

# Littoral macroinvertebrate communities: spatial scale and ecological relationships

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## SUMMARY

1. Spatial correlations between ecological patterns and processes are thought to be scale-dependent, yet surprisingly few studies have evaluated the correspondence between different levels of spatial scale and ecosystem structure and function.
2. We evaluated the strength of relationships between the benthic macroinvertebrate communities of stony littoral habitats and levels of ecological scale and geographical position, using partial constrained ordination. Our hypothesis was that correlation strength would be inversely related to ecological scale, i.e. habitat > ecosystem > riparian > catchment > ecoregion.
3. The effect of habitat was greater than that of other levels of spatial scale: 23% of the variance in taxonomic composition and 11% of that in functional composition was explained by habitat variables alone. However, greater spatial scales were also important. For example, the combined influence of riparian, catchment and ecoregion classification accounted for 24% (taxonomic) and 11% (functional) of the explained variance.
4. Relationships between organisms and scale variables were, however, non-linear and a substantial amount of the functional variance was hidden in joint effects. These findings were not unexpected, and presumably indicate a close interdependence between local and regional-scale variables.

*Keywords:* ecosystem, lakes, littoral, spatial scale, temperate, variance partitioning

## Introduction

Integrating pattern and scale is a central theme in ecology and, not surprisingly, a number of studies have addressed fine-scale distribution patterns of plants and animals (Levin, 1992). Much less attention, however, has been given to the correspondence between community structure and function at different levels of spatial scale (e.g. from habitat to landscape). The rather common 'reductionist approach' of studying small-scale processes and mechanisms has certainly increased our understanding of important ecosystem processes (e.g. the microbial loop of pelagic systems), but the conceptual segregation of

ecosystems hinders our understanding of interactions between them (Bunnell & Huggard, 1999). For example, the presence or absence of organisms may depend on rare or large-scale (region-specific) dispersal and colonisation events, while local abundance is more a function of frequent, fine-scale processes such as biotic interactions and habitat heterogeneity (e.g. Ricklefs, 1987). This implies that communities are structured by both abiotic and biotic factors nested along spatial and temporal scales, and that knowledge of the strength of relationships, and in particular ecological linkages, is important for understanding large- and small-scale variability.

Traditionally, position in the landscape, and especially the solid geology and land use, has provided insight into differences among aquatic systems. For example, the lake trophic classification schemes developed by Thienemann (1925) and Naumann (1932) and the River Continuum Concept of Vannote

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*et al.* (1980) are classical examples of the importance of interactions between terrestrial and aquatic systems. Although lake ecologists quickly appreciated the importance of the land on lake water chemistry, stream ecologists have addressed the linkage concept more formally, i.e. streams are considered as 'open systems that are intimately linked with their surrounding landscapes' (e.g. Hynes, 1975). Lake ecologists have, however, recently revisited the landscape position hypothesis and formalised paradigms that recognise more explicitly the importance of landscape position and its significance for describing among-lake variance (e.g. Neill, 1994; Kratz *et al.*, 1997; Soranno *et al.*, 1999; Riera *et al.*, 2000). Variability within and among lakes is driven by factors acting at both regional and local scales. Regional factors such as climate, geology and weathering are interrelated with other factors such as soil type and land cover/use, whereas local factors, like the input and retention of organic matter, are related to the vegetation type and topographical relief. Hence, *a priori*, a close linkage between regional and local scale variation is expected. However, geographical proximity alone is often not sufficient to predict the physical and chemical characteristics of individual lakes. For example, differences in lake morphometry and water retention time, internal processes such as nutrient cycling, and strengths of interactions with the surrounding landscape may singly or in concert confound the importance of regional-scale factors for ecosystem structure and function.

A better knowledge of spatial coherence and the strength of ecological linkages or interconnectedness is needed to understand how differences in land use affect aquatic communities (e.g. Ormerod & Watkinson, 2000). In the management of aquatic resources this information is essential for predicting how catchment-scale manipulations (e.g. forestry and agriculture) will affect the ecological quality of aquatic systems. Earlier analyses evaluated how well ecoregion classification can partition the among-site variance of macroinvertebrate communities of Swedish lakes (Johnson, 2000). Modest differences in community composition were found, these being more homogeneous within than between ecoregions. In this study we address how structural and functional aspects of the littoral macroinvertebrate community in lakes relate to local (e.g. habitat) and regional (landscape) patterns. First, we sought to elucidate

how patterns in community composition relate to local (small-scale) factors at sampling site or to larger scale features of the surrounding landscape. Secondly, we investigated how the strength of ecological relationships between the structural and functional composition of aquatic macroinvertebrate communities corresponds to various levels of spatial scale. Recognising that organisms are closely interlinked with their immediate physical environment, we expect that correlation strength would decrease with increasing levels of spatial scale, i.e. habitat > ecosystem > riparian > catchment > ecoregion.

## Methods

### *Sample collection and study area*

Littoral macroinvertebrate communities of 538 lakes (median lake surface area, 0.26 km<sup>2</sup>; lower and upper quartiles, 0.06 and 1.33 km<sup>2</sup>, respectively) were sampled in the autumn of 1995 as part of the Swedish national lake survey (Wilander *et al.*, 1998; Johnson & Goedkoop, 2000). A number of factors suggested that this data set was sufficiently robust to examine the importance of spatial scale on the structure and function of littoral macroinvertebrate communities. First, lakes were randomly selected, so the samples should be representative of littoral macroinvertebrates in Swedish lakes. Secondly, a number of measures were taken to reduce potentially confounding natural variability or operator error. To reduce within-lake variability, sample collection was stratified both temporally (autumn) and spatially (stony, wind-exposed littoral areas) and samples were collected using standardised kick-sampling (European Committee for Standardization, 1994) with a handnet (0.5 mm mesh size). Five kick-samples (collected during 20 s along a 1-m stretch) were taken from each site (one site per lake) and pooled to one sample for analysis. All macroinvertebrate samples were sorted at the Department of Environmental Assessment according to quality control and assurance protocols. Taxonomic identification was carried out on a predetermined list of some 500 'operable' taxonomic units by six experienced biologists, and an intercalibration of the frequency of misidentified or miscounted taxa was performed (Wilander *et al.*, 1998). Additionally, water samples were taken for physical and chemical analyses, habitats were classified

according to substratum type, and the riparian zone and catchments were classified by land use and cover (Wilander *et al.*, 1998).

