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SPATIAL SCALE AFFECTS COMMUNITY CONCORDANCE AMONG FISHES, BENTHIC MACROINVERTEBRATES, AND BRYOPHYTES IN STREAMS

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Abstract. Owing to the lack of information about the distribution patterns of many taxonomic groups, biodiversity conservation strategies commonly rely on a surrogate taxa approach for identifying areas of maximum conservation potential. Macroinvertebrates or fish are the most likely candidates for such a role in many freshwater systems. The usefulness of the surrogate taxa depends largely on community concordance, i.e., the degree of similarity in community patterns among taxonomic groups across a set of sites. We examined the effect of the spatial scale of a study on the strength of community concordance among macroinvertebrates, bryophytes, and fish by comparing the concordance between ordinations of these groups in 101 boreal stream sites. We specifically asked if communities spanning several drainages are more concordant than those originating from a single drainage system. Our results indicate that community concordance is affected by spatial extent, being variable and generally weak at the scale of individual drainages, but strong across multiple drainage systems and ecoregions. We attribute this finding to different taxonomic groups responding to similar environmental factors and sharing a similar latitudinal gradient of community structure when viewed across large spatial scales. We also identified a "gradient of concordance," with sites contributing disproportionately to community concordance being in relatively large streams with high microhabitat variability. Overall, our results suggest that the degree of community concordance among freshwater organism groups depends critically on the spatial extent of the study, and surrogate groups at the scale of single river systems should be used with caution.

Key words: benthic invertebrates; bioassessment; boreal streams; bryophytes; community concordance; fishes; spatial extent.

INTRODUCTION

Freshwater bioassessment typically relies on a few well-known organism groups that require no specific taxonomical expertise. As a result, taxonomically difficult groups are rarely included in bioassessment protocols. Owing to the wealth of information, benthic macroinvertebrates and fishes are obvious candidates for having such a key role in freshwater bioassessment and conservation (e.g., Angermeier and Winston 1999). Unfortunately, less well-known groups (e.g., chironomid midges, aquatic bryophytes, benthic algae) may have very different patterns of diversity and community structure than the "surrogate" groups and, accordingly, uniform management and conservation practices may be inappropriate. Despite a large amount of effort being spent to the development of the surrogate taxa approach, there has been little consideration of the impact that study scale may have on its applicability to practical conservation work. Therefore, clearly more information is needed about community concordance (sensu Jackson and Harvey 1993), i.e., the degree to which patterns in community structure across a set of sites are similar among different groups of freshwater taxa, and whether different groups are responding to similar environmental gradients across multiple spatial scales.

In spite of its importance, community concordance has been examined relatively little in aquatic ecosystems, and most of the studies conducted to date focus on lake communities. These studies have indicated rather strong concordance among such taxonomically unrelated groups as benthic invertebrates and fish (Jackson and Harvey 1993), aquatic birds and fish (Paszkowski and Tonn 2000), or diatoms and zooplankton (Allen et al. 1999). Although many lotic studies have compared responses of different organism groups

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to the same underlying gradient (e.g., Ormerod et al. 1994, Lammert and Allan 1999, Hirst et al. 2002, Wright and Li 2002), only Ormerod et al. (1987), Kilgour and Barton (1999) and Paavola et al. (2003) have directly addressed community concordance in streams. Ormerod et al. (1987) detected strong concordance between macrophyte and invertebrate assemblages in upland Welsh streams in relation to acidity, whereas Kilgour and Barton (1999) found concordant patterns of distribution between fish and benthos in a set of wadeable streams in Ontario, Canada. In contrast, Paavola et al. (2003) documented little concordance among benthic invertebrates, fish, and bryophytes in a boreal watershed in northern Finland. We suggested then that the detection of concordance among multiple taxonomic groups might be scale dependent, and strong concordance would only be found if a study spans large geographic areas with multiple drainage systems. Overall, present evidence suggests that fish or benthos might be useful surrogates for other freshwater organism groups, but because community concordance may be context dependent (e.g., region and scale specific), more studies, especially in running waters, are needed to better assess the usefulness of the surrogate taxa approach in freshwater bioassessment and conservation.

Our objective in this study was to assess whether benthic macroinvertebrates, fishes, and aquatic bryophytes exhibit similar patterns of community structure across 101 streams in Finland. We specifically addressed whether concordance among these groups is related to the spatial extent of the study, with higher concordance in studies spanning larger areas. We then related patterns in community structure to riparian and in-stream variables to see whether the communities responded to similar environmental gradients across the study area.

METHODS

Study area

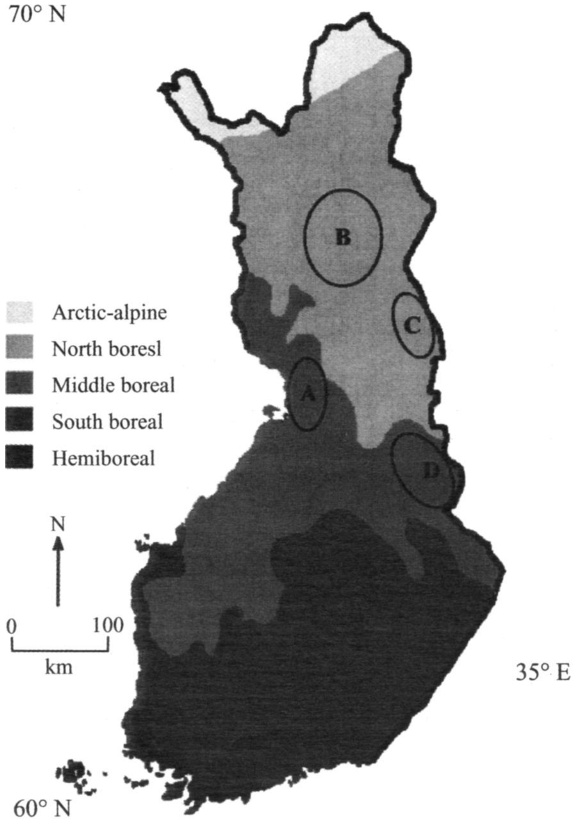


FIG. 1. Location of the study areas in Finland. The map also displays the ecoregional delineations of Finland.

