

Riku Paavola

Community Structure of Macroinvertebrates,
Bryophytes and Fish in Boreal Streams

Patterns from Local to Regional Scales,
with Conservation Implications

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ABSTRACT

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Community structure of macroinvertebrates, bryophytes and fish in boreal streams – Patterns from local to regional scales, with conservation implications

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Yhteenveto: Selkärangattomien, vesisammalten ja kalojen yhteisö rakenne pohjoisissa virtavesissä – säännönmukaisuudet paikallisesta mittakaavasta alueelliseen ja luonnonsuojelullinen merkitys

The alarming lack of information about the habitat requirements, biogeographical patterns and degree of concordance in community patterns of freshwater species seriously obstructs the implementation of conservation and monitoring programs. In addition to providing information on the basic community patterns of stream macroinvertebrates, bryophytes and fish, the major aims of this thesis were (1) to investigate the degree of concordance among patterns in community structure and species richness of the three taxonomic groups, (2) examine how patterns in concordance relate to spatial scale, and (3) assess the implications of concordance for stream conservation. Patterns in environmental characteristics and macroinvertebrate assemblages of boreal headwater streams were rather congruent with ecoregional delineations, but showed weaker correspondence with a finer classification at the level of subcoregions, implying that an ecoregional framework holds promise for a successful implementation of stream management programs. At a local scale, macroinvertebrate communities correlated mainly with stream size, acidity, and water colour, while bryophytes were mainly related to nutrient levels and in-stream habitat complexity, and fish communities to oxygen levels, depth and substratum size. At the scale of ecoregions, spatial coordinates, acidity and depth were important for all three taxonomic groups. Community concordance among macroinvertebrates, bryophytes, and fish was strong when viewed across drainage systems, but weak or variable at the scale of single river systems. Strong concordance at broad spatial scales was caused by the three groups responding largely to the same set of environmental cues, whereas weak concordance at the scale of individual river systems was attributed to each group correlating with distinctively different environmental gradients. Communities of headwater streams were less concordant than those of medium sized streams. Species richness patterns among macroinvertebrates, bryophytes and fish were significantly concordant, but the relationships had a low predictive power. These results show that surrogate measures may be of limited value in stream biodiversity inventories. Overall, there may be no cost-effective shortcuts for extensive inventories of lotic biodiversity, incorporating a wide array of taxonomic groups with differing sizes and ecologies.

Key words: Aquatic bryophytes; aquatic insects; benthic invertebrates; bioassessment; community concordance; community structure; conservation; fish; species richness; streams.

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LIST OF ORIGINAL PUBLICATIONS

This doctoral thesis is based on the following original articles, which will be referred to by their Roman numerals throughout this summary. I contributed to all phases of every paper, being mainly responsible for the study design, field work, data analysis and writing of papers I, III and V. In studies II and IV, I participated in the study design, field work, data analysis, and to a lesser extent, in writing of the manuscripts.

- I Paavola, R., Muotka, T. & Tikkanen, P. 2000. Macroinvertebrate community structure and species diversity in humic streams of Finnish Lapland. *Verhandlungen der internationalen Vereinigung für theoretische und angewandte Limnologie* 27: 2550-2555.
- II Heino, J., Muotka, T., Paavola, R., Hämäläinen, H. & Koskenniemi, E. 2002. Correspondence between regional delineations and spatial patterns in macroinvertebrate assemblages of boreal headwater streams. *Journal of the North American Benthological Society* 21: 397-413.
- III Paavola, R., Muotka, T., Virtanen, R., Heino, J. & Kreivi, P. 2003. Are biological classifications of headwater streams concordant across multiple taxonomic groups? Submitted.
- IV Heino, J., Paavola, R., Virtanen, R. & Muotka, T. 2003. Searching for biodiversity indicators in running waters: do bryophytes, macroinvertebrates, and fish show congruent diversity patterns in boreal streams? Submitted.
- V Paavola, R., Muotka, T., Virtanen, R., Heino, J. & Mäki-Petäys, A. 2003. Study scale affects the degree of community concordance among fishes, benthic macroinvertebrates, and bryophytes in boreal streams. Submitted.

1 INTRODUCTION

Natural river systems have become increasingly rare in the northernmost third of the world (Dynesius & Nilsson 1994). Together with rivers in other parts of the world, they continue to be threatened by a wide variety of human activities, including river regulation, alteration of water chemistry, direct additions and losses of biota, and climate change, all of which are driven by the rapidly expanding human population (Malmqvist & Rundle 2002). Many of the northern rivers still remaining in natural condition are situated in Fennoscandia (Dynesius & Nilsson 1994), which should therefore be an ideal area for conducting research on factors governing biodiversity of lotic ecosystems. However, until quite recently, stream research has concentrated heavily on temperate river systems, and systematic large scale studies implementing rigorous measurement of relevant environmental gradients have been lacking for Fennoscandian rivers. North-American boreal streams have been studied in more detail, but the existing knowledge is heavily biased with regard to habitat types and taxonomic groups. Unfortunately, headwater streams have suffered most from this bias, yet they comprise the largest portion of the drainage network of any river system. Increased research activity on Fennoscandian boreal streams has improved the situation for macroinvertebrates (e.g. Malmqvist & Mäki 1994, Malmqvist & Eriksson 1995, Sandin & Johnson 2000) and, to a smaller extent, for bryophytes (e.g. Muotka & Virtanen 1995, Englund et al. 1997, Virtanen et al. 2001). Thus, suitable background information has accumulated to set the stage for more detailed analyses of biodiversity of boreal river systems, although many aspects still remain poorly known (Naiman et al. 1995). For example, the role of humic substances, a key element of boreal waters, has not received much attention (but see Malmqvist & Mäki 1994, Vuori & Muotka 1999). Worldwide, the situation is even worse, with only a tiny fraction of biodiversity related research having been conducted in freshwater systems (Vinson & Hawkins 1998, Abell 2002). Habitat requirements and biogeographical patterns of many species are poorly known, and information

about the numbers of species living in different types of freshwater habitats is largely lacking (Abell 2002).

However, the distributions and habitat requirements of some lotic taxonomic groups, notably some macroinvertebrates and fish, are reasonably well-known (Matthews 1998, Angermeier & Winston 1999). Therefore, it would be tempting to use these groups as surrogates for complete stream biodiversity ('biodiversity indicators'; McGeoch 1998). Surrogate taxa can also be used in conservation biology as a shortcut for describing patterns and processes other than complete biodiversity (Caro & O'Doherty 1999). Nevertheless, even biodiversity indicators would be invaluable for effective conservation of freshwater biodiversity. Yet, even if species richness patterns for some habitats and taxonomic groups are rather well known, the reasons behind those richness patterns are still poorly understood (e.g. Voelz & McArthur 2000). Furthermore, less well-known groups, like aquatic bryophytes, may have very different patterns of diversity and community structure than the surrogate groups and uniform management practices and conservation measures may thus be entirely inappropriate.