The analyses used here are restricted to macroinvertebrate assemblages of sites considered as minimally impacted (Johnson, 1999). Sites affected by point source pollution, liming, acidification (> 0 exceedence of critical load of S), agriculture (catchments > 20% defined as arable), or sampling error (sampling effort in the county of Västernorrland did not comply with the national protocol) were removed from the data set. The remaining 364 lakes were distributed fairly evenly across the country (Fig. 1). The lakes were divided among the major ecoregions of Sweden using the boundaries given by the Nordic Council of Ministers (1984), but modified according to Gustafsson & Ahlén (1996). The ecoregions range from the nemoral region in the south, characterised by deciduous forests, a mean annual temperature higher than 6 °C and a relatively long growth period (180–210 days), to the arctic/alpine complex in the north, characterised by a relatively low mean annual temperature (< 2 °C) and short growth period (< 140 days). Fifty-seven lakes were situated in the arctic/alpine complex, 67 in the northern boreal, 116 in the middle boreal, 53 in the southern boreal, 63 in the boreonemoral and seven in the nemoral regions. For a more thorough description of the ecoregion characteristics see Johnson (2000).

Functional feeding guilds of macroinvertebrates were defined after Moog (1995). Feeding guild classification is based on the food consumed, the morphological adaptations of the feeding structures (mouthparts, legs) and the behaviour that drives these structures (e.g. modes of attachment that allow individuals positioned in the stream current to manipulate a filtering structure, and the construction of capture nets). Moog (1995) recognised 10 classes of functional feeding guilds, but only six classes are used here: shredders, grazers, deposit-feeding collector-gatherers, active and passive filter-feeders, and predators. Leaf borers were not represented in our material and only a few individuals of xylophages, parasites and 'other' feeding types were recorded. Consequently, these four groups were not included in the analysis. Recognising that during its life history an organism may be classified into more than one feeding guild a 10-point score is allotted to each taxon identifying its feeding guild(s). For example, accord-

ing to Moog (1995) the snail *Theodoxus* is scored for 10 points as a grazer, whereas the crustacean *Gammarus* is scored as a shredder (six points), grazer (one point), collector-gatherer (two points) and predator (one point).

Simpson's diversity was calculated as:

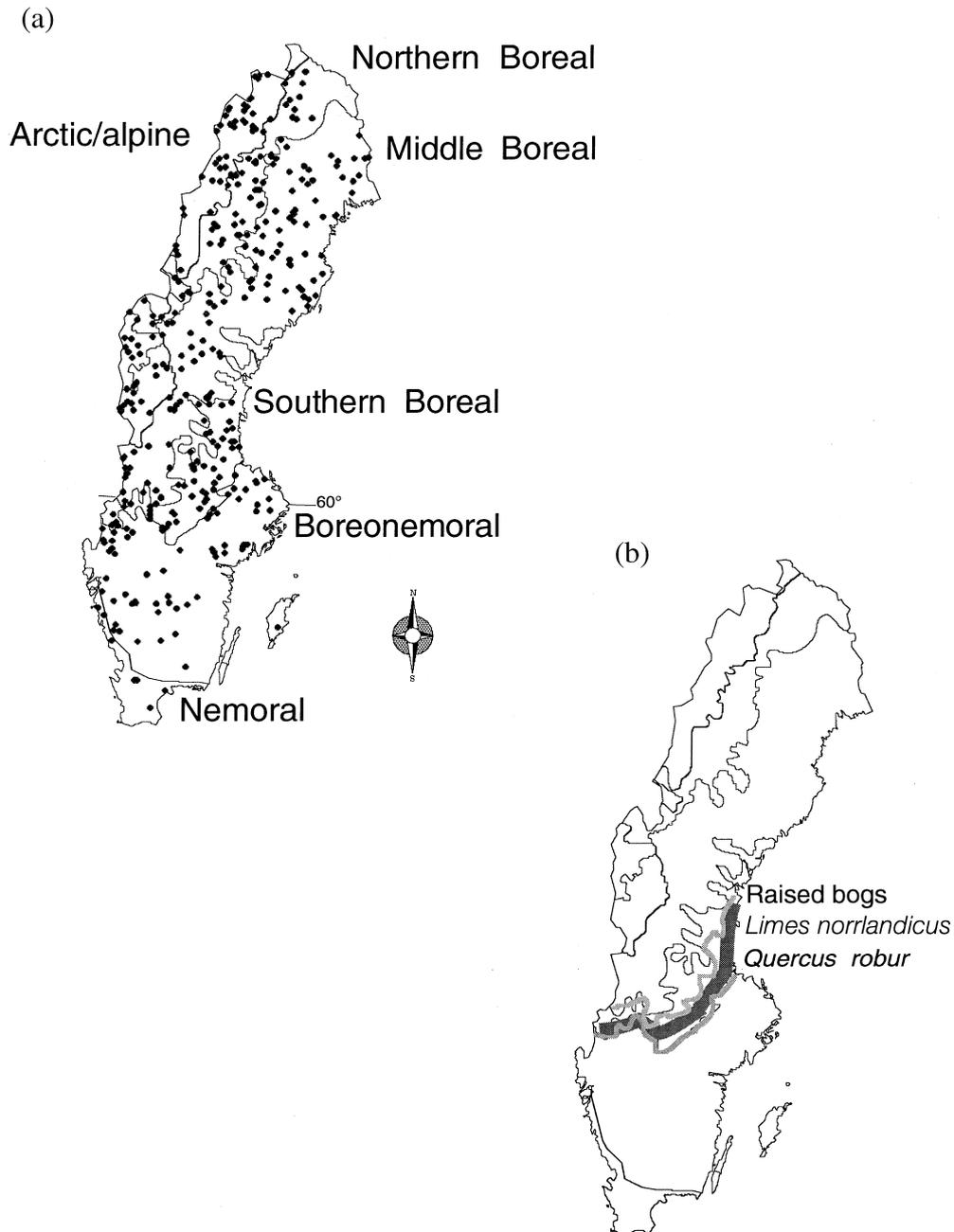
$$D_s = 1 - \frac{\sum n_i(n_i - 1)}{N(N - 1)}$$

where  $N$  is the number of individuals distributed among species, with  $n_i$  individuals in the  $i$ th species.