We sampled 101 first- to fourth-order streams in the drainage systems of Rivers Iijoki and Kiiminkijoki (sampling area A, $n = 13$ streams), Kemijoki (sampling area B, $n = 33$ streams), Koutajoki (sampling area C, $n = 9$ streams; see Plate 1), and Oulujoki (sampling area D, $n = 46$ streams) (Fig. 1). These rivers span two of the five ecoregions encompassing Finland: north boreal (Iijoki, Kemijoki, and Koutajoki) and middle boreal (Iijoki, Kiiminkijoki, and Oulujoki) ecoregions (Fig. 1; for more details on the ecoregional delineations of Finland, see Heino et al. [2002]). They all run through coniferous forest landscapes in northern and northeastern Finland (64–68° N, 25–31° E). Streams sampled in each drainage system were selected randomly, with two restrictions: accessibility (only streams within less than 2 km of the nearest road were included) and naturalness (streams with obvious human impact in the stream channel (channelization, removal of woody debris) or in the riparian zone (e.g., clearcuts, forestry ditches) were excluded). The catchments of most of the streams have been historically influenced by some forestry practices, but the present-day impact of forestry is modest, and the sampled streams thus represent near-pristine conditions.

Field sampling

We sampled bryophytes, macroinvertebrates, and fish at 101 streams in 1992, 1994, or 1998. Most sampling (approximately 70% of the sites) was conducted in 1994. Benthic invertebrates were sampled twice, in summer (June) and autumn (late September). We collected a 2-min kick-net sample (mesh size 0.3 mm), consisting of four 30-s subsamples at each site. We distributed the samples over a riffle area of 100 m^2, taking care to include all microhabitat variability present in a riffle. This sampling effort covers an area of about 1.2 m^2, capturing 70–75% of all taxa present in a corresponding 10-min sample (consisting of 20 30-s subsamples) (Mykrä et al., *in press*). We preserved the samples in 70% ethanol, and later sorted the animals in the laboratory. Invertebrates were mostly identified to species level. Early instar limnephilids and chiron-

