

Nutrient enrichment homogenizes lake benthic assemblages at local and regional scales

IAN DONOHUE,^{1,3} ANDREW L. JACKSON,¹ MARTIN T. PUSCH,² AND KENNETH IRVINE¹

¹*School of Natural Sciences, Department of Zoology, Trinity College, Dublin 2 Ireland*

²*Leibniz Institute of Freshwater Ecology and Inland Fisheries, Department of Lowland Rivers and Shallow Lakes, Müggelseedamm 301, 12587 Berlin, Germany*

Abstract. The compositional heterogeneity of biotic assemblages among sites, or β -diversity, regulates the relationship between local and regional species diversity across scales. Recent work has suggested that increased harshness of environmental conditions tends to reduce β -diversity by decreasing the importance of stochastic processes in structuring assemblages. We investigated the effect of nutrient enrichment on the compositional heterogeneity of lake benthic invertebrate assemblages in Ireland at both local (within-lake) and regional (among-lake) scales. At local scales, we found that the compositional heterogeneity of benthic assemblages was related inversely to the extent of nutrient enrichment (as indicated by measurements of water column total phosphorus, total nitrogen, and chlorophyll *a*), after effects of lake morphology (i.e., surface area, connectivity, and depth of sampling) and alkalinity were accounted for. At regional scales, we found that nutrient-rich lakes had significantly more homogenous benthic assemblages than nutrient-poor lakes, over and above the effect of alkalinity and across a similar range of lake morphologies. These findings have profound implications for global aquatic biodiversity, as the homogenization of benthic assemblages at both local and regional scales may have important and unpredictable effects on whole aquatic ecosystems, with potentially considerable ecological and evolutionary consequences.

Key words: disturbance; diversity; eutrophication; homogenization; invertebrate; Ireland; productivity; variability.

INTRODUCTION

The compositional heterogeneity of biotic assemblages among sites, or β -diversity, regulates the relationship between local and regional species diversity across scales (Whittaker 1972, Cornell and Lawton 1992, Lande 1996, Loreau 2000). β -diversity is itself a function of heterogeneity in both environmental conditions and species niches, of which the latter define the mechanisms by which species respond to environmental heterogeneity (Loreau 2000). Widespread anthropogenic homogenization of taxonomic, genetic and functional diversity, either indirectly through homogenization of environmental conditions (Balata et al. 2007, Brauns et al. 2007b, Passy and Blanchet 2007, Poff et al. 2007), or directly via alteration of biotic assemblages (Rahel 2002, Olden and Poff 2004, Olden and Rooney 2006, Chase 2007, Chalcraft et al. 2008) have, therefore, profound implications for ecology, evolution, and global biological diversity (Olden et al. 2004).

The compositional heterogeneity of biotic assemblages among sites has been correlated positively with productivity (Chase and Leibold 2002, Chase and

Ryberg 2004). It has, however, been demonstrated (Chalcraft et al. 2008) that anthropogenic nutrient enrichment can both increase and decrease the β -diversity of terrestrial grasslands, depending upon initial site productivity. Recently, Chase (2007) demonstrated that increased harshness of environmental conditions tends to reduce compositional heterogeneity among sites by decreasing the importance of stochastic processes in structuring assemblages. Moreover, anthropogenic enrichment of ecosystems with nutrients frequently increases the harshness of environmental conditions for biota indirectly by, for example, reducing availability of resources such as light and oxygen and modifying habitat structure, food webs, predation pressure and other interspecific interactions (e.g., Cadotte et al. 2006, Fukami et al. 2006, Brauns et al. 2007a, Declerck et al. 2007). This suggests that reductions in β -diversity may be expected wherever nutrient enrichment increases the harshness of environmental conditions for biota, irrespective of changes in productivity.