### Statistical analyses

Analysis of variance (ANOVA) and the Tukey–Kramer HSD test (Tukey, 1949; Kramer, 1956) were used to test if metrics of community structure (taxon richness and diversity) and function (feeding guild classification) differed among ecoregions. All tests were performed using the statistical program JMP (SAS, 1994, version 3.1, SAS Institute Inc., Cary, NC, U.S.A.).

Direct gradient analysis (also known as constrained ordination, ter Braak, 1988, 1990) was used to select environmental variables that could explain significant amounts of variability in structural and functional composition among the littoral macroinvertebrate communities. Detrended correspondence analysis (DCA) of square-root transformed species abundance, with downweighting of rare taxa, detrending by segments and non-linear rescaling was used to determine the biological turnover, or gradient length, of the species data set. From this the appropriate model (ordination procedure) for the constrained ordination was chosen. The DCA of the taxonomic composition of the 364 lakes gave gradient lengths of 3.627 for axis 1 and 3.265 for axis 2, indicating that a unimodal response would adequately fit the species data. The DCA of functional classification gave, on the other hand, gradient lengths of 1.365 for axis 1 and 1.433 for axis 2, indicating that a linear model was more appropriate. For these reasons, canonical correspondence analysis (CCA) was used in the ordination of taxonomic data (species abundances), whereas redundancy analysis (RDA) was used in constrained ordination of functional feeding guilds. In CCA and RDA, the species abundance data were square-root transformed and, where necessary, the environmental variables were  $\log_{10}$ -transformed in order to approximate normally distributed random errors. Both CCA



**Fig. 1** (a) Location of the 364 lakes sampled for littoral macroinvertebrates in autumn 1995 and location of the six major ecoregions in Sweden and (b) the approximate location of the *limes norrlandicus* ecotone and the northernmost distribution of raised bogs and oak (*Quercus robur* Linnaeus).

and RDA were run using the species downweighting option and forward selection of environmental variables. Significance of the environmental variables was tested with 999 Monte Carlo permutations. TWINSpan analysis (Hill, 1979) was used to select taxa indicative of the variability among community types. Only taxa

selected as strong preferential taxa in the first three divisions of TWINSpan are shown in the CCA ordination of community composition.

The total variation in an ecological data set can be partitioned into: (i) unique or pure variation from a specific variable, (ii) common variation contributed by

all measured variables and (iii) random error (Hopke, 1992). Constrained ordination, as used above, does not explicitly test for the unique effect of the categories of spatial scale on taxonomic and functional composition. A number of techniques have been developed recently, however, for analysing and partitioning the variance of multiscale studies (e.g. Gustafson, 1998). The approach used here is based on constrained ordination (ter Braak, 1988); partial constrained ordination is used to explore the relationships between single environmental variables and biological response variables (e.g. Borcard, Legendre & Drapeau, 1992). Here, partial constrained ordination was used to test the strength (i.e. the unique effect) of relationships between spatial scale and community composition and function.

Both partial canonical correspondence analysis (pCCA) and partial redundancy analysis (pRDA) were run for community composition and functional feeding guilds, respectively, according to Borcard *et al.* (1992) and Liu (1997). Univariate constrained ordinations were first run to determine which environmental variables could explain significant ( $P < 0.001$ ) amounts of variance of taxonomic or functional feeding guild composition. Only significant variables were included in the aggregations of environmental variables used in the partial constrained ordinations. Table 1 shows the variables included in the six categories as well as the variance explained by the individual variables ( $\lambda_1$ ). Six categories, five levels of spatial scale: ecoregion (six variables), catchment (12), riparian (10), ecosystem (eight) and habitat (17), and geographical position (three variables) were used in pCCA and pRDA. In brief, in the first step, pCCA or pRDA was run using community structure (taxonomic composition) or function (functional composition), respectively, as the response variable and all six categories as explanatory variables. Not including covariables in the first run gave the total amount of variation explained by all six categories. In the second step, CCA or pRDA was rerun using one of the six categories as explanatory variables and the remaining five categories as covariables, i.e. with and without the covariables (see Liu, 1997 for a thorough description of the steps). Partial constrained ordination was thus run four times within each combination of the six categories. By doing so we obtained the unique effect of the five levels of spatial scale (ecoregion, catchment, riparian, ecosystem and

habitat variables) as well as geographical position. For simplicity, the joint effects were not subdivided beyond the six categories. A bootstrap randomisation test (Efron, 1982) was used to determine if the variance explained in partial constrained ordination was significantly different ( $P < 0.05$ ) from the null hypothesis of no difference between classes of spatial scale. Confidence limits were obtained based on 1000 sets of simulated data and using Efron's percentile (Efron, 1979; Manly, 1997).

## Results

Macroinvertebrate taxon richness and diversity in the stony littoral varied significantly among the six major ecoregions (ANOVA,  $P < 0.0001$ ). The lowest taxon richness and diversity were noted in the arctic/alpine region ( $9.0 \pm 0.52$  and  $0.50 \pm 0.025$ , mean  $\pm 1$  SE) (Fig. 2). However, the most obvious landscape-level pattern was noted between the middle and southern boreal regions. Both taxon richness and diversity were higher in the southern boreal ( $16.8 \pm 0.88$  taxa and  $0.72 \pm 0.020$  diversity) compared with the middle boreal region ( $11.8 \pm 0.42$  taxa and  $0.61 \pm 0.177$  diversity). These differences correspond to the approximate location of the *limes norrlandicus* ecotone or the transition zone between the mixed forests that predominate in the south and the coniferous boreal forests in the north.