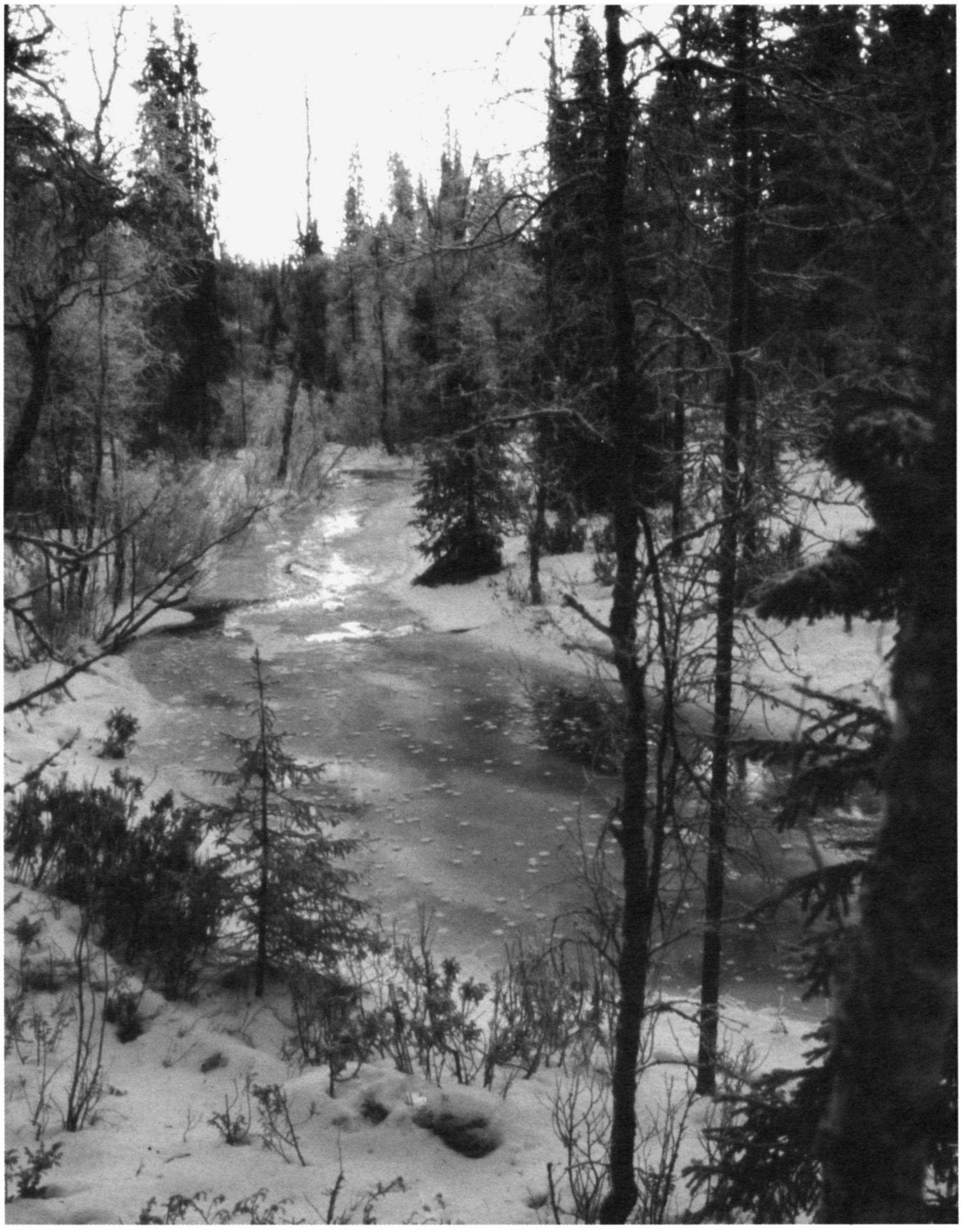


PLATE 1. A study stream from sampling area C during early winter. Photo credit: Arto Huhta.

omid larvae were only identified to family level, and were thus excluded from all statistical analyses.

We collected bryophyte samples at the same riffle sites simultaneously with the autumnal benthic sampling. We sampled bryophytes from 10 randomly placed plots (0.5 × 0.5 m) at each site. Plots were placed in only those areas of the stream bed that remain wetted at mean water level. We recorded all bryophyte species and estimated their relative abundances (percentage of cover) for each plot. Nearly all bryophyte sampling was conducted by the same person (R. Paavola). Two study sites were devoid of bryophytes and were thus removed from all data sets.

We collected fish by electrofishing the same riffle sites in early September. We used a DC backpack electroshocker with low voltage (350 V). The number of passes per site varied (one to three), with more passes at sites with heterogeneous substratum (and thus lower catchability). We counted and identified all stunned fish, after which we released them back to the stream. Seventeen sites were fishless, as confirmed by electrofishing an additional area of at least 50 m^2 immediately upstream of the study reach.

A suite of environmental characteristics was measured at each site. We estimated riparian zone integrity (percentage of the riparian zone without human impact) and the proportion of deciduous trees along both banks in a 50-m section directly upstream of a sampling site. Shading (percentage of canopy cover) was measured at 20 locations in evenly spaced cross-channel transects covering the whole study section. Depth, current velocity (at 0.4 × depth), and substratum size were measured at 40 random locations along the same transects. To determine substratum size, we measured three perpendicular dimensions of each stone, then applying the formula of Graham et al. (1988) to estimate stone surface area. We measured stream gradient (cm/m) with a carpenter's level. The amount of large woody debris (LWD; m^3/ha) in the stream channel was quantified using a technique modified from Carlson et al. (1990). We measured the length and average diameter of each wood particle at least 5 cm in diameter, 1 m in length, and at least partly in the channel at base flow. We assessed stream bank cover, an estimate of cover provided by stream bank for fishes, along both shores using a scale of 1 to 5, with higher values indicating more cover habitat. Distance to nearest upstream lake was measured from topographic maps. We used coefficients of variation for water velocity, depth, and substratum size as indicators of in-stream habitat heterogeneity. We also calculated an index of bed instability by dividing tractive force (based on bankfull depth and stream slope; see Newbury [1984]) by the median substrate diameter (Cobb and Flannagan 1990). Low index values indicate stable substratum. We collected water samples simultaneously with benthic sampling, and they were analyzed for pH, alkalinity, conductivity, water color, total N, total P, and Fe at Oulanka Biological Station or the Environmental Centres of Lapland, North Ostrobothnia, or Kainuu within 24 h of sampling.

Data analysis

We pooled macroinvertebrate abundance data (number of individuals per sample) from the two sampling dates for each site to obtain a composite of the whole assemblage. Prior to analysis, abundance data for macroinvertebrate and fish species were log $(x + 1)$ transformed and bryophyte data (percentage of cover) were arcsine square-root transformed to reduce the influence of numerically dominant species and to better approximate multinormality. Species that occurred in only one sample were deleted. Because 19 sites were fishless, we conducted an additional set of analyses using only sites containing fish. Environmental variables were transformed as needed (logarithmic or arcsine square-root) to approximate normal distributions.

We aimed to compare the degree of concordance in data sets of variable spatial extent. For this purpose, we partitioned our data into two sets of differing spatial extent: (1) complete data set with the 101 sampling sites across six river systems and two ecoregions (spatial extent of about 106 400 km^2); and (2) two spatially restricted data sets: Kemijoki river system (area B, spatial extent approximately 8800 km^2), and Oulujoki river system (area D, spatial extent approximately 3100 km^2) (Fig. 1). We chose areas B and D because they contained sufficient numbers of fish-inhabited sites (31 and 32, respectively) for meaningful multivariate analyses. Further, to ascertain that any differences in community concordance among the complete and spatially restricted data sets were not simply caused by unequal sample sizes, we constructed 10 subsets of 32 sites from the complete data set, using stratified random sampling. We randomly selected sites from each of the four sampling areas, thus retaining the spatial structure of the original data set. Although a direct test of the null hypothesis (no difference among study scales in the degree of concordance) would have been preferable, this was not possible in our case, because the data sets for areas B and D are subsets of our larger data set. Therefore, any comparison would not involve independent data sets, compromising any formal statistical evaluations.

We first used nonmetric multidimensional scaling (NMDS) to summarize patterns in each biotic data set. NMDS is an ordination method based on ranked distances, and it performs well with ecological data that typically contain numerous zero values (Minchin 1987). It is robust to deviations from multinormality (McCune and Mefford 1999). We used stress value to determine the number of dimensions in NMDS. Stress is a measure of deviation from monotonicity in the relationship between distance in the original space and the reduced ordination space, and the analysis was stopped when the stress value did not change appreciably with additional dimensions. To avoid the problem of local minima, we ran the NMDS analyses in an autopilot mode, letting the program choose the best solution (i.e., solution with the lowest stress value) from 100 separate runs of real data (McCune and Mefford 1999). We used the Sørensen coefficient as the distance measure in all NMDS analyses. Correspondingly, principal components analysis (PCA) on a correlation matrix was used to reduce the dimensionality of the environmental data into a few principal components representing the major environmental gradients of the data.