Cultural eutrophication from nutrient enrichment comprises a globally important anthropogenic impact on aquatic ecosystems (Smith et al. 2006, Schindler and Vallentyne 2008). In spite of this, current understanding of its effects on benthic assemblages remains poor,

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³ E-mail: ian.donohue@tcd.ie

particularly in lakes. This owes largely to their high spatiotemporal variability at scales among and within both lakes and habitats (White and Irvine 2003, Stoffels et al. 2005, Brauns et al. 2007a). The negative effects of nutrient enrichment are, however, arguably manifested most strongly in the benthic zone owing to decreased oxygen availability (Charlton 1980) and reduction of phytobenthic production (Vadeboncoeur et al. 2003, Chandra et al. 2005) and structural complexity (Scheffer et al. 1993, Egertson et al. 2004). We tested the hypothesis that nutrient enrichment homogenizes lake benthic assemblages by analyzing data from both littoral and profundal/sublittoral invertebrate assemblages extracted from a national lakes database for Ireland. Further, as spatial scale can affect the nature of productivity–biodiversity relationships (Chase and Leibold 2002, Chase and Ryberg 2004), and productivity is generally related strongly to nutrient concentrations (Schindler 1978, Smith 1979), we also examined whether relationships between the extent of nutrient enrichment and the compositional heterogeneity of benthic assemblages varied between local (within-lake) and regional (among-lake) scales.

METHODS

Sampling and laboratory analyses

Littoral invertebrates were collected by kick sampling in stony substrates (gravels, pebbles, or cobbles without obvious macrophyte presence) for 30 seconds with a 1-mm mesh pond net for the analysis at within-lake scales, and for 2 minutes with a 670- μ m mesh pond net for the analysis among lakes. Two hundred and four littoral invertebrate taxa were collected and identified to the lowest practicable taxonomic level (60% to species and 31% to genus, with the remainder identified to family, except for Hydrachnidia, Lepidoptera, Oligochaeta, Ostracoda, and Turbellaria). Profundal/sublittoral invertebrates (range of water depths sampled 1.1–71.9 m; Appendices A and B) were sampled with an Ekman grab (sampling area 0.0225 m²) and passed through a 500- μ m mesh. Ninety seven profundal/sublittoral invertebrate taxa were found, of which 26% were identified to species (including Oligochaeta and Hirudinea), 53% to genus (including Chironomidae), and the remainder to family except for Hydrachnidia, Nematoda, Ostracoda, and Turbellaria.

Concurrent measures of water column total phosphorus (TP), total nitrogen (TN), chlorophyll *a*, and alkalinity (quantified following Eisenreich et al. 1975, Standing Committee of Analysts 1980, Clesceri et al. 1998, Grasshoff et al. 1999) were made on every sampling occasion. Lakes exposed to minimal anthropogenic disturbance in Ireland have been shown consistently to be oligotrophic (Leira et al. 2006). This supports the assertion that lakes of higher trophic analyzed here have undergone anthropogenic nutrient enrichment, particularly since the mid-1970s.

Data analyses

Data from six samples of littoral invertebrates from each of 25 lakes and three samples of profundal/sublittoral invertebrates from each of 12 lakes (Appendix A), sampled as described above, were extracted from an Irish lakes database and used to quantify the compositional heterogeneity of benthic assemblages (see *Statistical methods*) within lakes. The samples were taken from a number of locations throughout each lake between 1996 and 2002 on sampling occasions distributed throughout the year (Appendix A). Sampling of profundal/sublittoral assemblages was, however, limited to the period between March and September. Owing to availability of data, it was not possible to disentangle the individual contributions of spatial and temporal variability. The data were instead used to estimate total spatiotemporal heterogeneity in the composition of benthic assemblages. In cases where in excess of six samples of littoral invertebrates (21 out of 25 lakes) or three of profundal/sublittoral invertebrates (10 out of 12 lakes) were available from a particular lake, samples included in the analyses were selected randomly from the pool of those available (mean number of available littoral samples per lake [\pm SD] = 8.6 ± 2.3 , range = 6–15; mean number of available profundal/sublittoral samples per lake = 5.6 ± 2.4 , range = 3–11).

Data from single samples of both littoral and profundal/sublittoral invertebrate assemblages, collected between 1996 and 2005 from, respectively, 40 and 52 lakes (Appendix B) distributed throughout Ireland were also extracted from the database and used to quantify compositional heterogeneity at among-lake scales. These samples were extracted from the database on the basis of their concurrent water chemistry fulfilling criteria for either oligotrophic (nutrient-poor) or eutrophic (nutrient-rich) status; lakes classified as oligotrophic (littoral, $n = 20$; profundal/sublittoral, $n = 26$) had both TP and chlorophyll *a* concentrations less than 10 and 2.5 μ g/L, respectively, at the time of sampling. Those with concentrations of greater than, respectively, 35 and 8 μ g/L were classified as eutrophic (littoral, $n = 20$; profundal/sublittoral, $n = 26$), following Organisation for Economic Cooperation and Development (1982). Owing to subsequent analytical requirements for equal numbers of lakes in each trophic group, lakes included in the analyses from the group with greater numbers of samples were selected randomly from those available (littoral, 46 oligotrophic lakes available; profundal/sublittoral, 37 oligotrophic lakes available). In cases where in excess of one sample fulfilling the water chemistry criteria was available from any particular lake (littoral, 7 out of 40 lakes; profundal/sublittoral, 4 out of 52 lakes), the sample included in the analyses was selected randomly from the pool of those available.