Functional composition of the littoral community also differed among the six ecoregions (ANOVA,  $P < 0.0001$ ). The mean number of collector-gatherer and predator taxa (7.3 and 8.7, respectively) was two times higher than that for shredders and grazers (3.5 and 4.8). Not surprisingly, both active (0.2) and passive (1.03) filter-feeders were poorly represented in these littoral habitats. The three northernmost ecoregions were functionally depauperate compared with the three regions in the south (Fig. 3). For example, the number of collector-gatherer taxa ranged from 5.4 (arctic/alpine) to 6.6 (middle boreal) in lakes in the north, compared with 9.3 (southern boreal) to 10 (nemoral) for the three regions in the south. Similar to community structure, the most marked differences in functional aspects also occurred between the middle and southern boreal regions.

Although lakes in the northern ecoregions had lower functional richness, the sites were not 'functionally' poor when functional composition was normalised

**Table 1** Environmental variables included as groups or covariables in partial constrained ordination of littoral macroinvertebrate communities.  $\lambda_1$  shows the variance explained as a per cent of total variance

Variable	Unit	$\lambda_1$
Geographical position		
Latitude	Decimal degrees	14
Longitude	Decimal degrees	3
Altitude	m a.s.l.	12
Ecoregion classification*		
Arctic/alpine	Dummy variable	11
Northern boreal	Dummy variable	5
Middle boreal	Dummy variable	4
Southern boreal	Dummy variable	4
Boreonemoral	Dummy variable	8
Nemoral	Dummy variable	1
Catchment classification		
Total forest	Per cent	9
Spruce	Per cent	8
Pine	Per cent	6
Deciduous	Per cent	3
Alpine forest	Per cent	10
Heath/grassland	Per cent	1
Arable	Per cent	6
Mire	Per cent	4
Alpine	Per cent	2
Water	Per cent	1
Riparian classification		
Coniferous	Classified 0–3†	2
Deciduous	Classified 0–3	4
Mixed forest	Classified 0–3	2
Clear-cut	Classified 0–3	1
Heath/grassland	Classified 0–3	2
Arable land	Classified 0–3	1
Mire	Classified 0–3	5
Alpine	Classified 0–3	7
Urban	Classified 0–3	2
Ecosystem classification		
Lake surface area	km <sup>2</sup>	9
Total phosphorus	µg L <sup>-1</sup>	5
Total nitrogen	µg L <sup>-1</sup>	9
Conductivity	mS m25	8
Chloride	meq L <sup>-1</sup>	12
Acid neutralising capacity	meq L <sup>-1</sup>	5
Exceedence of S critical load	meq m <sup>-2</sup> year <sup>-1</sup>	2
Colour	Absorbance of filtered water	11
Habitat classification		
Substratum		
Block/boulders	Classified 0–3	3
Cobble	Classified 0–3	6
Pebble	Classified 0–3	6
Gravel	Classified 0–3	4
Sand	Classified 0–3	4
Silt/clay	Classified 0–3	2
Fine detritus	Classified 0–3	4
Coarse detritus	Classified 0–3	5

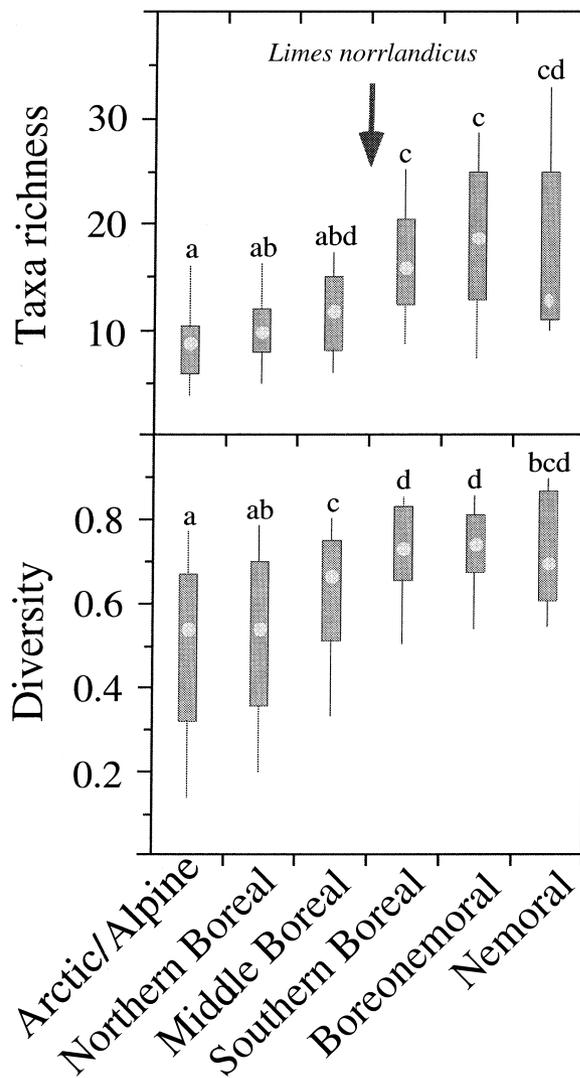
Table 1 (Continued)

Variable	Unit	$\lambda_1$
Vegetation		
Total coverage	Per cent	6
Emergent	Classified 0–3	7
Floating-leaved	Classified 0–3	5
Isoetid	Classified 0–3	4
Broad-leaved submerged	Classified 0–3	2
Fine-leaved submerged	Classified 0–3	2
<i>Fontinalis</i>	Classified 0–3	1
Other mosses	Classified 0–3	3
Filamentous algae	Classified 0–3	2

\*Six major ecoregions according to the Nordic Council of Ministers (1984) and Gustafsson & Ahlén (1996).

†Classified as per cent coverage; 0 = < 5%, 1 = 5–25%, 2 = 25–75%, 3 = > 75%.