The usefulness of the surrogate taxa approach largely depends on the degree of similarity of patterns in community structure and species diversity among taxonomic groups across a set of sites, i.e. community concordance (*sensu* Paszkowski & Tonn 2000). Most aquatic studies of community concordance have been conducted on lake communities. These have shown rather strong congruence in community patterns among such remote taxonomic groups as benthic macroinvertebrates and fish (Jackson & Harvey 1993), aquatic birds and fish (Paszkowski & Tonn 2000), or diatoms and zooplankton (Allen et al. 1999b). By contrast, studies examining community concordance in streams are rare. Although there is a wealth of literature dealing with responses of different lotic organism groups to the same underlying gradient (e.g. Ormerod et al. 1994, Lammert & Allan 1999, Hirst et al. 2002, Wright & Li 2002), only Ormerod et al. (1987) and Kilgour & Barton (1999) have directly addressed community concordance in streams. Ormerod et al. (1987) reported strong concordance between macrophyte and invertebrate assemblages in upland Welsh streams in relation to an acidity gradient, and Kilgour & Barton (1999) found strong spatial congruence between fish and benthos in a set of wadeable streams in Ontario, Canada. Most of the existing direct tests of community concordance have been conducted at rather large spatial scales, encompassing several river systems (e.g. Kilgour & Barton 1999) or lakes from large areas (e.g. Allen et al. 1999a,b). Studies at smaller scales, i.e. within single ecoregions or river systems, where many bioassessment programs are still being conducted (Cao & Larsen 2001), do not exist for streams. Moreover, studies explicitly testing the effect of spatial scale on the degree of community concordance are completely lacking. The existing evidence thus suggests that fish or benthos might be useful surrogates for other freshwater biotic groups, but since patterns in community concordance may be context-dependent (e.g. region- and scale-specific), many more studies, especially in running waters, are needed to assess

better the usefulness of the surrogate taxa approach in freshwater biodiversity assessment and conservation.

Stream management and conservation might be further improved through geographical stratification. Ecoregions based on climate, vegetation, geology, and relief might serve as a framework for stratifying natural variation for the needs of stream management. However, to fulfill this role ecoregions would need to correspond rather well with biotic communities and environmental characteristics. Differences in environmental characteristics between catchments within ecoregions may, however, override the influence of regional factors. Alternatively, human impact on the vegetation structure of a region may disrupt the correspondence between invertebrate assemblages and regional delineations (Corkum 1990). In a similar vein, Quinn & Hickey (1990) suggested catchment land use as the reason for their inability to connect stream invertebrate assemblages to ecoregions. Nevertheless, several authors have been successful in linking invertebrate assemblages to ecoregions (Whittier et al. 1988, Hughes et al. 1990, Harding et al. 1997, Rundle & Ramsay 1997, Rabeni & Doisy 2000), and regional delineations thus hold considerable promise for improved management and conservation of stream biodiversity.

This thesis concentrates on the patterns of community structure and diversity of benthic macroinvertebrates, bryophytes and fish in boreal streams, and on the relationships of these patterns with environmental factors and spatial scale. In comparison to temperate stream systems, the biodiversity of boreal streams remains inadequately known, a condition which severely hampers any conservation attempts. In addition to providing the kind of basic information needed for conservation planning, I also tackled the little studied question of concordance of patterns in community structure among stream macroinvertebrates, bryophytes and fish. Further, I examined the previously unexplored role of spatial scale in stream community concordance. The main objectives were to identify the major environmental gradients associated with macroinvertebrate community structure and species diversity in boreal streams (I, II), and to test the congruence between in-stream environmental factors, macroinvertebrate assemblages and regional delineations (II). I also investigated how consistently macroinvertebrates, bryophytes and fish classify stream sites (III). Finally, I examined the environmental correlates of and spatial congruence in the species richness patterns of bryophytes, macroinvertebrates and fish (IV), assessed whether these stream organisms exhibit similar patterns of community structure across streams and whether the patterns of concordance observed were scale-dependent (V).

2 MATERIALS AND METHODS

2.1 Study areas

The study areas of papers I, III, IV and V were in middle boreal and north boreal ecoregions in northern and northeastern Finland (64°N to 68°N and 25°E to 31°E), whereas those of paper II ranged throughout the country (60°N to 70°N and 20°E to 32°E), encompassing all five ecoregions of Finland (hemiboreal, south boreal, middle boreal, north boreal and arctic-alpine). Ecoregional delineations are based on climate, vegetation, geology, and land use, and follow the Atlas of Finland (1988) and the Nordic Council of Ministers (1984).

2.2 Field surveys

Field sampling was conducted between 1992 and 1998 at riffle sites of 1st to 5th order streams, with paper II streams being restricted to 1st to 3rd order headwater streams and only paper I including data from larger, 5th order river sites. Using topographic maps, the selection of sampling sites was performed as randomly as possible, the only restrictions being accessibility (only streams within less than 2 km of the nearest road were included) and "naturalness" (streams with obvious human impact were excluded). Catchments of most of the streams are under the influence of modest forestry activities, but the sampled streams otherwise represent reasonably pristine stream conditions. Data from 23, 156, 32, 101, and 101 streams were included in papers I, II, III, IV, and V, respectively. The streams of study III are a subset of the streams investigated in studies IV and V. Field data consisted of semiquantitative macroinvertebrate (all papers), bryophyte (III, IV, V), and fish (III, IV, V)

samples, complemented by simultaneous measurements of physical and chemical environmental characteristics.

Macroinvertebrates for papers I, III, IV and V were collected by taking a two-minute kick-net sample (consisting of four 30 s subsamples) at each site on two dates (early summer and early autumn), whereas only early autumnal samples were collected for paper II. The subsamples were distributed over a riffle area of c. 100 m², and care was taken to include as much of the microhabitat variability present in a riffle as possible. The samples were immediately preserved in 70% ethanol, and animals were later sorted in the laboratory by trained personnel. Invertebrates were mostly identified to species or genus. Data were then pooled across the two sampling dates to obtain a site-specific composite of the whole assemblage.

Bryophyte samples were collected at the same riffle sites simultaneously with the autumnal benthic sampling. Bryophytes were harvested from ten randomly placed plots (0.5 x 0.5 m) at each site. The plots were placed in only those areas of the streambed that remain wetted at mean water level. All bryophyte species and their relative abundances (% cover) were recorded.

Fish were collected by electrofishing a 100 m² area in 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 (1-3), with more passes at sites with heterogeneous substratum or large numbers of fish. All stunned fish were counted, identified, and measured (TL in mm), after which they were released back to the stream. Only native, naturally reproducing fish were included in data analyses.

A suite of physical environmental characteristics was measured at each site, including both riparian (tree composition, riparian integrity, riparian zone width, and shading) and in-stream factors (current velocity, depth, particle size and moss cover). In papers I, III, IV and V, stream slope, stream bank cover, the amount of large woody debris (LWD) in stream channel, and distance from nearest upstream lake were also measured. Coefficients of variation for water velocity, depth and substratum size and an index of bed instability were used to quantify in-stream habitat heterogeneity and substrate stability, respectively. Water samples were collected in early autumn, and were analysed for pH, alkalinity, conductivity, total nitrogen, total phosphorus, iron and colour at the regional environment centres of Finland or at Oulanka Biological Station.