At the next step, we used Procrustes rotation analysis to investigate the degree of concordance among the biotic data sets. One of the advantages of this method is that it does not assume linear relationships between the biotic and/or abiotic variables (Jackson 1995). Procrustes analysis works by scaling, rotating, and dilating one ordination solution and then superimposing it on a second ordination, maximizing the fit between corresponding observations of the two ordination configurations. The most frequently used method for Procrustean fitting is based on the least-squares criterion that minimizes the sum of the squared residuals (m^2) between the two configurations; the m^2 statistic is thus a measure of association (i.e., concordance) between

TABLE 1. Results of ProTest analyses (Jackson 1995) on the biotic (nonmetric multidimensional scaling [NMDS]) and environmental (principal components analysis [PCA]) ordinations on each of the regional data sets and the complete data set.

	N		Environment		Invertebrates		Bryophytes	
Component	Sites	Taxa	m^2	P	m^2	P	m^2	P
Area B								
Invertebrates	32	80	0.8022	0.0029				
Bryophytes	32	25	0.8554	0.0190	0.9659	0.5253		
Fish	32	9	0.8440	0.0138	0.8212	0.0060	0.9100	0.1086
Area D								
Invertebrates	31	76	0.6008	0.0001				
Bryophytes	31	18	0.8887	0.0637	0.7675	0.0021		
Fish	31	7	0.8635	0.0316	0.8402	0.0149	0.8951	0.0835
Complete data set								
Invertebrates	99	122	0.6170	0.0001				
Bryophytes	99	45	0.7757	0.0001	0.8087	0.0001		
Fish	82	10	0.8575	0.0001	0.8422	0.0001	0.8858	0.0001

Notes: Procrustean P values indicate how many of the 9999 random permutations provided a better fit than the original configuration. Two ordination dimensions were used for areas B and D and three for the complete data set. The sum of the squared residuals (m^2) between the two configurations is a measure of association (i.e., concordance) between the two ordinations.

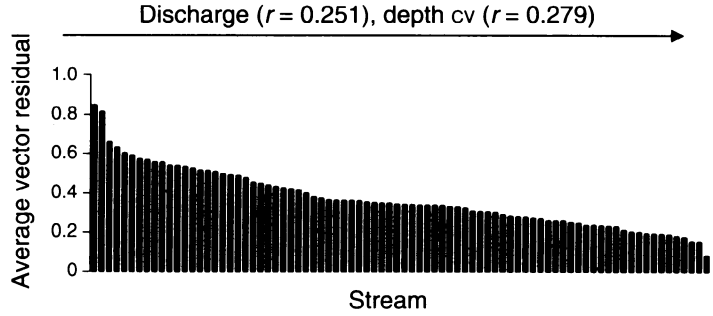
the two ordinations (Gower 1971, Digby and Kempton 1987). Low values of m^2 indicate strong concordance. ProTest extends Procrustes analysis by providing a permutation procedure to assess the statistical significance of the Procrustean fit (Peres-Neto and Jackson 2001). ProTest randomly permutes the original observations of one matrix so that each site can be assigned any of the values attributed to other sites (Jackson 1995). The m^2 statistic is then recalculated for each permutation, and the proportion of the statistics smaller than or equal to the observed value provides the significance level of the test. We used ProTest (with 9999 permutations) for pairwise comparisons of the biotic (NMDS) ordination configurations. The vector residuals given by ProTest for each sample provide a means of investigating the deviation in the positions of individual samples between the two superimposed ordinations (Olden et al. 2001). The length of the vector residual represents the lack of fit of ordination scores for an individual sample, with low values indicating strong concordance. We used vector residuals from the three pairwise ordination superimpositions (invertebrates vs. bryophytes; invertebrates vs. fish; bryophytes vs. fish) based on the complete data set, without fishless sites, to arrange our sample sites along a "concordance gradient." We first standardized the vector residuals to range between 0 and 1. We then averaged the residuals from the three analyses to obtain a single "grand residual" for each sample. Finally, we placed the 82 samples in a descending order based on their average residuals, and calculated Spearman rank correlations between the average residuals and environmental variables to see

TABLE 2. Summary of the results of ProTest analyses on the biotic (NMDS) and environmental (PCA) ordinations of the 10 random subsets of the complete data set.

	Environment		Invertebrates		Bryophytes	
Parameter	m^2	P	m^2	P	m^2	P
Invertebrates						
Average	0.4915	0.0001				
Minimum	0.3787	0.0001				
Maximum	0.7133	0.0003				
Bryophytes						
Average	0.7190	0.0019	0.6903	0.0054		
Minimum	0.5288	0.0001	0.4905	0.0001		
Maximum	0.8349	0.0119	0.8834	0.0500		
Fish						
Average	0.7199	0.0046	0.7754	0.0021	0.8225	0.0247
Minimum	0.6230	0.0001	0.6935	0.0001	0.7479	0.0003
Maximum	0.8768	0.0412	0.8312	0.0074	0.9104	0.1202

Notes: The original spatial structure of the complete data set was retained when the random subsets were created. Two dimensions were used in all ordinations. Averages and ranges are given for the m^2 statistics and associated P values. The number of permutations was 9999 in all analyses.