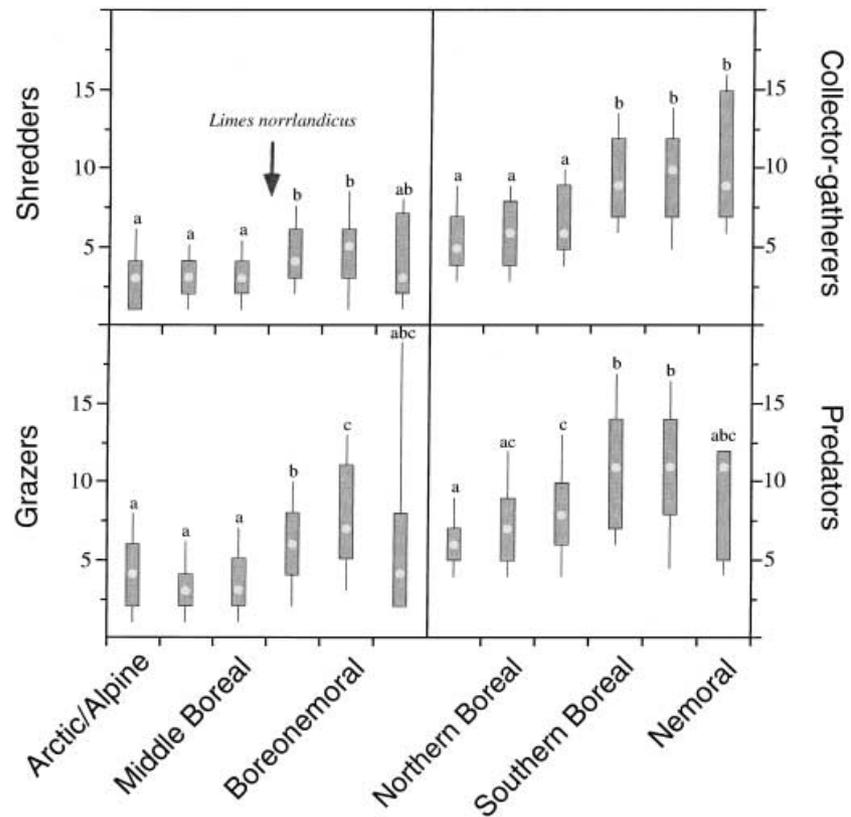
for taxon richness. When functional groups were expressed as a percentage of total richness, functional diversity was surprisingly constant across the



six ecoregions (Fig. 4); collector-gatherers (30%) and predators (35%) still predominated, followed by shredders (13%) and grazers (18%), and active (0.07%) and passive (3.7%) filter-feeders. With the exception of filter-feeders, the 'taxon-normalised' feeding guilds varied by less than 10% among the six ecoregions; the proportion of shredders ranged from 12 to 15%, grazers from 15 to 21%, collector-gatherers from 29 to 36% and predators from 31 to 37%.

In the constrained ordination of taxonomic composition, 25 variables were selected. The first two axes accounted for 9.7% of the variance in taxonomic composition among communities (eigenvalues for axis 1 and 2 were 0.202 and 0.135, respectively). Variables indicating geographical position (latitude, longitude and altitude), as well as ecosystem characteristics (lake surface area, water colour and chloride concentration) and habitat features (pebble substratum, floating-leaved vegetation and coarse detritus) were among the first 10 variables selected (Table 2). Taxa indicative of arctic/alpine regions, for example the plecopterans *Diura nanseni* (Kempny) and *Capnia atra* Morton, were positively correlated with riparian areas classified as alpine and with the arctic/alpine ecoregion (Fig. 5a). The isopod *Asellus aquaticus* Linnaeus was negatively correlated with altitude and positively correlated with the southern boreal region,

◀  
**Fig. 2** Box plots of macroinvertebrate taxon richness and Simpson's diversity for the six major ecoregions in Sweden. Littoral macroinvertebrate samples were taken from 364 lakes in autumn 1995 (circle, median; box, 25th and 75th quantiles; whiskers, interquartile range). Box plots with the same letter are not significantly different (Tukey–Kramer HSD test,  $P > 0.05$ ).



**Fig. 3** Box plots of four functional feeding guilds for the six major ecoregions in Sweden. Littoral macroinvertebrate samples were taken from 364 lakes in autumn 1995. The feeding guilds active and passive filter-feeders averaged < 1% and are not shown (circle, median; box, 25th and 75th quantiles; whiskers, interquartile range). Box plots with the same letter are not significantly different (Tukey–Kramer HSD test,  $P > 0.05$ ).

while the mayfly species group composed of *Caenis luctuosa* (Burmeister) and *Caenis macrura* Stephens and *Heptagenia fuscogrisea* Retz were positively correlated with lake surface area and low latitude.

In the constrained ordination of functional composition, only nine variables were needed to explain 25% (axes 1 and 2) of the among-lake variance. The majority of the variance was loaded on the first axis (eigenvalue, 0.323) and the second axis accounted for only 2.3% of the residual variance. Similar to the CCA ordination of taxonomic composition, variables indicating geographical position (latitude, longitude and altitude), ecosystem characteristics (lake surface area and water colour) and habitat features (cobble substratum, per cent vegetation) were important descriptors. All functional feeding guilds were negatively correlated with latitude and altitude. Grazers, and to some extent even shredders, were positively correlated with lake surface area and cobble substratum (Fig. 5b).

Partial constrained ordination showed that local factors explained a large portion of the explained variance in taxonomic composition (Fig. 6). Habitat

variables explained 23% of the variance among lakes, followed by ecosystem (11%) and catchment-level variables (10%). The other three categories (riparian, ecoregion and geographical) each explained less than 10% of the variance in taxonomic composition. Habitat variables also explained the largest portion of variance in the classification by functional composition. However, the amount of variance explained was less than half (11%) of that for taxonomic composition. This is, in part, because of the amount of variance that is 'hidden' in joint effects among the variables. In the ordination of taxonomic composition, only 4.2–7.3% of the explained variance was hidden in joint-effects between categories, whereas in the ordination of functional composition a much larger share of the variance was attributed to joint effects between variables (range 14–24%).