2.3 Specific methods

2.3.1 Macroinvertebrate community structure and species diversity in humic streams (I)

Multivariate methods were used to identify the major environmental gradients associated with macroinvertebrate community structure and species diversity

in a set of north boreal streams. Invertebrate data from the two sampling dates were pooled to obtain a composite of the whole assemblage. The data were $\ln(x+1)$ transformed prior to analysis to reduce the effect of numerically dominant species and better to approximate multivariate normality. Rare species (i.e. those occurring in only one sample) were omitted from analyses other than calculations of species-rank curves.

Two-Way Indicator Species Analysis (TWINSpan, Hill 1979), a hierarchical classification method based on reciprocal averaging, was used to produce an ecologically meaningful site classification of assemblage types, with indicator species for each division. It uses species composition of the study sites to build a site classification. Despite some drawbacks (Belbin & McDonald 1993, Legendre & Legendre 1998), TWINSpan has been shown to perform better than alternative clustering methods in the classification of benthic macroinvertebrate assemblages (Moss et al. 1999).

To reduce the dimensionality of the environmental data, Principal Components Analysis (PCA) on a correlation matrix was used to extract orthogonal, uncorrelated gradients which were then used in subsequent analysis. Canonical Correspondence Analysis (CCA), a direct gradient (constrained) ordination method that simultaneously analyses species and environmental data by combining multiple regression and ordination (ter Braak 1995), was used to identify and visualize the major environmental gradients (PCA components) related to the macroinvertebrate assemblage types identified by TWINSpan.

Finally, species-rank curves were constructed for each sampling site to visualize the diversity patterns in each TWINSpan group.

2.3.2 Regional delineations and stream macroinvertebrate assemblages (II)

Multivariate techniques were used to investigate the congruence between in-stream environmental factors, macroinvertebrate assemblages and regional delineations (five ecoregions and 11 subcoregions).

PCA was used to extract major gradients in stream environmental data. A varimax rotation was used to maximize loadings of the original variables on each extracted principal component to facilitate interpretation of PCA (e.g. Legendre & Legendre 1998). Variables were log or arcsine-squareroot transformed as needed. Mean subcoregional scores on each principal component were plotted for visual examination of among-regional differences.

Nonmetric multidimensional scaling (NMDS) was used to summarize patterns in macroinvertebrate assemblage structure. 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 also robust to deviations from multinormality (McCune & Mefford 1999). Sørensen's coefficient based on $\log(x+1)$ transformed macroinvertebrate data was used as the dissimilarity measure. To avoid the problem of local minima, several NMDS analyses were run, and the one with the lowest stress value was chosen. Stress is a measure of departure from monotonicity in the relationship between

distances in the original space and in the reduced ordination space. A three-dimensional solution of NMDS was used since the change in stress value was minor with further dimensions. Differences in NMDS site scores among ecoregions, as well as among subcoregions, were compared using one-way ANOVA.

Discriminant Function Analysis (DFA) was used for two purposes. First, DFA was used to examine the degree of correspondence of stream environmental characteristics to ecoregions and subcoregions. Distances of stream sites to group (ecoregion or subcoregion) centers were calculated, and each site was allocated to the group it was closest to (Manly 1994). Environmental variables were transformed when necessary, better to approximate normal distributions and to remove heteroscedasticity. Second, DFA was used to assess the correspondence of macroinvertebrate assemblage structure to the ecoregions and subcoregions. For this purpose, site scores on the three NMDS dimensions were used as variables, but otherwise the procedure followed that of the analysis of stream environmental variables. Cross-validated classifications were used to determine the fidelity of sites to their source regions in all analyses.

The classification strength (CS) of the ecoregions and subcoregions was tested using a randomization method following Van Sickle (1997). Sørensen similarity coefficient was used in the analysis. To examine if there were differences among the ecoregions and subcoregions in the functional feeding group composition of macroinvertebrate assemblages, MRPP analyses were performed. MRPP is a data-dependent Monte Carlo permutation test based on pair-wise distance measures, and it makes few assumptions about the distribution structure of the data (Zimmerman et al. 1985) which makes it ideal for testing among-group differences in ecological data sets. Finally, Indicator Value method (IndVal) was used to detect significant indicator taxa for ecoregion delineations. IndVal is based on the comparison of relative abundances and relative frequencies of occurrence of taxa in different a priori site groups. It identifies indicator taxa that vary more between groups than would be expected by chance, testing their significance through a Monte Carlo randomisation procedure (Legendre & Legendre 1998).

2.3.3 Concordance of biological stream classifications (III)

The concordance among biological classifications of fish, benthic macroinvertebrates, and bryophytes in 1st to 4th order streams within a single large watershed (River Kemijoki) was tested using multivariate methods. The goal was to test how consistently different taxonomic groups classify stream sites. Direct ordination analyses were performed to identify the major environmental correlates for each biotic group. All abundance data were $\log(x+1)$ transformed (except for IndVal which uses untransformed abundances). Species occurring in only one sample were deleted.

A hierarchical site classification was first created separately for each taxonomic group by using TWINSpan. Each TWINSpan division was then

validated by using a combination of Multiresponse Permutation Procedures (MRPP) (Zimmerman et al. 1985, Biondini et al. 1988) and the indicator value method (IndVal) (Dufrêne & Legendre 1997, see also McGeoch & Chown 1998). A TWINSpan division was only accepted if the groups differed significantly according to MRPP. To be certain that the resulting typology represents meaningful ecological entities, we further required that at least one significant indicator species be identified by IndVal for each TWINSpan division.

The performance of each TWINSpan site classification on the other two taxonomic groups was tested by subjecting the final groupings and the first division of each 'benchmark' typology to MRPP and IndVal analysis using the other biotic data sets. The classification strength (CS) approach of Van Sickle (1997) was also used to assess the performance of these cross-tests. CS is based on a comparison of the mean of all between-class similarities (B) and the mean within-class similarity (W). Sørensen similarity coefficient was used in the analysis. CS is defined as the difference between these similarities ($CS = W - B$). Values of this measure range from 0 to 1, values near zero indicating that sites are randomly assigned to classes.

A Detrended Correspondence Analysis (DCA) was performed separately for each taxonomic group to assess the gradient length of the first DCA axis (in S.D. units). After seeing that gradients were long enough to justify the use of methods based on a unimodal response model, CCA was performed separately on each biotic group to visualize the classifications in relation to major environmental gradients. Due to the large number of environmental variables, the analysis was run using the automatic forward selection mode, accepting up to five significant variables for each taxonomic group. This approach avoids the problem of noisy or irrelevant variables (McCune 1997).

2.3.4 Congruence of diversity patterns in boreal streams (IV)

Environmental correlates of and congruence in the patterns of species richness among bryophytes, macroinvertebrates and fish were examined in this study using mainly correlation and regression techniques. Rare species were retained in the analyses.

Environmental variables were first subjected to PCA to produce uncorrelated composite variables representing the major environmental gradients among the data. A varimax rotation was performed to facilitate interpretation of the PCA components. If necessary, appropriate transformations (logarithmic or arcsine-squareroot) were performed to approximate normal distributions.