Statistical methods

Global relative multivariate dispersion (calculated following Warwick and Clarke 1993, Clarke and

Warwick 2001) was used as a holistic measure of compositional heterogeneity (Anderson et al. 2006) both within and among lakes. All multivariate analyses of biotic data were based on Bray-Curtis similarity matrices (Bray and Curtis 1957) and were calculated from $\log(x + 1)$ -transformed abundances in the case of profundal/sublittoral data and proportional abundances in the case of the littoral invertebrate data, the latter owing to the nonquantitative nature of kick sampling. Multivariate dispersion, which is not confounded with estimates of α - or γ -diversity (Lande 1996), comprises a relative multivariate measure of variability in different groups of samples and is calculated by comparing ranked distance/similarity measures within and among groups in a similarity matrix. This was calculated independently for littoral and profundal/sublittoral assemblages.

Multiple regression (linear first-order main effects with normal errors) was used to test the significance and nature of relationships between multivariate dispersion within lakes and each of three measures of nutrient enrichment: mean water column concentrations of TP, TN, and chlorophyll *a*. The significance of each measure of nutrient enrichment was determined in separate multiple regression analyses. Owing to the fact that water column alkalinity, surface area, and connectivity of lakes are all likely to influence strongly the composition and taxonomic richness of their biotic assemblages (Nilsson and Nilsson 1978, Browne 1981, Dodson 1992, Chase and Ryberg 2004, Smith et al. 2005), these factors were offered as independent variables to the multiple regression analyses in conjunction with each measure of nutrient enrichment in the maximal model. We used the number of lakes connected directly to the sampled lakes as our measure of lake connectivity. In addition, the mean depth of sampling was incorporated into the analyses of profundal/sublittoral invertebrates. Step-wise model selection was performed based on Akaike's information criterion (AIC_c), corrected to account for small sample size biases (Burnham and Anderson 2004), using forward and backward selection to identify the minimum adequate model (Whittingham et al. 2006). Significance of the effects of the various measures of nutrient enrichment on compositional heterogeneity at within-lake scales was then quantified by its contribution to model fit determined by AIC_c . Each of TP, TN, chlorophyll *a*, and lake surface area were \log_{10} -transformed to normalize distributions prior to analysis.

A combination of permutational analysis of multivariate dispersions (PERMDISP; Anderson 2006) and permutational multivariate analysis of variance (PERMANOVA; Anderson 2001, McArdle and Anderson 2001) was used to test whether the compositional heterogeneity of littoral or profundal/sublittoral invertebrate assemblages varied between nutrient-poor and nutrient-rich lakes (i.e., at among-lake scales). PERMDISP comprises a distance-based test of the homogeneity