## Discussion

Understanding the concurrent effects of large- (landscape) and fine-scale (habitat) patterns on community structure is becoming increasingly important in

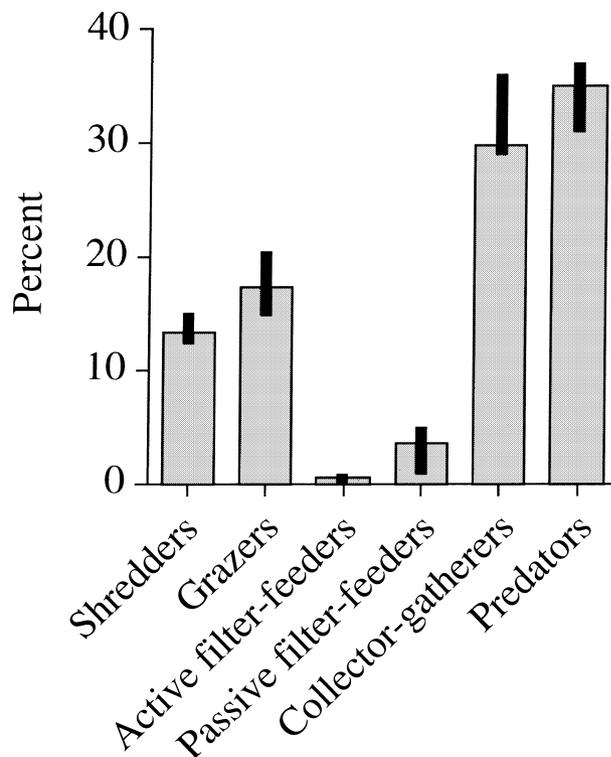


Fig. 4 Mean functional diversity normalised for species richness (in per cent) of littoral habitats of 364 lakes sampled in autumn 1995. Error bars give the range for six ecoregions.

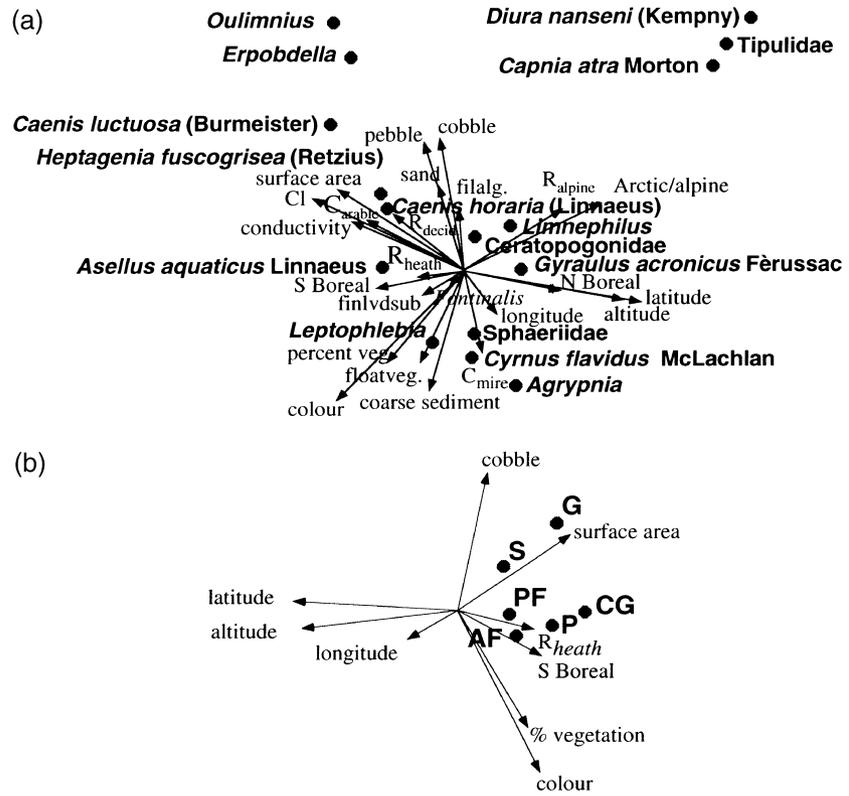
monitoring and assessment programmes because agencies and managers want to shift their efforts from single lakes to populations of lakes. In this

study, we analysed the strength of correlations between levels of spatial scale, ranging from the habitat (stony littoral zone of a lake) to the ecoregion, and community structure and function. Our main findings support the conjecture that correlation strength varies inversely with spatial scale. We showed regional differences in the functional composition of macroinvertebrate assemblages across Sweden, patterns that corresponded reasonably well with large-scale (regional) patterns of the landscape. Although a relatively strong north–south (or latitudinal) gradient was apparent, the most obvious differences in functional composition occurred between the middle and southern boreal regions. These landscape-level patterns coincide with the approximate location ( $\approx 60^\circ\text{N}$  latitude) of *limes norrlandicus*, an ecotone denoting the transition between the northern coniferous (pine and spruce) and southern mixed forests. Further, in Sweden, the transition zone between the northern coniferous and southern mixed forests also coincides with another biologically important gradient, namely the highest postglacial coastline. The highest postglacial coastline is recognised as the highest level the sea reached after the last ice age and below which fluvial sediments have been deposited. Lakes situated in areas below this important geomorphological landscape delineation are often more nutrient rich (Johnson, 1999).

A number of earlier studies have shown the effect of latitude and altitude on macroinvertebrate aquatic

Table 2 The first 10 variables selected in stepwise forward selection of CCA ordination of taxonomic and RDA ordination of functional composition of 364 lakes. The variables selected are also classified according to five categories of spatial scale and geographical position. The sum of all unconstrained and canonical eigenvalues are for complete models (i.e. all significant variables). RDA of lake function only resulted in nine significant variables. Category abbreviations are: GEO, geographical; ECOREG, ecoregion; CATCH, catchment; RIPAR, riparian; ECOSYS, ecosystem; HABIT, habitat

Taxonomic composition			Functional composition		
Variable	Model	Category	Variable	Model	Category
Latitude	0.14	GEO	Latitude	0.19	GEO
Colour	0.08	ECOSYS	Longitude	0.05	GEO
Longitude	0.06	GEO	Lake surface area	0.03	ECOSYS
Pebble	0.04	HABIT	Cobble	0.01	HABIT
Lake surface area	0.03	ECOSYS	Per cent vegetation	0.01	HABIT
Chloride	0.03	ECOSYS	Riparian <sub>heath</sub>	0.01	RIPAR
Floating-leaved vegetation	0.03	HABIT	Altitude	0.01	GEO
Arctic/alpine	0.02	ECOREG	Colour	0.01	ECOSYS
Coarse detritus	0.02	HABIT	Southern boreal	0.01	ECOREG
Altitude	0.02	GEO			
$\Sigma$ Unconstrained eigenvalues	3.48			1.00	
$\Sigma$ Canonical eigenvalues	0.676			0.325	