Stepwise regression analysis was used to model variation in the species richness of each taxonomic group. This method takes independent variables (here, site scores on each principal component, and latitude and longitude) in the model, in order of importance, according to how much of the variation in the dependent variable they explain. Finally, Pearson correlations were calculated between the three groups as a direct test of concordance in species richness.

Beta-diversity in each taxonomic group was assessed using the formula of Harrison et al. (1992), measuring the degree by which regional richness exceeds maximum local richness. Beta-diversity was used to measure species turnover for each taxonomic group across the whole study area.

2.3.5 Effects of study scale on the degree of stream community concordance (V)

Several multivariate methods were used to assess whether benthic macroinvertebrates, fishes and aquatic bryophytes exhibit similar patterns of community structure across streams and to test whether the patterns of concordance observed were scale-dependent. Two spatial scales were used in this study: (1) the scale of individual river systems and (2) a regional scale encompassing several river systems and two ecoregions. To ascertain that any differences in patterns of community concordance among the complete and spatially-restricted data sets were not simply caused by unequal sample sizes, ten random subsets were constructed by selecting 32 sites from the complete data set, using stratified random sampling. We thus randomly selected sites from each of the four sampling areas, thereby preserving the spatial structure of the original data set. Patterns in biotic communities were further related to environmental characteristics of the study sites to see if biotic communities were responding to similar environmental gradients across the study area.

NMDS was used to summarize patterns in each biotic data set. To avoid the problem of local minima, NMDS were run 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 & Mefford 1999). Sørensen coefficient was used as the distance measure in all analyses. PCA on correlation matrix was used to reduce the dimensionality of the environmental data into a few interpretable principal components representing the major environmental gradients of the data.

Procrustes rotation analysis was used to investigate the degree of concordance among the biotic NMDS ordinations and between the biotic and environmental ordinations (PCA). 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 which minimizes the sum of the squared residuals (m^2) between the two configurations; the m^2 statistic is then used as a measure of association (i.e. concordance) between the two ordinations (Gower 1971, Digby & 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 & 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.

ProTest further provides site-specific vector residuals that describe deviation in the positions of individual samples between 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, low values indicating strong concordance. Averaged vector residuals from the three pair-wise ordination superimpositions (invertebrates vs. bryophytes; invertebrates vs. fish; bryophytes vs. fish) were used to arrange the sampling sites along a 'concordance gradient'. Spearman rank correlations between the averaged vector residuals and environmental variables were then calculated to see which, if any, environmental factors were associated with the 'concordance gradient'.

Lastly, ProTest was used to examine directly the strength of congruence 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, an additional set of NMDS ordinations was run, this time extracting only two dimensions to match the dimensionality of the spatial factors.

Mantel test was also used for pair-wise comparisons of concordance between the three biotic data sets. It compares the degree of concordance among two similarity (or dissimilarity) matrices using the standardized Mantel statistic (r), analogous to the correlation coefficient, to evaluate the strength of the relationship between the two matrices. High values of r indicate strong congruence (McCune & Mefford 1999, Legendre & Legendre 1998). It was not used for comparisons involving environmental ordinations, however, because the level of significance obtained from the Mantel test is known to be sensitive to the distance measure used (Jackson 1995) (in this case, Sørensen distance for the biotic and Euclidean distance for the environmental data set, respectively).

To identify the major environmental gradients related to each biotic group, CCA was performed on each taxonomic group separately. Due to the large number of environmental variables, we ran the analyses using the automatic forward selection mode, accepting up to five most significant variables for each taxonomic group.

3 RESULTS AND DISCUSSION

3.1 Macroinvertebrate community structure and species diversity in humic streams (I)

Unambiguous patterns in community structure of macroinvertebrates were extracted from the multivariate analyses. Three distinct groups of streams emerged: large rivers, clear-water streams and humic streams. Lake outlets mingled with humic streams in the ordination space although according to the TWINSpan classification they were a separate entity. The PCA components represented clearly interpretable environmental gradients, the first component being a gradient of decreasing water quality with high loadings for total nitrogen, water colour and chemical oxygen demand. In the CCA ordination humic streams and lake outlets separated from large rivers and clear-water streams along this gradient. The second PCA component was mainly related to stream size with high loadings for discharge and depth. This component separated large river sites from the others. The third PCA component was related to in-stream habitat features, such as LWD and substrate size, although it also incorporated aspects of water chemistry, notably alkalinity and conductivity. Large rivers, clear-water streams, and humic streams separated rather well along this gradient. That all of the four stream groups harboured characteristic faunas was evident in the CCA ordination. Species richness was generally high and the degree of dominance low in the large river and clear-water stream sites. Contrastingly, humic streams and lake outlets supported species-poor communities dominated by relatively few species, these being shredders and collector-gatherers in humic streams and filter feeders in lake outlets.

The finding that water chemistry emerged as a predominant factor underlying macroinvertebrate community structure was somewhat unexpected, because such results normally stem from large-scale studies (see Hildrew & Giller 1994). However, in the present data even adjacent streams had distinctly

different regimes of water colour, nutrients and pH, and harboured differing macroinvertebrate communities. This would suggest that local factors do sometimes predominate over regional ones in structuring macroinvertebrate communities. Further, humic streams were shown to harbour relatively depauperate benthic communities, a possible explanation being the staining effect of humic substances, whereby transmission of light into the water is impaired. This might have an inhibitory effect on autochthonous production (Otto & Svensson 1983) and, hence, affect scraping macroinvertebrates, leading to changes in community structure. The pivotal role of water colour in affecting macroinvertebrate communities, although similar to the results of Malmqvist & Mäki (1994), differed sharply from that reported by Winterbourn & Collier (1987), who showed that adjacent humic and clearwater streams had rather similar faunas in New Zealand streams. Clearly, there is a need for further studies on the role of water colour in influencing lotic communities.

3.2 Regional delineations and stream macroinvertebrate assemblages (II)

Ecoregions and patterns in stream environmental characteristics matched rather closely, while macroinvertebrate assemblages exhibited slightly weaker correspondence with ecoregional delineations. In general, correct DFA classifications of streams decreased from the pristine arctic-alpine ecoregion to the more human-altered southern ecoregions for both environmental characteristics and macroinvertebrates. Stream classifications at the subecoregion level produced more variable results than at the level of ecoregions. Significant regional differences were found, however, for assemblage structure, functional feeding group composition, and taxon richness at both levels.

Regional differences in the prediction success might result from natural reasons or anthropogenic factors. For example, hemiboreal streams showed a poor classification success both in terms of environmental characteristics and macroinvertebrate assemblages. Landscapes of this ecoregion have been modified by forestry and agriculture for a longer time than in any of the other ecoregions. In the north boreal and arctic-alpine ecoregions, the variable relationships of stream macroinvertebrate assemblages to subecoregions were more likely driven by natural within-subecoregion variation in environmental conditions. For instance, clear-water streams with riparian zones dominated by deciduous trees occur in each subecoregion of the north boreal and arctic-alpine ecoregions, and these streams were highly similar in macroinvertebrate community structure, regardless of their location.