FIG. 2. Average site-specific vector residuals from the biotic ProTest comparisons of the NMDS (nonmetric multidimensional scaling) ordinations of macroinvertebrate, bryophyte, and fish communities, using abundance data from 82 sites (i.e., sites with fish). Significant environmental correlates and their direction are also given.



which, if any, environmental factors were associated with the "concordance gradient."

We further employed ProTest to investigate the degree of concordance between each biotic (NMDS) and environmental (PCA) ordination. Finally, as a direct test for the existence of any spatial structure among the data sets, we used ProTest to examine the strength of concordance between the spatial coordinates (longitude and latitude) of the study sites and the biotic and environmental ordinations of the complete data set. For this purpose, we ran an additional set of NMDS and PCA ordinations of the complete data set, this time extracting only two dimensions to match the dimensionality of the spatial factors.

To identify the major environmental gradients related to each taxonomic group, we performed a canonical correspondence analysis (CCA), separately for each group, at both local (areas B and D) and regional (complete data set) scales. The environmental matrix was identical in all three analyses, except that the variable "total bryophyte cover" was removed from the bryophyte CCA. Owing to the large number of environmental variables (25 altogether), we ran the analysis using the automatic forward selection mode, accepting up to five most significant variables for each taxonomic group. This approach avoids the problem of noisy or irrelevant variables (McCune 1997). At each step, we only included variables explaining a significant ($P <$ 0.05, Monte Carlo test with 999 permutations) proportion of the remaining variation.

We conducted the multivariate analyses using the PC-Ord computer package (version 4.17, McCune and Mefford 1999), with the exception of Procrustes analyses, for which we used the ProTest program (Peres-Neto and Jackson 2001), and CCA which was run using Canoco for Windows (version 4.0; ter Braak and Šmilauer 1998).

RESULTS

Concordance comparisons

Stress values indicated that three dimensions were sufficient for the NMDS ordinations of the taxonomic groups for the complete data set, whereas only two dimensions were needed for areas B and D and the random subsets. All NMDS solutions on both the actual data sets and random subsets of bryophyte and invertebrate abundance data were significant at $P < 0.01$, and those for fish at $P < 0.05$ (Monte Carlo tests with 100 permutations).

ProTest analysis of area B data indicated significant ($P < 0.05$) concordance between the environmental (PCA components 1 and 2) and biotic (NMDS axis 1 and 2 for each organism group) ordinations (Table 1). In contrast, concordance among the taxonomic groups was weak, the only significant association being that

TABLE 3. (A) Summary of the canonical correspondence analysis (CCA) of the complete data set using forward selection of variables. (B) The five best explanatory variables for each analysis are given in order of importance.

	Invertebrates		Bryophytes		Fish	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
A) CCA summary						
Eigenvalue	0.262	0.213	0.386	0.271	0.435	0.228
Variance of species data explained (%)	6.5	5.3	6.2	4.3	12.4	6.6
Variance of species–environment relationship explained (%)	35.7	29.0	38.8	27.3	49.1	25.8
Species–environment correlation	0.909	0.845	0.804	0.774	0.821	0.643
B) Five best variables						
1	pH		pH		pH	
2	east coordinate		east coordinate		depth	
3	north coordinate		total P		particle size	
4	depth		north coordinate		north coordinate	
5	conductivity		depth		outlet distance	

Notes: All canonical axes were significant at $P < 0.001$. The number of permutations was 999 in all cases.

TABLE 4. Ranges and means of selected environmental variables in each data set.

Parameter	Shading (%)	Particle size (dm^3)	Moss cover (%)	Discharge (m^3/s)	Depth (cm)	Water velocity (cm/s)
Area B						
Minimum	0	0.59	0	0.01	13	16
Mean	18.7	10.9	37.2	1.23	26	31.5
Maximum	59	45.38	92.8	7.5	40	57
Area D						
Minimum	8	4.62	7	0.04	12	13
Mean	35.5	23.8	54.6	0.5	26.9	25.5
Maximum	79	63.68	95	4.05	45	53
Complete data set						
Minimum	0	0.5	0	0.01	2	10
Mean	31.6	18.2	42.2	0.8	26.0	35.2
Maximum	79	74.9	95	7.5	45	97

† Large woody debris.
‡ Units are millisiemens per meter.
§ Pt, platinum.

between fish and invertebrates. Similar ProTest analysis for area D indicated somewhat weaker, though mostly significant, concordance between the environmental gradients and the taxonomic groups. With the exception of fish vs. bryophytes, other taxonomic groups were significantly concordant (Table 1). However, analysis of the complete data set revealed much stronger ($P < 0.001$) concordance, both between the environment and the taxonomic groups, and among the three taxonomic groups.

ProTest analysis of the random subsets indicated consistently strong concordance between the environment and the three taxonomic groups (Table 2). Concordance between pairs of taxonomic groups was also strong, with only one bryophyte–fish comparison failing to indicate significant concordance.

Averaged standardized sample residuals from the ProTest comparisons among the taxonomic groups in the complete data set revealed a distinct among-site "concordance gradient" (Fig. 2). However, only discharge and depth CV were significantly correlated with sample residuals (Fig. 2), indicating that concordance among the groups tended to increase with stream size.

Concordance between spatial (latitude and longitude) and environmental factors (first two PCA components of the complete data set) was very strong ($m^2 = 0.594$, $P = 0.0001$). Similarly, spatial factors and patterns in invertebrate ($m^2 = 0.693$), bryophyte ($m^2 = 0.743$), and fish ($m^2 = 0.594$) community structure (NMDS ordinations) were strongly concordant (all $P < 0.0001$). These results indicate a strong spatially structured component to the variability of environmental factors and biotic communities of boreal streams.