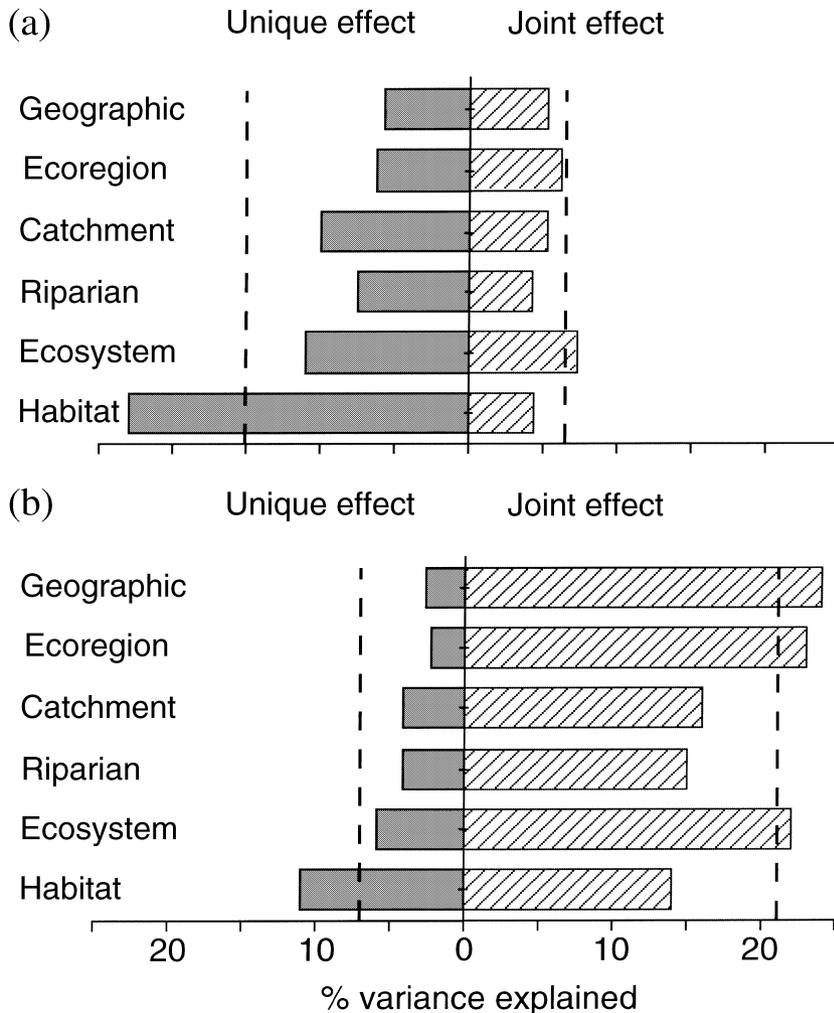
**Fig. 5** Constrained ordination of littoral macroinvertebrate communities of 364 lakes sampled in autumn 1995. The first two axes of (a) CCA of species and environmental variables and (b) RDA of functional feeding guilds and environmental variables are shown. The arrows show the direction and proportional influence of the environmental variables. *C<sub>arable</sub>*, catchment arable; *C<sub>mire</sub>*, catchment mire; *R<sub>alpine</sub>*, riparian alpine; *R<sub>decid</sub>*, riparian deciduous; *R<sub>heath</sub>*, riparian heath; filalg., filamentous algae; finlvds, fine-leaved submerged vegetation; floatveg., floating-leaved vegetation; per cent veg., per cent vegetation cover; S, shredders; G, grazers; P, predators; CG, collector-gatherers; PF, passive filter-feeders; AF, active filter-feeders.

communities (e.g. Jacobsen, Schultz & Encalada, 1997). Consequently, we anticipated the importance of a strong latitudinal gradient on macroinvertebrate composition and expected that littoral communities in the north would be more species-poor and less diverse than communities in the south. The finding that both structural and functional diversities were lower in the north supports this conjecture, although sites were not 'functionally' poor when functional composition was normalised for taxon richness. The lower diversity may, however, be an artefact of our study design. For example, chironomid midges, a functionally diverse and important taxonomic group in high altitude and latitude systems (e.g. Lindegaard & Brodersen, 1995), were not identified in species.

Similar to the landscape-level patterns noted for community composition, constrained ordination showed the importance of latitude for macroinvertebrate assemblages. Both community composition and function were strongly correlated with latitude ( $\lambda_1$  was 14% for composition and 19% for function). In fact, all three geographical variables (latitude, longitude and altitude) explained significant portions of variance in both taxonomic and functional compo-

sition, and were found among the first 10 (for taxonomic composition) or nine (for functional composition) variables selected in CCA or RDA, respectively. However, ecosystem or habitat variables seemed more important. For example, three variables that depict ecosystem characteristics (water colour, lake surface area and chloride concentration) and three variables that characterise habitat features (pebble, floating-leaved vegetation and coarse detritus) were included in the first 10 variables selected in the ordination of taxonomic composition. Similar results were found in the ordination of functional composition, although the specific ecosystem and habitat variables selected varied. These results indicate that not only geographical position, but also ecosystem and habitat characteristics, are good predictors of community composition and function.

In contrast to the relatively strong importance of geographical variables in constrained ordinations, pCCA and pRDA showed that the unique effects of geographical variables were relatively low (< 6% of the explained variance) compared with other (e.g. habitat) variables. The strongest relationships were expected between habitat and community compo-



**Fig. 6** Percentage of variation explained (unique effect and joint effects) in littoral macroinvertebrate communities of 364 lakes sampled in autumn 1995 by five metrics of spatial scale and geographical position. Taxonomic composition was analysed using partial canonical correspondence analysis and functional composition was analysed using partial redundancy analysis. The dashed line shows the upper 95% confidence of Efron's percentile and a bootstrap randomisation test with 1000 iterations.

tion, as this is the template experienced directly by the organisms. Simply put, although taxonomic composition is constrained by the size of the regional species pool, habitat heterogeneity and the outcome of biotic interactions are considered to be more important descriptors of site-specific community composition in streams (Allan, 1995). Similarly, for lakes we expected that correlation strength would decrease with increasing levels of spatial scale, i.e. habitat > ecosystem > riparian > catchment > ecoregion. For example, recognising that the riparian zone directly influences the quality and quantity of organic matter inputs, and that catchments set upper limits with their large-scale control on hydrology and chemistry, we expected that higher levels of spatial scale might explain a significant portion of the community variance. This conjecture, namely that correlation strength would decrease with increase in

scale, was partly supported here; the unique effect of habitat was greater than that of the other levels of spatial scale (Efron's percentile test, Efron, 1979). The relationships between organisms and scale variables were clearly non-linear and a substantial amount of the functional variance was hidden in joint effects. These findings indicate a close interdependence between local- and regional-scale variables, lending support to the notion that catchments may set upper limits and that, nested within these limits, local factors become important.

