that other aspects of the environment, including anthropogenic factors, were much weaker in their influence and more assemblage specific. To the extent that biological diversity affects ecosystem function, lake morphology may therefore influence energy and nutrient cycling through its simultaneous influence on diversity patterns at multiple trophic levels. Nonanthropogenic factors were more important than anthropogenic factors as determinants of richness, so the former must be considered prior to assessing effects attributable to the latter. This is an important consideration for developing indices of biotic integrity (IBI's) (Karr 1991) to monitor anthropogenic effects on lakes because IBI's often incorporate richness measures. The relatively weak responses of our lake assemblages to land use are consistent with Schindler's (1987) observation that the richness of lake assemblages is affected only by the most severe environmental perturbations. Moreover, responses of our assemblages to human development varied; thus, our results were consistent with neither the disturbance literature, which predicts a richness peak with intermediate disturbance (Huston 1979), nor the stress literature, which predicts monotonic declines in richness (Odum 1985). Taxonomic richness may therefore be of ambiguous value as an indicator of biological integrity in lakes.

Assemblage-specific richness models explained $\leq 42\%$ of the variance, so in addition to measurement variability, other factors not considered here were likely also important. However, even a complete understanding of the factors influencing taxonomic richness would be insufficient to fully appreciate the organization, dynamics, and controlling mechanisms of these assemblages because other aspects of assemblage structure are obscured in richness measures (Tonn and Magnuson 1982). For example, our results indicate that fish introductions have increased the species richness of lake fish assemblages in much of this region despite the fact that many of these same introduced species are littoral predators that have been implicated in the extirpation of native cyprinid species from lakes in southern New England (Whittier et al. 1997). It is therefore likely that while fish species introductions have enhanced overall fish species richness for individual lakes, these same introductions have also homogenized the piscifauna at the regional scale by replacing the diverse cyprinid group with smaller numbers of nonnative sport fish species (Whittier et al. 1997). These additional insights could only be obtained through qualitative consideration of the species present in the fish assemblages. Community structural aspects other than assemblage richness must therefore also be examined to evaluate how natural and anthropogenic factors affect the biota.

Acknowledgments

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