Variation in stream size is generally thought to underlie the relative contribution of different functional feeding groups (FFGs) to lotic macroinvertebrate assemblages (e.g. Vannote et al. 1980, Grubaugh et al. 1996).

Despite the narrow size distribution of streams in this study, the relative abundances of FFGs differed among ecoregions and sub-ecoregions, reflecting among-region variation in stream characteristics. Scrapers were generally abundant in subcoregions with clear-water streams, suggesting that their abundance may be controlled indirectly by water colour through its effects on light conditions and algal abundance (Otto & Svensson 1983, Vuori & Muotka 1999). Brown-water streams in the middle boreal ecoregion, by contrast, were characterised by low numbers of scrapers and high abundance of shredders. This variability in shredder versus scraper abundance may reflect the known acid-tolerance of many shredding invertebrates (e.g. many stoneflies). The high numbers of filterers in hemiboreal streams was probably related to lake connections, because streams in this region are typically short and connect series of small lakes to one another. Therefore, they are continuously fed by lake-derived organic material, an abundant and predictable resource base for filterers. Also, lakes tend to reduce discharge variations, resulting in stable flow conditions suitable for many filterers (e.g. hydropsychid caddisflies). These patterns emerged despite the fact that true lake outlets were not sampled, indicating long-distance influences of lakes on riffle-dwelling macroinvertebrates.

Congruence among ecoregions and macroinvertebrate assemblage characteristics was evident, but the presence of wide within-region variability implies that regional delineations alone do not provide a satisfactory framework for stream management programs. Rather, it appears that boreal headwater streams, and perhaps lowland streams in general, are governed by a mosaic of locally acting factors, combined with a regional control of local communities (Heino et al. in press a). Thus, a combined framework of regional delineations, landscape features and in-stream environmental predictors would probably yield the most effective tools available for the characterization of macroinvertebrate assemblages of boreal headwater streams.

3.3 Concordance of biological stream classifications (III)

Community classifications of macroinvertebrates, bryophytes, and fish in headwater streams were clearly not concordant, at least not at the within river-system scale used in this study. This pattern occurred despite clear, statistically validated and ecologically interpretable structure of each individual organism group along major environmental gradients. Each of the three biotic classifications gave clearly non-significant results when subjected to cross tests using data from the other two biotic groups. The lack of concordance reflected the fact that all three groups were responding to different environmental factors. Invertebrate community structure was mainly correlated with stream size and pH, whereas bryophytes were more influenced by water colour, nutrient content, and factors related to in-stream habitat variability. Water

colour was the only shared descriptor of community structure for both invertebrates and bryophytes. Fish community structure was best described by stream depth, substratum particle size, and water quality (oxygen concentration). Of these, only oxygen concentration was shared with invertebrates, and none with bryophytes.

The near lack of other studies on community concordance among running water biota precludes a wider comparison, and any explanations for the lack of parallel environmental responses by different taxonomic groups are necessarily tentative. Fish, due to their high mobility and long life-span, might be expected to reflect environmental conditions across broad spatial scales (Kilgour & Barton 1999), and therefore the rather site-specific sampling of environmental factors of this study may not have adequately covered all the factors relevant to lotic fish. However, Lammert & Allan (1999) also attributed lack of concordance in site rankings among macroinvertebrate and fish communities to differential environmental responses by these two organism groups in Michigan lowland streams. Jackson & Harvey (1993) also reported that fish and invertebrate communities in lakes were associated with different environmental factors, yet they found similar patterns of community structure for both groups across the study lakes, i.e. the two groups were strongly concordant. Paszkowski & Tonn (2000) and Allen et al. (1999b) also found significant concordance among groups of lake organisms. Considering the hypothesis of Allen et al. (1999b) that community concordance should be strongest among relatively similar-sized organisms, one might have anticipated more spatial congruence among macroinvertebrates and mosses in this study. Apparently, however, lotic macroinvertebrates and bryophytes are regulated by environmental factors operating at partly different scales, macroinvertebrates being more influenced by landscape-scale factors (e.g. stream size, drainage area, pH) and bryophytes by locally controlled, in-stream factors (e.g. substrate size and heterogeneity). Many recent studies have shown that macroinvertebrate communities are strongly influenced by catchment-scale land use patterns (e.g. Richards et al. 1997, Stone & Wallace 1998, Lammert & Allan 1999). While bryophytes are much less studied in this respect, recent papers have consistently shown that their community structure is strongly regulated by the availability of large substrate particles providing refugia during spates (Englund 1991, Suren & Ormerod, 1998) and suitable microhabitats for species specialized on the extremely variable microenvironment at the water-air interface (Muotka & Virtanen 1995, Virtanen, Muotka & Saksa 2001). While not arguing that bryophytes are unaffected by catchment-scale factors (indeed they are affected by e.g. altitude; Ormerod et al. 1994), the present results suggest that they are more directly controlled by reach-scale factors, especially as these relate to flow variability, than are the much more mobile macroinvertebrates.

A key element of this study was that it is based on data from a single, albeit large, river system. While this undoubtedly restricts the potential for broader generalisations, it also reduces the influence of any confounding factors, e.g. wide (and often unknown) species ranges and other biogeographic

factors. Since many freshwater taxonomic groups in northern Europe are known to exhibit broadly similar biogeographic patterns, related to climatic and historical factors (Heino 2001), a study encompassing large geographic areas would likely indicate stronger among-group concordance. However, many bioassessment programs have a more regional scope, and it is therefore imperative that we understand the associations in community patterns between taxonomic groups at several spatial scales, ranging from local (within drainages) to biogeographic (across drainages and/or ecoregions) ones. The results of this study do not support the contention that classifications based on a single taxonomic group can be easily generalized across other biotic groups. These results apply at the scale of single river systems, and the apparent discrepancy with results of studies conducted at larger spatial scales implies that the effects of spatial scale need to be explicitly studied. Overall, care should be taken when benthic invertebrates, or any other component of freshwater biota, are targeted as a surrogate for other taxonomic groups in freshwater biodiversity research.

3.4 Congruence of diversity patterns in boreal streams (IV)

Congruence in patterns of species richness among the biotic groups was generally low. Bryophytes and macroinvertebrates showed the strongest congruence, but even this relationship had a relatively weak predictive power. The observed weak, albeit significant, concordance stemmed mainly from the variable responses of the taxonomic groups to major environmental gradients. Bryophyte diversity showed the strongest relationship with water colour, followed by habitat stability and stream size. Macroinvertebrate diversity increased with stream size, and further variation was accounted for by water colour and acidity. Fish species richness showed a weak and complex relationship with geographical location, stream size and in-stream habitat characteristics. Regression models explained less than half of the variation in species richness: 23% for bryophytes, 45% for macroinvertebrates, and 26% for fish. Furthermore, there was clear geographical variation in stream site scores along some of the PCA components. These correlations suggest a strong spatially structured component to variation in stream conditions. At the local scale of stream riffle, macroinvertebrates were the most species-rich group, followed by bryophytes and fish. Species turnover was, however, highest for bryophytes, followed by macroinvertebrates and fish.