Our findings that habitat- and ecosystem-level variables were good predictors of both taxonomic and structural composition lend support to other studies, albeit mainly from lotic systems. As stony lake-littoral habitats are similar to stony stream habitats, we would, however, expect similarities in the factors regulating community composition

between littoral lake sites and streams. For example, both lake-littoral and lotic foodwebs have been shown to be similarly driven by allochthonous detrital carbon and periphytic algae (France, 1995a,b). Furthermore, in lotic systems, habitat-level predictors such as productivity (e.g. Hildrew & Townsend, 1987), disturbances and competition (e.g. McAuliffe, 1984), and predation (e.g. Peckarsky, 1984) are known to be important. Although the relative importance of biotic and abiotic processes in structuring macroinvertebrate communities of littoral habitats is largely unknown, it has been suggested that biotic interactions may be more important in lakes than in streams (Harrison & Hildrew, 1998a). For example, heterogeneity in lake littoral macroinvertebrate communities has been attributed to oviposition behaviour (Harrison & Hildrew, 1998b) and intrinsic factors of habitat choice and life history phenologies (Harrison & Hildrew, 2001).

A number of studies have shown that habitat-level descriptors, in particular substratum type and the presence of filamentous algae, are good predictors of littoral macroinvertebrate communities (e.g. Claassen, 1987; Dall, Lindegaard & Jónasson, 1990; Brodersen, 1995; Tolonen *et al.*, 2001). Similarly, ecosystem-level characteristics such as lake productivity, water chemistry and lake morphometry have been shown to be good predictors for discriminating community types among lakes (e.g. Kansanen, Aho & Paasivirta, 1984; Brodersen & Lindegaard, 1999; Tolonen *et al.*, 2001). However, trying to separate the importance of habitat and ecosystem variables is precarious. For example, macroinvertebrate communities of stony littoral regions of Danish lakes were found to be correlated with mean lake depth, Secchi depth and chlorophyll *a* concentration (Brodersen, Dall & Lindegaard, 1998). Mean depth, in particular, was shown to be a good predictor of community composition in Danish lakes; stratified lakes displayed a more oligotrophic character compared with shallow lakes with similar nutrient loading and concentration. Jeppesen *et al.* (1997) argued that deep stratified lakes trap nutrients in the hypolimnion resulting in lower pelagic production, thereby improving conditions for littoral communities because of increased primary production of submerged macrophytes and periphyton. Hence, ecosystem-level variables (like lake surface area, depth and morphometry) may influence habitat-level characteristics such as periphyton production, and

subsequently taxonomic and functional characteristics of the benthic community.

Spatial correlation or the interconnectedness between macroinvertebrate assemblages and levels of spatial scale other than habitat and ecosystem were also important in our study. For example, the combined influence of riparian, catchment and ecoregion classification accounted for 24% (taxonomic) and 11% (functional) of the explained variance, compared with the combined unique effects of habitat and ecosystem (i.e. 34 and 17%, for taxonomic and functional composition, respectively). As spatial position of an ecosystem (lake) in the landscape generally influences the properties of that ecosystem (e.g. Soranno *et al.*, 1999), this finding was not unexpected. Although the strength of the relationships was not known, earlier studies found a correlation between landscape characteristics and aquatic communities. Whittier, Hughes & Larsen (1988) showed, for example, a general correspondence between ecoregions and spatial patterns of stream fish, macroinvertebrate and periphyton communities. Landscape features have even been proposed to be more useful than hydrological variables in determining the spatial distribution of stream macroinvertebrate assemblages (Corkum, 1989).

However, some discord remains as to how well landscape characteristics can be used to partition biological variance. Hawkins *et al.* (2000) recently compiled information from a number of studies designed to assess how well landscape classification schemes (often ecoregions) account for patterns in aquatic biota. Ecoregions were found to be effective in partitioning variance when distinct differences in geomorphology or strong gradients in physiology and/or climate occurred. Such gradients are found in Sweden, in particular the large-scale, regional effect of the *limes norrlandicus* ecotone. However, none of the studies included in the review by Hawkins *et al.* (2000) used methodologies designed to test explicitly the unique effects of partitioning biological variance by spatial scale. Our findings show that ecoregion classification accounted for 6.3% (taxonomic composition) and 2.3% (functional composition) of the variance in littoral macroinvertebrate communities. Although we show that habitat-level descriptors are of primary importance for explaining variance in littoral macroinvertebrate communities, we also demonstrate that other levels of spatial scale can explain

significant amounts of the among-lake variance. These findings imply that lake communities are not isolated but integral parts of the landscape.

Part of the contention surrounding whether local or regional factors drive ecosystem structure and function may be because of how we design our studies. Indeed, artefacts of study design may strongly influence and confound our interpretations of what factors are driving community composition both within and among lakes. As Poff & Allan (1995) noted, our ability to detect significant relationships is in part dependent on scale and range of variability within the group of interest. For example, simply whether a study is spatially or temporally extensive will emphasise different mechanisms (e.g. Wiley, Kohler & Seelbach, 1997). Temporally extensive studies will emphasise biotic control or factors such as predation, competition and the effects of pathogens, whereas spatially extensive studies (like our study) will emphasise abiotic structuring factors such as habitat-level descriptors. Knowledge of the strength of correlations and ecological linkages is important for how we view aquatic ecosystems; in particular, this information is needed for making informed decisions regarding their management and restoration.

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