TABLE 5. (A) Summary of the CCA for the two spatially restricted data sets. Forward selection of variables was used to identify up to five best explanatory variables for each analysis; the selected variables are shown in order of importance in panel (B).

	Area B					
	Invertebrates		Bryophytes		Fish	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
A) CCA summary						
Eigenvalue	0.241	0.153	0.416	0.296	0.241	0.185
Variance of species data explained (%)	13.1	8.4	11.1	7.8	11.7	9.0
Variance of species–environment relation explained (%)	35.9	22.8	39.6	27.9	42.5	27.3
Species–environment correlation	0.915	0.915	0.890	0.835	0.794	0.694
B) Five best variables						
1	pH		total P		particle size	
2	discharge		water velocity		oxygen	
3	oxygen		LWD		depth	
4	moss cover		color			
5	color		water vel. CV			

Notes: The first canonical axis of both fish CCAs was significant at $P < 0.05$, and the first axis of bryophyte CCA for area D was significant at $P < 0.01$. For all other analyses, the first CCA axis was significant at $P < 0.001$. The number of permutations was 999 in all cases.

TABLE 4. Extended.

LWD† (m^3/ha)	Outlet distance (km)	Conductivity (mS/m)‡	pH	Color (mg Pt/L)§	Total N (μg/L)	Total P (μg/L)
0	0.01	0.94	5.7	12.5	99	3
16.2	7.5	8.6	7.3	70.2	261.8	22.8
226.28	18	18.85	8	160	1000	140
0	0	1.6	4.5	80	180	7
29.3	2.0	2.1	5.9	130.6	283.4	20.2
141.4	8	3	6.4	200	440	52
0	0	0.94	4.5	10	99	2
19.1	4.1	5.0	6.5	128.9	334.4	19.4
226.28	18	20.4	8.3	400	1200	140

CCA ordinations

All CCA analyses of the complete data set displayed significant relationships between the species data and the explanatory variables (Table 3). All variables selected by the forward selection option exhibited wide ranges of variation, especially in the complete data set (Table 4). Interestingly, the spatial and environmental variables that emerged as the best correlates of the biotic patterns at the regional scale (across drainages) were strikingly similar for all taxonomic groups studied (Table 3, Fig. 3). CCAs for invertebrates and bryophytes shared four of the five best explanatory variables, whereas the fish CCA shared three variables with the invertebrate and bryophyte CCAs. Water pH, depth, and spatial coordinates appeared as the strongest environmental correlates for all three groups (Table 3). In contrast, few environmental correlates were shared between the groups when the analysis was conducted at the local, within-drainage scale (Table 5). An overview of the flow of data and sequence of the main statistical analyses is shown in Fig. 4.

DISCUSSION

The key finding of our study was that concordance between the taxonomic groups, as well as between the environmental factors and the groups, was rather weak at the scale of single river systems, whereas the complete data set spanning multiple drainage systems and two ecoregions revealed strong concordance among the groups, and among the groups and the environment. *P* values based on random subsets of the complete data indicated that the observed differences in concordance among the complete and the two spatially restricted data sets were not caused simply by variable sample sizes, but mainly by the greater spatial extent of the complete data set. This effect might be attributed to a sampling artifact, however: increased sample extent may result in increased correlation between environment and community composition simply because samples spread over a larger area capture a larger portion of variability in environmental factors and biological communities, resulting in spatial autocorrelation between communities and the environment (Reed et al.

TABLE 5. Extended.

Area D					
Invertebrates		Bryophytes		Fish	
Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
0.318	0.132	0.214	0.113	0.422	0.383
18.2	7.5	12.1	6.4	16.7	15.1
49.0	20.3	65.4	34.6	31.9	28.9
0.931	0.801	0.805	0.745	0.824	0.799
outlet distance		outlet distance		discharge	
pH		discharge		bed instability	
depth				alkalinity	
COD				total N	
Fe				depth	

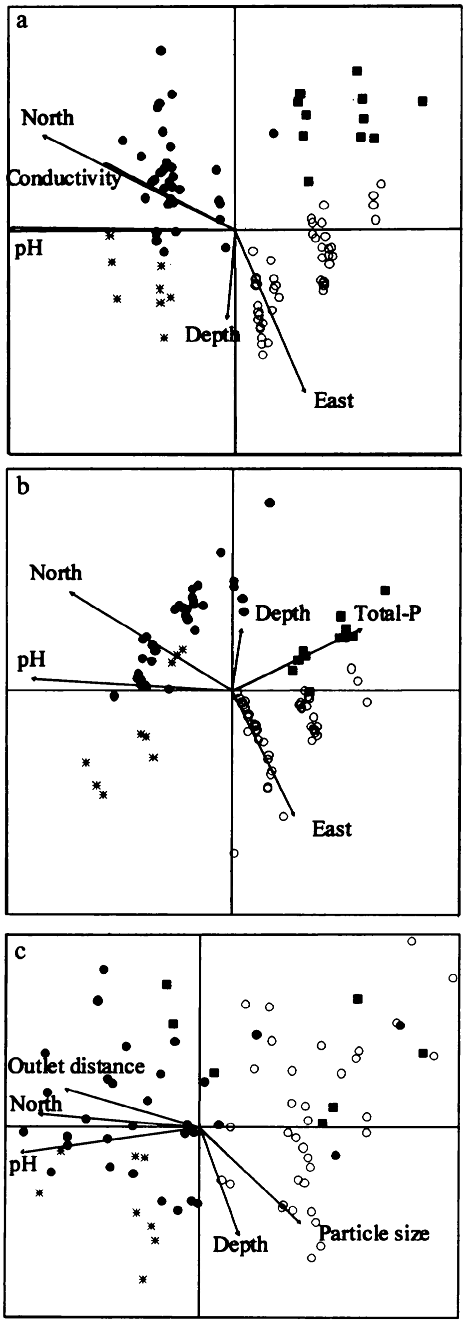


FIG. 3. Forward-selection CCA (canonical correspondence analysis) ordinations of the 99 stream sites based on (a) macroinvertebrate abundance and (b) bryophyte cover data. (c) Fish ordination was based on abundance data from 82 sites. The five best explanatory variables are included for each taxonomic group. Areas are indicated by solid squares (area A), solid circles (area B), asterisks (area C), and open circles (area D).