One might expect strongest concordance in diversity patterns among taxa of similar size (e.g. Allen et al. 1999b), or those with strong inter-taxa relations (e.g. Jackson & Harvey 1993, Paszkowski & Tonn 2000). However, even similar-sized organisms, such as different groups of stream insects, may exhibit surprisingly low spatial covariation (Heino et al. in review). Thus, bryophytes, invertebrates and fish may simply be too different in terms of size and general

ecology to exhibit strong congruence in diversity patterns. Bryophytes, being sessile organisms, are strongly affected by streambed stability (e.g. Muotka & Virtanen 1995, Suren & Ormerod 1998), whereas more mobile invertebrates and fish reflect environmental factors prevailing at larger spatial scales. However, because bryophytes provide habitat for invertebrates (e.g. Suren 1991, Muotka & Laasonen 2002), and may facilitate the recovery of invertebrate communities from disturbance (see Muotka et al. 2002), a diverse bryophyte assemblage including species with different growth forms could be hypothesized to support a diverse macroinvertebrate assemblage. In our study, the highest degree of congruence in species richness was indeed observed among bryophytes and macroinvertebrates, but it must be noted that even this association may be too weak to be used for any predictive purposes.

The taxonomic groups studied showed differing degrees of turnover diversity across the streams. This pattern is probably related to the relative dispersal capability of each group, i.e. taxa with limited capability of dispersal should exhibit the highest degree of spatial turnover (but see Harrison et al. 1992). Bryophytes, relying on passive means for among-stream dispersal, probably have a relatively low capability of dispersal, although not much is known about this aspect of stream bryophyte biology (Stream Bryophyte Group 1999). By contrast, the low turnover diversity of fish results from a highly impoverished regional species pool typical of boreal streams, thereby allowing little among-site turnover in species composition. In fact, many of our streams were either fishless or were inhabited by one to three of the core fish species of boreal streams, i.e. brown trout (*Salmo trutta*), bullhead (*Cottus gobio*), and burbot (*Lota lota*).

Low among-taxa concordance in diversity patterns has been a common result in many recent studies, suggesting low utility for single taxonomic groups as biodiversity indicators across local systems (e.g. Lawton et al. 1998, Ricketts et al. 2002). This is somewhat problematic because it is at the level of local communities where the evaluation and conservation of wholesale biodiversity ought to be most effective. If the use of indicator taxa gives no shortcut for conservation evaluation, then physical habitat surrogates should be considered as an alternative. The use of habitat surrogates is supported by a considerable amount of information on macroinvertebrates and fish showing that collections of major habitat types, by complementing each other, capture a large proportion of the regional variability in lotic biodiversity (e.g. Angermeier & Winston 1999, Malmqvist & Eriksson 1995, Malmqvist & Hoffsten 2000, see also paper I). Because most lotic taxa will remain poorly-known, and because indicator groups appear ineffective in guiding conservation efforts, a habitat-based approach might bear more promise for the conservation of lotic biota.

3.5 Effects of study scale on the degree of stream community concordance (V)

The degree of community concordance observed between the three biotic groups was clearly scale-dependent. At the scale of single river systems, both ProTest analyses and Mantel tests indicated variable and generally weak concordance among the groups studied, as well as between the environmental factors and the taxonomic groups. In contrast, the complete data set spanning multiple drainage systems and two ecoregions revealed strong congruence among the groups, and among the biotic groups and the environment. Randomized subsets of the complete data further indicated that the observed differences in the strength of 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 and longer environmental gradients of the complete data set. In a similar vein, congruence between spatial (latitude and longitude) and environmental factors (PCA components of complete data set), and between spatial factors and patterns in invertebrate community structure (NMDS ordinations of complete data set) was very strong. These results indicate a strong spatially structured component to the variability of environmental factors and biotic communities of boreal streams. Direct gradient analyses (CCA) revealed a striking similarity in the key environmental correlates for macroinvertebrates, fish, and bryophytes, indicating that closely similar suites of environmental factors underlie the major patterns of community structure of these groups, when viewed across broad spatial scales. The roles of pH, spatial coordinates, and depth were particularly conspicuous, these being the strongest environmental correlates for all three groups.

Although it is possible for biotic communities responding to different environmental cues to exhibit concordant patterns of community structure (Jackson & Harvey 1993), our results rather concur with those of Paszkowski & Tonn (2000) and Kilgour & Barton (1999) showing that concordance results from both groups responding to the same set of environmental factors. In paper III, the degree of concordance between biotic classifications (benthic invertebrates, bryophytes, fish) of 32 stream sites (i.e. one of the spatially restricted data sets of this study) within a single river system was investigated, and little evidence for community concordance was found. Direct gradient analyses in paper III (CCA with forward selection of variables) showed that the three biotic groups were responding to different sets of environmental cues. Interestingly, Lammert & Allan (1999) also reported that patterns of fish and macroinvertebrate community structure in the River Raisin drainage system in southern Michigan 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 the underlying environmental gradients, and such predominant gradients are likely to emerge only if relatively large geographical areas, spanning multiple drainage systems, are included. The observation that benthic invertebrate

communities exhibited a strong latitudinal pattern reiterates the earlier findings of Sandin & Johnson (2000) for stream (see also paper II), and Johnson (2000) and Johnson & Goedkoop (2002) for lake communities. It thus appears that the general trend of freshwater taxa to exhibit strong latitudinal distribution patterns across northern Europe (see Heino 2001), most likely resulting from climate and largely similar postglacial colonization routes, sets the stage for strong community concordance among the biotic groups of boreal streams, even when examined at the scale of local habitats and across a much shorter latitudinal gradient (in our case, c. 400 km).

Site-specific residuals from the ProTest analyses enabled the identification of a 'concordance gradient' which was positively related to discharge (i.e. stream size) and microhabitat variability (depth CV). This finding suggests that larger streams contribute disproportionately to concordance among lotic communities. This result is well in line with one of the basic premises of the River Continuum Concept (RCC; Vannote et al. 1980) that stream habitats become more stable as the stream size increases from headwaters to mid-sized, fourth to fifth order streams. Accordingly, mid-sized streams are expected to harbour 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 seem to support biotic assemblages that show unpredictable among-stream variability, thus providing little scope for community concordance among lotic taxonomic groups (see Heino et al. in press b).

Since information on the distribution patterns of many groups of stream organisms is clearly inadequate, benthic macroinvertebrates or fishes are routinely used as surrogates of wholesale biodiversity, or as overall indicators of stream condition. Our observations suggest that cross-taxon surrogacy based on macroinvertebrates bears great promise for stream biodiversity assessment at broad geographical scales, but less so at the regional or watershed scales where many bioassessment programs are still being conducted (Cao & Larsen 2001). Our results show that it is exactly at these small to intermediate scales where community concordance in streams is most variable and generally rather low. 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 lotic biodiversity, incorporating a wide array of taxonomic groups with differing sizes and ecologies.