of multivariate dispersions among groups of a single factor, comprising essentially a multivariate extension of Levene's test (Levene 1960). Although similar ranges in alkalinity, surface area, connectivity, and depth of sampling were present in both trophic groups (Appendix B), (\log_{10} -transformed) alkalinity was significantly higher in the eutrophic lakes in both the littoral (*t* test; $t_{38.8} = 4.28$, $P \leq 0.0001$) and profundal/sublittoral ($t_{37.9} = 5.92$, $P \leq 0.0001$) analyses, reflecting geographical association between intensive grassland agriculture in Ireland and alkaline soils. Consequently, to disentangle the possible confounding effects of alkalinity and trophic status on compositional heterogeneity, we categorized lakes into three alkalinity groups (low alkalinity, <20 mg CaCO_3/L ; moderate alkalinity, 20 – 100 mg CaCO_3/L ; high alkalinity, >100 mg CaCO_3/L) following the Irish lake classification scheme (EPA 2005) under the EU Water Framework Directive (2000/60/EC). PERMDISP was then used to calculate the distances between samples and their trophic group centroids separately for each alkalinity group. Similar to standard PERMDISP analyses, PERMANOVA was then used to compare these distances, except we used a two-factor PERMANOVA design, with 9999 permutations of the residuals under a reduced model, as recommended by Anderson (2005), with trophic status (fixed factor, two levels) crossed with alkalinity group (fixed factor, three levels). This model design was also used to examine whether the spatial distances among lakes differed significantly between the nutrient-rich and nutrient-poor lakes used in the among-lake analysis. Among-lake distances were calculated as the Euclidian distances among the eastings and northings of lake midpoints. Taxa that were contributing most to the dissimilarities between nutrient-poor and nutrient-rich lakes were identified using similarity percentages (SIMPER) analyses (Clarke and Warwick 2001) with alkalinity and trophic status incorporated as independent variables. All multivariate analyses were done with PRIMER Version 6.1 (PRIMER-E Ltd., Plymouth, UK). Finally, in order to test whether changes in the compositional heterogeneity of benthic assemblages were a result of reductions in the frequency of occurrence of intolerant taxa (see Chase 2007) and, hence, less sporadic occurrences of taxa in nutrient-enriched lakes, we conducted independent-samples *t* tests (without assuming equal variances; Welsh 1947) comparing the frequency of occurrence of taxa in nutrient-poor and nutrient-rich lakes. This was done at among-lake scales for both littoral and profundal/sublittoral assemblages. An α significance level of 0.05 was used for all analyses.

RESULTS

Each of our covariates measuring nutrient enrichment were retained in the models best describing multivariate dispersion of both littoral and profundal/sublittoral invertebrate assemblages at the within-lake scale (Table

1). Further, these relationships were inverse in every case (Table 1, Fig. 1). Comparison of AIC_c values indicate that the model containing chlorophyll *a*, alkalinity, connectivity, and surface area best explained the data for littoral assemblage heterogeneity, whereas a model containing TN and surface area was best for profundal/sublittoral assemblages.

At among-lake scales, the composition of both littoral and profundal/sublittoral invertebrate assemblages was significantly (Table 2) less heterogeneous (Fig. 2) in nutrient-rich than nutrient-poor lakes, while there was no effect of water column alkalinity and no significant interaction between trophic status and alkalinity. Further, the relative variability of the distances among lakes was not affected by trophic status (Appendix C). *Asellus aquaticus*, *Gammarus* sp., and oligochaete worms were found to be the three taxa from littoral samples contributing most to the dissimilarity between nutrient-poor and nutrient-rich lakes while the two oligochaete taxa *Limnodrilus* sp. and *Potamothrix hammoniensis* together with the Chaoboridae contributed most to this dissimilarity for the profundal/sublittoral zone (Appendix D). The oligochaetes were also consistently more abundant in the nutrient-rich lakes. There was, however, no difference in the frequency of occurrence of taxa between nutrient-poor and nutrient-rich lakes (*t* test; littoral, $t_{150,25} = 0.08$, $P = 0.94$; profundal/sublittoral, $t_{63,77} = 1.2$, $P = 0.24$); of the littoral taxa observed in at least one of the nutrient-poor lakes, each was observed in 4.72 ± 1.01 (mean \pm 95% CI) of the nutrient-poor lakes, while of those sampled from nutrient-rich lakes, each was sampled from 4.78 ± 1.2 of the nutrient-rich lakes. Similarly, each profundal/sublittoral taxon found in at least one of the nutrient-poor lakes was found in 4.64 ± 1.21 of the nutrient-poor lakes, while for those found in nutrient-rich lakes, each was sampled from 6.19 ± 2.3 of the nutrient-rich lakes.

DISCUSSION

Our results indicate strongly that nutrient enrichment homogenizes the composition of lake benthic assemblages. The fact that similar results were obtained from independent analyses of both littoral and profundal/sublittoral invertebrate assemblages within and among lakes suggests that this pattern occurs throughout the benthic zone of lakes at both local and regional scales. Two mechanisms could account for these patterns. First, if nutrient enrichment promotes homogenization of habitat structure, increased compositional similarity of biotic assemblages is likely to occur among sites at both local and regional scales (Chase and Leibold 2002). Habitat heterogeneity is recognized as one of the most important mechanisms generating β -diversity (Connor and McCoy 1979, Loreau 2000), and empirical field surveys have shown that decreased habitat heterogeneity owing to anthropogenic disturbance can reduce β -diversity significantly (Passy and Blanchet 2007). Although we did not quantify habitat heterogeneity

TABLE 1. Results of multiple regression analyses with multivariate dispersion within lakes as the dependent variable for two benthic zones (littoral and profundal/sublittoral).