1993). In our case, this is potentially relevant only for some of the water chemistry variables (pH, water color) because most other variables varied as much within as between the drainages. It should also be noted that many correlations between the environment (PCA components) and the communities (NMDS ordinations) were in fact significant even at the within-drainages scale. Finally, the relationship between sample extent and environment-community correlation may not always be that simple; for example, Reed et al. (1993) failed to show any scale dependence in the vegetation–environment relationship, mainly because of the larger number of interacting factors and greater data complexity encountered when sampling across large areas. Similarly, Ohmann and Spies (1998) detected relatively little variability (9–15%) in total variation explained in the community composition of woody plants in Oregon forests at three hierarchical geographical extents. Nevertheless, we must emphasize that, due to the data structure (i.e., spatial dependence among data subsets), we were unable to produce an unequivocal, direct test of the scale dependence of community concordance. Indeed, such a test would require data completely lacking spatial dependence, that is, data sets with different spatial extents would have to come from spatially separate systems. Acquiring such data, however, presents a formidable task, not only because of the enormous amount of field effort needed, but also because different data sets would necessarily span completely different environmental gradients, thereby hindering any direct comparison among the data sets.

The fundamental importance of spatial extent was further emphasized by the strong concordance of both the biotic and the environmental ordinations with the spatial coordinates of the study sites. To our knowledge, no previous study has assessed the effects of scale on community concordance in streams, or in any other freshwater ecosystem. The study by Kilgour and Barton (1999) included three separate data sets from partly different authors who used slightly differing sampling designs and methodology. In contrast to our near-pristine streams, many of their study sites were variously modified by human activities, and such anthropogenic filters are likely to have a major influence on most lotic organisms. Thus, it should not be surprising that their data exhibited significant concordance among fish and macroinvertebrates. Each of the data sets in Kilgour and Barton (1999) included sites from more than one river system, thus resembling our broad-scale data set. Similarly, Ormerod et al. (1987) found macrophyte and invertebrate communities to be highly concordant in a study spanning 88 sites in the headwaters of 16 river systems in Wales.

Direct gradient analyses (CCA) revealed a striking similarity in the key environmental correlates for macroinvertebrates, fish, and bryophytes, indicating that, when viewed across broad geographical scales, closely similar suites of environmental factors underlie the patterns of community structure of these groups. The roles of pH, spatial coordinates, and water depth were particularly striking, these being the strongest environmental correlates for all three groups. Although biotic