4 CONCLUDING REMARKS

The alarming lack of information about the habitat requirements and biogeographical patterns of freshwater species has recently raised pleas for concentrating more research effort on freshwater biodiversity (Abell 2002). Running waters are already among the most impacted ecosystems, and unfortunately the pressure from human activities is likely to increase in the future (Malmqvist & Rundle 2002). Therefore, priority areas for conservation need to be identified and protected. Biodiversity hotspots, areas containing high numbers of species, endemic species, rare or threatened species (Reid 1998), ought to be the best candidates for priority areas. The only absolutely reliable method for identifying biodiversity hotspots would be to attempt to enumerate nearly all species in each taxonomic group living in a given area. However, due to their high costs, such thorough inventories of lotic biodiversity will not be readily conducted in many parts of the world. Taxonomic expertise for many groups of organisms is also lacking. Therefore, cost-efficient shortcuts for locating priority areas would enormously ease the task of protecting lotic biodiversity. The surrogate taxa approach is certainly among the best candidates for such a shortcut, although recent terrestrial studies have identified serious limitations to the applicability of this method (Jaarsveld et al. 1998, Lawton et al. 1998, Mac Nally et al. 2002).

The implementation of bioassessment programs would further benefit from a usable framework of geographical stratification, which would enable a better understanding of broad-scale patterns in the structure of stream communities (see Hawkins et al. 2000). According to our results, ecoregions might provide such a framework for stratifying natural variation for the needs of stream management. Patterns in environmental characteristics and macroinvertebrate assemblages of boreal headwater streams corresponded rather well with ecoregional delineations, but less so with a finer-scale classification at the level of subcoregions (II). Further, ecoregions differed significantly with respect to local species numbers and functional feeding group composition, implying that ecoregions partition a large proportion of variation in macroinvertebrate community structure.

Macroinvertebrates or fish are probably the best candidates for biodiversity surrogates in streams, simply because their habitat requirements, distributions and species richness patterns are better known than those of other biotic groups (e.g. Angermeier & Winston 1999). Often, however, the reasons behind the richness patterns are inadequately understood (e.g. Voelz & McArthur 2000). According to the present data, fish species richness has a weak and complex relationship with geographical location, local environmental conditions, and stream size. Further, due to the highly impoverished regional species pool typical of Fennoscandian streams, the turnover diversity of fish was low (IV, see also Oberdorff et al. 1997). The finding that invertebrates may be more efficient than vertebrates as predictors of the overall biodiversity is not a novel one (e.g. Moritz et al. 2001). Overall, the patterns of community structure and species richness of macroinvertebrates were clear, being governed by the interplay of stream size and water chemistry (I, IV). Macroinvertebrate diversity increased with stream size, and additional variation was accounted for by water colour and acidity, with clear-water streams of high pH harbouring the most species-rich communities. Further, the turnover diversity of macroinvertebrates, though surpassed by that of bryophytes, was reasonably high, indicating their potential usefulness as proxies of lotic biodiversity.

The success of the surrogate taxa approach ultimately depends on the degree of community concordance among the taxonomic groups in question. If patterns in community structure and species richness of the biotic groups do not converge, then the approach has little chance of success. The present results suggest that community concordance among macroinvertebrates, bryophytes and fish is strong at the scale of ecoregions (V), but weak or variable at the scale of single river systems (III). This would severely limit the usefulness of the approach for many riverine assessment programs, as these are often conducted at the scale of single watersheds (Cao & Larsen 2001). It also seems that, by comparison to larger rivers, headwater streams harbour less congruent communities (V), perhaps because of their physically harsh and variable environmental conditions. Environmental variability has been shown to cause assemblage variability and decreased species richness in European stream fish (Oberdorff et al. 2001). The lower degree of concordance observed in headwater streams has further negative implications for the management of stream biodiversity, simply because a large proportion of streams are headwaters. The rather weak concordance of species richness patterns among macroinvertebrates, bryophytes and fish (IV, V) poses further challenges for the successful management of stream biodiversity. Furthermore, even in cases of high predictive power detected among candidate taxonomic groups, the efficiency of surrogacy may still be asymmetric; for example, snails and insects may be strong predictors for vertebrates, but not vice versa (Moritz et al. 2001). Habitat-based approaches advocating the use of physical surrogates of overall biodiversity may thus be more useful in the conservation of lotic biodiversity. However, it appears that, despite the highly similar environmental cues underlying the patterns of community structure (V), partly different

environmental factors govern the local species richness of different lotic organism groups (IV). This might make the identification of universal physical proxies for the wholesale lotic biodiversity very difficult. However, many aspects of lotic community concordance have not yet been sufficiently explored. More studies conducted similarly in different parts of the world and across multiple spatial scales are needed for a rigorous evaluation of the patterns reported here. The inclusion of more biotic groups, such as stream algae and meiofauna, would also help to judge how universal the observed patterns are.

In summary, the present evidence suggests that there are no cost-effective yet reliable shortcuts for extensive inventories of lotic biodiversity, incorporating a wide array of taxonomic groups with differing sizes and ecologies (see also Lawton et al. 1998, van Jaarsveld et al. 1998). Keeping in mind the steadily increasing pressure from human activities (Malmqvist & Rundle 2002), this finding may have important implications for the monitoring and management of lotic biodiversity in various countries, especially among the members of the European Union. Through the Water Framework Directive, environmental authorities are responsible for the evaluation, monitoring and conservation of freshwater biodiversity. The task is already daunting, but it may well become impossible to do acceptably, unless environmental authorities have proper resources for extensive inventories of biodiversity in the form of money and personnel.

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YHTEENVETO

Selkärangattomien, vesisammalten ja kalojen yhteisörakenne pohjoisissa virtavesissä – säännönmukaisuudet paikallisesta mittakaavasta alueelliseen ja luonnonsuojelullinen merkitys

Luonnontilaiset jokisysteemit ovat voimakkaasti harvinaistuneet kaikkialla maailmassa. Jäljellä olevia luonnontilaisia jokisysteemejä, joista monet sijaitsevat Fennoskandiassa, uhkaavat monet ihmistoiminnasta aiheutuvat tekijät. Useimmat näistä tekijöistä tulevat jatkossa pahenemaan, jo pelkästään voimakkaan väestönkasvun aiheuttaman kasvavan paineen vuoksi. Virtavesien biologisen monimuotoisuuden suojelutoimilla on siis kiire, mutta tehtävää vaikeuttaa olennaisesti jokivesissä elävien eliöryhmien puutteellinen tuntemus: monien taksonomisten ryhmien ekologiset vaatimukset, levinneisyys sekä lajirunsautteen vaikuttavat seikat ovat pitkälti selvittämättä. Erityisen huonosti tunnettuja ryhmiä ovat virtavesisammalet, makroskooppiset levät sekä meiiofaunaan luettavat selkärangattomat pohjaeläimet. Optimaalisesti toimiva luonnonsuojelullisten painopistealueiden valintajärjestelmä edellyttäisikin kattavia, kaikki eliöryhmät sisältäviä inventaarioita. Tällaiset ohjelmat ovat kuitenkin kalliita, koska ne vaativat suuren määrän asiantuntevaa henkilökuntaa ollakseen toteuttamiskelpoisia. Niinpä luonnonsuojelubiologisin tutkimuksin on pyritty löytämään edullisia ja helppokäyttöisiä biologisen monimuotoisuuden ilmentäjälajeja tai -lajiryhmiä (surrogate taxa). Näillä tarkoitetaan kohtalaisen hyvin tunnettujen eliöryhmien edustajia, joita voisi käyttää ennustamaan vaikkapa erilaisissa jokihabitaateissa elävien lajien kokonaismäärää. Tämä lähestymistapa onkin osoittautunut toimivaksi mm. troopiikin rikkaiden eliöyhteisöjen lajimäärien ennustamisessa, erityisesti toimittaessa laajoilla eliömaantieteellisillä mittakaavoilla. Monet vesiluonnon arviointi- ja seurantaohjelmat kuitenkin toimivat selkeästi paikallisemmilla mittakaavoilla, usein yksittäisten jokisysteemien tasolla. On kokonaan selvittämättä, miten hyvin ilmentäjälajeihin perustuva lähestymistapa toimisi paikallisilla mittakaavoilla jokiympäristöjen biodiversiteetin ennustamisessa. Koska kritiikki monimuotoisuuden ilmentäjiä vastaan on viime aikoina lisääntynyt maaekosysteemienkin puolella, on tarpeen huolellisesti testata ilmentälajien soveltuvuus virtavesien eliöyhteisöjen lajirunsauden ennustamiseen.