Independent variable	<i>B</i> (2.5%, 97.5% CI)	AIC_c (null model)
Littoral zone ($n = 25$)		
a)		
log ₁₀ (area)†	-0.31 (-0.50, -0.12)	
Alkalinity	-0.00 (-0.00, 0.00)	
Connectivity	removed	
log ₁₀ (TP)‡	-0.47 (-0.73, -0.21)	5.97 (24.47)
b)		
log ₁₀ (area) †	-0.35 (-0.57, -0.12)	
Alkalinity	removed	
Connectivity	removed	
log ₁₀ (TN) §	-0.52 (-0.92, -0.12)	10.22 (24.47)
c)		
log ₁₀ (area)	-0.30 (-0.48, -0.01)	
Alkalinity	-0.00 (-0.00, -0.00)	
Connectivity	-0.04 (-0.07, -0.00)	
log ₁₀ (chlorophyll <i>a</i>)	-0.48 (-0.68, -0.03)	1.84 (24.47)
Profundal/sublittoral zone ($n = 12$)		
d)		
log ₁₀ (area)	-0.54 (-0.94, -0.13)	
Alkalinity	removed	
Sample depth	removed	
Connectivity	removed	
log ₁₀ (TP)	-0.68 (-1.1, -0.27)	10.12 (15.86)
e)		
log ₁₀ (area)	-0.50 (-0.87, -0.13)	
Alkalinity	removed	
Sample depth	removed	
Connectivity	removed	
log ₁₀ (TN)	-1.10 (-1.67, -0.54)	7.84 (15.86)
f)		
log ₁₀ (area)	-0.41 (-0.83, 0.00)	
Alkalinity	removed	
Sample depth	removed	
Connectivity	removed	
log ₁₀ (chlorophyll <i>a</i>)	-0.64 (-1.04, 0.00)	10.64 (15.86)

Notes: The maximal model included all covariates as listed for models specifically including total phosphorus (TP; a and d), total nitrogen (TN; b and e) and chlorophyll *a* (c and f) as independent covariates. Results for the minimal adequate models based on AIC_c are presented. Parameter estimates are given by *B* with 2.5% and 97.5% confidence intervals in parentheses. The AIC_c value for the corresponding null model (i.e., with the overall mean as the only model parameter) is also given in parentheses for comparison. Area was measured in hectares, alkalinity in mg CaCO₃/L, sample depth in m, TP in μ g/L, TN in mg/L, and chlorophyll *a* in μ g/L. Connectivity was measured as the number of lakes connected directly to the sampled lakes.

directly, increased homogeneity of habitats both within and among lakes with increasing trophy, owing to blanketing of the lakebed with organic sediments and reduction of structural heterogeneity from macrophytes (Scheffer et al. 1993, Egertson et al. 2004), may have contributed to the observed homogenization of benthic assemblages. Similarly, decreased importance of trophic heterogeneity within and among benthic habitats owing to greater reliance on open-water productivity with increasing extent of nutrient enrichment (Vadeboncoeur et al. 2003, Chandra et al. 2005) could also lead to reduced heterogeneity of benthic communities. The