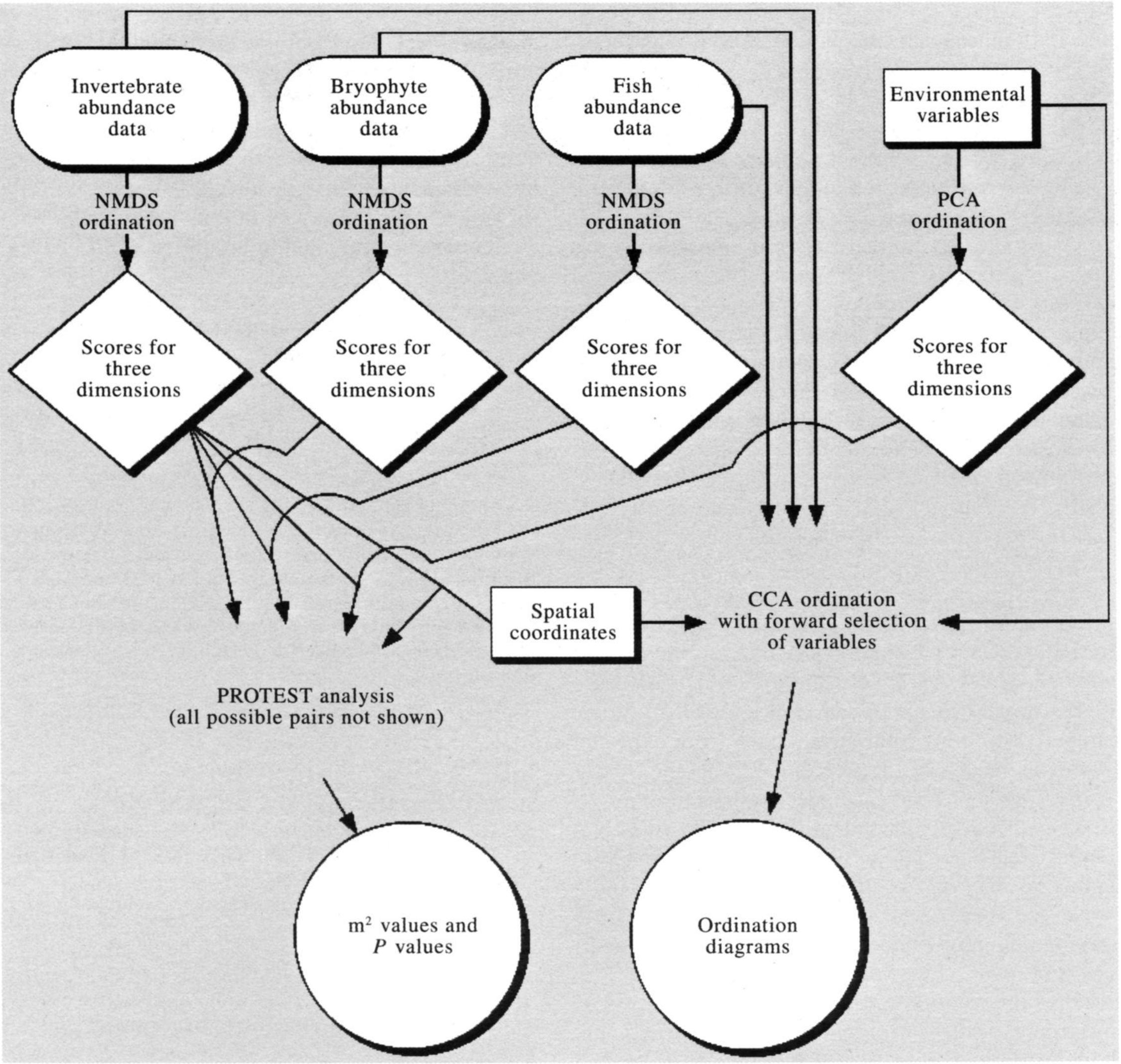


FIG. 4. Flow of data and sequence of the main statistical analyses.

communities responding to different environmental cues may exhibit concordant patterns of community structure (Jackson and Harvey 1993), our results rather concur with those of Paszkowski and Tonn (2000) and Kilgour and Barton (1999) suggesting that concordance results from both groups responding to the same set of environmental factors. In contrast, less evidence for community concordance was found within single river systems, paralleling the fact that at this scale, the three taxonomic groups were responding to different sets of environmental cues. It thus appears that the community compositions of these three major taxonomic groups of boreal streams are controlled by largely similar regional-scale environmental filters (sensu Tonn 1990), whereas local filters are weaker and more taxon-specific (see also Heino 2002). Interestingly, in a study of 18 warm-water streams in a single river system in southern Michigan, Lammert and Allan (1999) reported that patterns of fish and macroinvertebrate community structure were related to different environmental gradients. For the most part, available evidence thus suggests that strong concordance is most likely to emerge if different organism groups exhibit similar responses to underlying environmental gradients, and that such predominant gradients are likely to emerge only if relatively large geographical areas, spanning multiple drainage systems, are included. Studies confined at more local scales may still imply strongly concordant community patterns, if the environmental domain is controlled by a single dominant gradient (e.g., altitude; see Ormerod et al. 1994), creating distinct and parallel shifts in the community composition of all taxonomic groups involved.

Our finding that benthic invertebrate communities exhibited a strong latitudinal gradient reiterates the findings of Sandin and Johnson (2000) and Heino et al.

(2002) for boreal stream communities, and Johnson (2000) and Johnson and Goedkoop (2002) for lake communities. In fact, many freshwater organism groups share a similar north-to-south gradient in species richness (Heino 2002) and assemblage structure (Heino 2001), when viewed across the biogeographical provinces of northern Europe. It thus appears that this general trend of freshwater taxa to exhibit strong latitudinal distribution patterns in northern Europe, most likely resulting from largely similar postglacial colonization routes, sets the stage for community concordance among multiple taxonomic groups in boreal streams, even when examined across a much shorter latitudinal gradient (in our case, approximately 400 km).

Using the site-specific residuals from the ProTest analyses, we were able to identify a "concordance gradient" among our data that was positively related to discharge (i.e., stream size) and microhabitat variability (coefficient of variation for depth). This finding suggests that larger streams contribute disproportionately to concordance among lotic communities. This result parallels one of the basic premises of the river continuum concept (Vannote et al. 1980): that stream habitats should become less variable as the stream size increases from headwaters to mid-sized (fourth- to fifth-order) streams. Accordingly, mid-sized streams are expected to harbor more diverse biotic communities than those typically found in headwater streams (Vannote et al. 1980). The physically harsh and variable environments of boreal headwater streams appear to support biotic assemblages that vary somewhat unpredictably among streams (see Heino et al. 2003), thus providing little scope for community concordance between lotic organism groups.

Because information on the distribution patterns of many groups of stream organisms is still inadequate, benthic macroinvertebrates or fishes are routinely used as surrogates of the wholesale biodiversity, or as overall indicators of stream condition. This rationale seems to be based on an implicit assumption that these groups indicate reliably the responses of other, less-well known taxonomic groups to anthropogenic stressors. Little effort, however, has been put into quantifying the strength of concordance between lotic organism groups, and to the potential scale-dependence of this pattern. Our results suggest that cross-taxon surrogacy based on macroinvertebrates bears great promise for stream bioassessment at broad geographical scales, but much less so at the regional or watershed scales where many biomonitoring programs are still being conducted (see Cao et al. 2001). In fact, our results suggest that community concordance in streams is most variable and generally rather low exactly at these small to intermediate scales. Apparently, for the surrogacy approach to be successful, biodiversity surveys will need to encompass a rather wide range of biotic and abiotic variability. Thus, this scale-related phenomenon is not a mere sampling artifact of larger geographical extents unavoidably resulting in stronger environment–community correlations, but is rather an integral ecological attribute of the study system. Therefore it may well be, as suggested by Lawton et al. (1998) and van Jaarsveld et al. (1998) for terrestrial systems, that in many situations pertinent to practical conservation work or bioassessment, there are no cost-effective short cuts for extensive inventories of biodiversity, incorporating a wide array of taxonomic groups with differing sizes and ecologies.

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