Koska kalojen ja makroskooppisten selkärangattomien tuntemus on sisävesien eliöryhmistä parhaimmalla tasolla, tarkastelen tässä väitöskirjassa lähinnä näiden kahden ryhmän soveltuvuutta ilmentämään jokihabitaattien biologista monimuotoisuutta. Jotta ilmentäjälajit voisivat toimia luotettavasti, on jokisysteemeissä esiintyvien eliöryhmien osoitettava riittävän voimakkaasti yhteneviä piirteitä yhteisörakenteessa (community concordance) ja paikallisessa lajirunsaudessa (diversity concordance). Näiden yhtenevyksien olisi lisäksi ilmentävä luonnonsuojelubiologisesti tärkeillä paikallisilla mittakaavoilla. Niinpä keskityinkin selvittämään, ovatko piirteet eri selkärangattomien, vesisammalten ja kalojen yhteisörakenteissa ja lajimäärissä yhteneviä yksittäisten jokisys-

teemien mittakaavalla, vai kenties yli jokisysteemien ja ekoregioiden (kasvillisuudeltaan ja geologialtaan yhtenäinen alue) ulottuvalla laajemmalla mittakaavalla.

Makroskooppisten selkärangattomien yhteisörakenteiden ja lajirikkauden selkeät yhteydet havumetsävyöhykkeen jokisysteemien kannalta olennaisiin ympäristögradientteihin osoittivat, että makroskooppiset selkärangattomat soveltuvat ilmentäjälajeiksi paremmin kuin kalat. Selkärangattomien paikalliset lajimäärät kasvoivat jokikoon myötä, mutta korreloivat negatiivisesti happamuuden ja veden värin kanssa. Myöskin kohtalaisen suuri lajien vaihdunta (nk. β -diversiteetti) näytepaikkojen välillä viittasi makroskooppisten selkärangattomien soveltuvuuteen biologisen monimuotoisuuden ilmentäjiksi. Lajien vaihdunta oli kaloilla vähäistä, johtuen niukasta alueellisesta lajimäärästä, eikä paikallisten lajimäärien yhteys ympäristögradientteihin ollut yhtä selkeä kuin selkärangattomilla.

Latvapurojen selkärangatonyhteisöjen lajistolliset piirteet, kuten myös purojen ympäristötekijät noudattivat varsin hyvin ekoregioiden muodostamaa alueellista stratifikaatiota, mutta yhteys alaekoregioiden muodostamaan hienosyisempään alueelliseen jaotteluun oli heikompi. Ekoregioiden muodostama maantieteellinen stratifikaatio saattaisi siis toimia hyödyllisenä viitekehyyksenä jokiluonnon seurantaohjelmissa, erityisesti mikäli tueksi otetaan paikallisemmän mittakaavan, kuten valuma-alue, tason tekijöitä. Esille tulleet ekoregioiden väliset varsin selvät erot sekä selkärangattomien paikallisessa lajirunsaudessa että ravinnonkäyttöryhmien suhteellisissa osuuksissa osoittivat, että ekoregioihin perustuva stratifikaatio kykenee varsin hyvin jaottelemaan selkärangatonyhteisöissä esiintyvää variaatiota.

Ekoregioiden yli ulottuva mittakaava osoittautui yksittäisten jokisysteemien tasoa selkeästi lupaavammaksi kehyykseksi yhteisörakenteiden ja lajirunsauden yhtenevyyksien kannalta. Kaikki kolme eliöryhmää osoittivat ekoregioiden yli ulottuvalla mittakaavalla tilastollisesti erittäin merkitsevää yhtenevyyttä yhteisörakenteen piirteiden osalta, mutta yksittäisten jokisysteemien mittakaavalla yhtenevyys vaihteli suuresti, ollen kuitenkin enimmäkseen tilastollisesti ei-merkitsevää. Yhteisörakenteiden yhtenevyys oli kuitenkin voimakkaampaa keskikokoisissa joissa elävien yhteisöjen välillä kuin latvapurojen eliöyhteisöjen välillä, johtuen mahdollisesti latvapurojen epäennustettavasta ympäristövaihtelusta, joka estää voimakkaan yhtenevyyden kehittymisen eliöryhmien välille. Tämä heikentää ilmentäjälajeihin perustuvan lähestymistavan käyttökelpoisuutta paljon, koska suurin osa virtavesistä on juuri latvapuroja. Ongelmallista on myös paikallisen lajirunsauden varsin heikko yhtenevyys selkärangattomien, vesisammalien ja kalojen välillä. Yhtenevyys lajimäärissä oli kyllä tilastollisesti merkitsevää ekoregioiden yli ulottuvalla mittakaavalla, mutta lajimääräsuhteiden heikko ennustettavuus (regressioiden alhainen selityssaste) heikentää ratkaisevasti näiden ryhmien käyttömahdollisuuksia jokien biotisen kokonaismonimuotoisuuden ilmentäjänä. Ympäristötekijöiden käyttö ilmentäjälajien tai -lajiryhmien sijasta kokonaisbiodiversiteetin ilmentäjänä olisi eräs vaihtoehto, mutta pohjaeläinten, vesisammalien ja kalojen lajimäärien

osoittamat, keskenään varsin erilaiset suhteet ympäristömuuttujiin näyttäisivät estävän tämänkin oikotien käytön.

Tämän väitöskirjan päätulokset osoittavat, ettei ilmentäjälajeista ole merkittävää hyötyä jokiympäristöjen kokonaisbiodiversiteettiä selvitettäessä. Niinpä kattaville, useita jokien eliöryhmiä perusteellisesti luotaaville selvityksille ei näytä olevan halpoja, mutta hyvin toimivia vaihtoehtoja, ainakaan toimittaessa pienillä mittakaavoilla kuten yksittäisten jokisysteemien alueella.

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