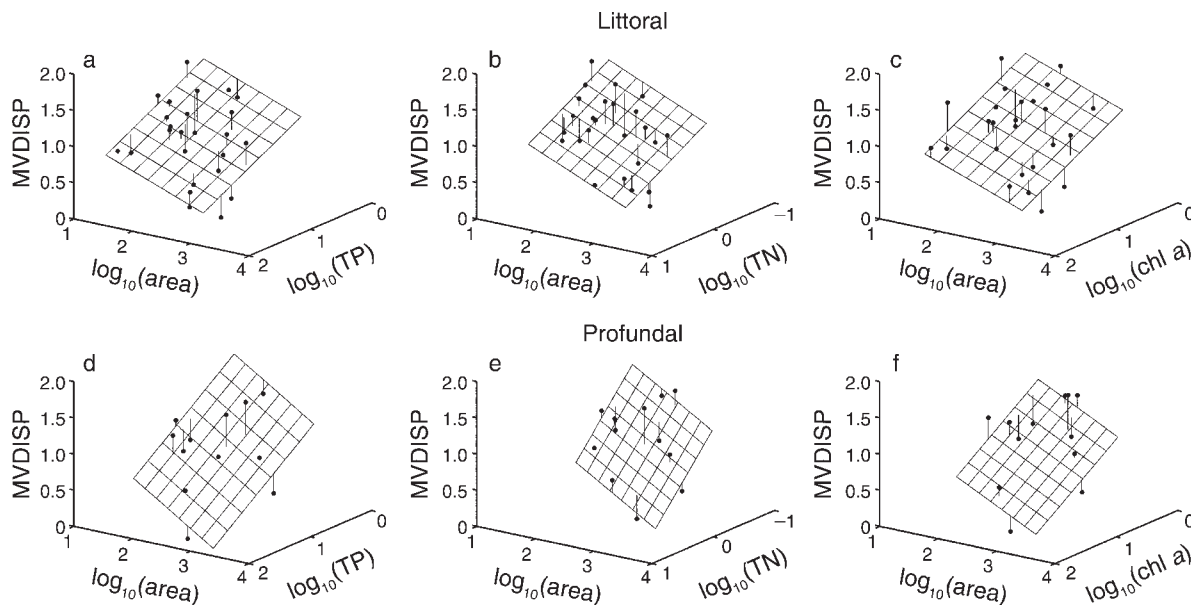


FIG. 1. Raw data (dots) with the fitted model (grid) detailed on Table 1 showing multivariate dispersion (MVDISP, a unitless measure) within lakes as a function of lake surface area and (a, d) TP, (b, e) TN, and (c, f) chlorophyll *a* for both littoral and profundal/sublittoral invertebrate assemblages. Stem lines join the raw data points to the fitted model surface indicating their relative position. Axes for the measures of nutrient enrichment are plotted in reverse direction. Models (a) and (c) contained additional covariates (see Table 1 for details), which were fixed at their mean value for the purposes of graphical representation.

important contribution of oligochaete worms, which normally exhibit a general preference for fine organic-rich sediments, to the dissimilarity between nutrient-poor and nutrient-rich lakes, coupled with their increased abundance in nutrient-rich lakes, supports these assertions.

Second, recent work by Chase (2007) suggests that harsh “ecological filters,” such as those resulting from strong anthropogenic disturbance, reduce the importance of stochastic processes in structuring biotic communities and, hence, reduce the compositional heterogeneity of biotic assemblages among sites. This process is driven by niche selection resulting in the exclusion of intolerant taxa and could occur independently of alterations to habitat heterogeneity (cf. Loreau 2000). The fact that there was no difference in the

frequency of occurrence of taxa between nutrient-poor and nutrient-rich lakes suggests strongly, however, that this mechanism was not a significant driver of the patterns observed here.

In contrast to our results, Chase and coworkers (Chase and Leibold 2002, Chase and Ryberg 2004) found positive associations between periphyton productivity and the compositional heterogeneity of whole biotic assemblages (including fish, amphibians, benthic and free-swimming invertebrates, plants, and algae) in ponds located along a natural gradient in productivity. This indicates that the effects of relatively recent anthropogenic nutrient enrichment on β -diversity may differ from those of more natural variability in productivity. Recent work by Chalcraft et al. (2008), which found that initial site productivity determines

TABLE 2. Results of PERMANOVA analyses examining the effects of lake water column alkalinity and trophic status on the compositional heterogeneity of littoral and profundal/sublittoral invertebrate assemblages at among-lake scales.

Source	df	Sum of squares	Mean square	Pseudo <i>F</i>	<i>P</i>
Littoral					
Alkalinity (Alk)	2	24.25	12.12	0.45	0.64
Trophic status (TS)	1	870.32	870.32	32.5	≤ 0.0001
Alk \times TS	2	17.79	8.89	0.33	0.71
Residual	34	910.41	26.78		
Total	39	2245.1			
Profundal/sublittoral					
Alkalinity	2	199.22	99.61	1.23	0.3
Trophic status	1	1666.9	1666.9	20.56	≤ 0.0001
Alk \times TS	2	468.29	234.14	2.89	0.07
Residual	46	3730.4	81.1		
Total	51	9131.6			

whether compositional heterogeneity increases or decreases with nutrient enrichment provides a potential mechanism for these contrasting findings. Whereas the gradual natural eutrophication of ponds over relatively long timescales supports the assembly of communities comprised of species adapted to increasingly productive conditions, the rapid increases in productivity caused by anthropogenic nutrient enrichment likely induce unfavorable conditions for biotic assemblages in situ, and may, therefore, affect compositional heterogeneity in entirely different ways.

Empirical surveys (Chase 2003, Chase and Ryberg 2004), experimental (Forbes and Chase 2002, Cadotte and Fukami 2005), and theoretical (Hastings and Gavrilets 1999, Mouquet and Loreau 2002, 2003, Loreau et al. 2003) work has shown that greater dispersal or connectivity among localities reduces β -diversity by homogenizing metacommunities. The inverse effect of lake area on the compositional heterogeneity of benthic communities within lakes observed in our study concurs with this (cf. Loreau 2000). That our results reveal a greater importance of lake area compared with connectivity among lakes in mediating β -diversity at within-lake scales likely reflects greater connectivity among metacommunities within, compared with among, lakes. In spite of this, we found that nutrient-rich lakes contained significantly less heterogeneous benthic assemblages than nutrient-poor lakes, across a large range of lake sizes and connectivities and over and above the effect of water column alkalinity, which concurs with our results from independent analyses at within-lake scales. Our results have, therefore, profound implications for the conservation and management of global aquatic biodiversity, owing to the primacy of nutrient enrichment as one of the most pervasive anthropogenic impacts on aquatic ecosystems worldwide (Smith et al. 2006, Schindler and Vallentyne 2008) and because the problem is expected to increase considerably in coming decades (Tilman 1999). Benthic assemblages provide important roles in aquatic food-webs and in the sequestration and recycling of materials (Underwood 1991, Schindler and Scheuerell 2002, Lohrer et al. 2004), which attests to their importance to overall ecosystem functioning. Homogenization of benthic assemblages at both local and regional scales may, therefore, have important and unpredictable effects on whole aquatic ecosystems at the regional scale, with potentially considerable ecological and evolutionary consequences (Olden et al. 2004). Moreover, the compositional homogenization of biotic assemblages at both local and regional scales suggests that studies done at local scales alone underestimate the effects of anthropogenic nutrient enrichment significantly.

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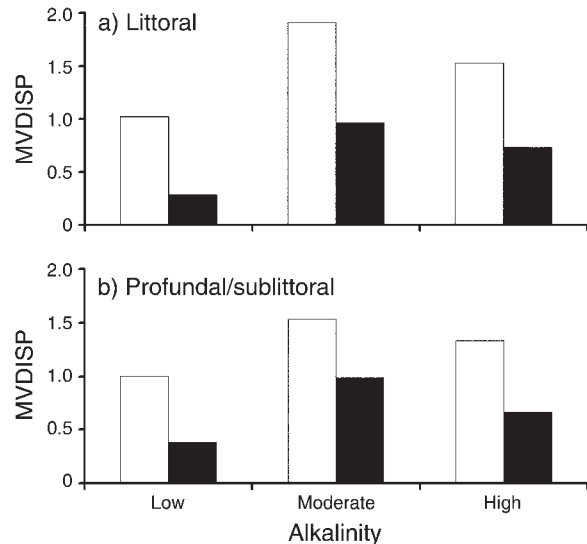


FIG. 2. Multivariate dispersion values of (a) littoral and (b) profundal/sublittoral invertebrate assemblages calculated at among-lake scales for the nutrient-poor (open bars) and nutrient-rich (solid bars) lakes in each alkalinity group.

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APPENDIX A

Lake morphology, water chemistry, mean number of taxa per sample, and the total number of taxa found for the analysis of the compositional heterogeneity of invertebrate assemblages within lakes (*Ecological Archives* E090-241-A1).

APPENDIX B

Morphology and concurrent water chemistry of the lakes used to investigate the compositional heterogeneity of invertebrate assemblages at among-lake scales (*Ecological Archives* E090-241-A2).

APPENDIX C

Results of PERMANOVA analyses examining the effects of lake alkalinity and trophic status on the relative variability of the spatial distances among lakes sampled for invertebrates (*Ecological Archives* E090-241-A3).

APPENDIX D

Results of SIMPER analyses identifying the five taxa contributing most to the dissimilarity between nutrient-poor and nutrient-rich lakes and indicating the relative changes in the abundance of each taxon in lakes of differing trophic status (*Ecological Archives* E090-241-A4).