

Jani Heino

Spatial Variation of Benthic
Macroinvertebrate Biodiversity
in Boreal Streams

Biogeographic Context and Conservation Implications

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Editors

Jukka Särkkä

Department of Biological and Environmental Science, University of Jyväskylä

Pekka Olsbo, Marja-Leena Tynkkynen

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ABSTRACT

Heino, Jani

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Yhteenveto: Pohjaeläinyhteisöjen monimuotoisuuden spatiaalinen vaihtelu pohjoisissa virtavesissä - eliömaantieteellinen yhteys sekä merkitys jokivesien suojelulle

Biodiversity patterns of most lotic animal and plant groups remain poorly known, which hinders the implementation of effective conservation, monitoring, and restoration programs. The major aims of this thesis were (i) to examine spatial variation in macroinvertebrate assemblage structure and diversity across natural environmental gradients, and (ii) to assess the utility of such information as the basis of stream conservation programs. Stream environmental characteristics and macroinvertebrate assemblage structure exhibited a clear, yet variable correspondence with regional delineations. The northernmost arctic-alpine and north boreal streams showed the highest degree of correspondence with ecoregion delineations, whereas streams of the southernmost hemiboreal ecoregion showed an opposite pattern. These findings were further supported by direct ordination analyses, showing that latitude was the best predictor of variation in macroinvertebrate assemblage structure across headwater streams. Such patterns were likely related to the fact that the distributions of ectothermic organisms, such as aquatic insects, are largely controlled by temperature. Latitudinal patterns in assemblage structure were further accentuated by geographical gradients in stream environmental conditions. However, there was no clear latitudinal gradient in local macroinvertebrate diversity. Local richness of macroinvertebrates showed a positive linear relationship with regional richness, though there was considerable within-region variation in local diversity accounted for by local environmental factors. These results suggest that the determination of macroinvertebrate diversity in streams constitutes a complex series of processes, which probably act differently on different ecological and taxonomic groups. Dissecting macroinvertebrate assemblages into taxonomic subgroups yielded additional insights into the biodiversity patterns in headwater streams. Although some pairwise comparisons of taxon richness and turnover diversity among mayflies, stoneflies, caddisflies, and chironomid midges were statistically significant, the correlations were overall low. It thus appears that no single group of stream insects can be used as an effective indicator of biodiversity in other taxa. By contrast, high degrees of congruence in provincial biodiversity were found among macrophytes, dragonflies, aquatic beetles, and fish. Patterns of decreasing species richness with latitudinal and altitudinal gradients were paralleled by variation in large-scale climatic conditions. There was, however, an exception to the general pattern: stoneflies showed an opposite pattern to those of the other groups in that their species richness was positively related to province altitude. Based on the main results of this thesis, stream conservation and bioassessment programs would benefit from regional stratification. Such spatial stratifications could, for instance, guarantee that (i) the conservation of lotic ecosystems is conducted within biogeographically and ecologically meaningful frameworks, and that (ii) predictive models for stream bioassessment are more robust and accurate than those generated for larger, more heterogeneous areas.

Key words: Aquatic insects; benthic invertebrates; bioassessment; community structure; conservation; environmental gradients; latitudinal gradients; species richness; streams.

J. Heino, Department of Biological and Environmental Science, University of Jyväskylä, P. O. Box 35, FIN-40014 University of Jyväskylä, Finland

Author's address

Jani Heino
University of Jyväskylä
Department of Biological and Environmental Science
P. O. Box 35
FIN-40014 University of Jyväskylä
Finland
E-mail: jheino@cc.jyu.fi

Supervisor

Docent Timo Muotka
Finnish Environment Institute
P. O. Box 140
FIN-00251 Helsinki
Finland

Reviewers

Associate Professor Dean Jacobsen
Freshwater Biological Laboratory
University of Copenhagen
Helsingørsgade 51
DK-3400 Hillerød
Denmark

Professor Jari Niemelä
Department of Ecology and Systematics
University of Helsinki
P. O. Box 65
FIN-00014 University of Helsinki
Finland

Opponent

Professor Richard K. Johnson
Department of Environmental Assessment
Swedish University of Agricultural Sciences
P. O. Box 7050
S-750 07 Uppsala
Sweden

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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 papers I to IV, being mainly responsible for data analyses and writing of the manuscripts. I was alone responsible for all phases of papers V and VI.

- I 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.
- II Heino, J., Muotka, T., Mykrä, H., Paavola, R., Hämäläinen, H. & Koskenniemi, E. 2002. Defining macroinvertebrate assemblage types of headwater streams: implications for bioassessment and conservation. Submitted.
- III Heino, J., Muotka, T. & Paavola, R. 2002. Determinants of macroinvertebrate diversity in headwater streams: regional and local influences. Submitted.
- IV Heino, J., Muotka, T., Paavola, R. & Paasivirta, L. 2002. Among-taxa congruence in biodiversity patterns: can stream insect diversity be predicted using single taxa groups? Submitted.
- V Heino, J. 2002. Concordance of species richness patterns among multiple freshwater taxa: a regional perspective. *Biodiversity and Conservation* 11: 137-147.
- VI Heino, J. 2001. Regional gradient analysis of freshwater biota: do similar biogeographic patterns exist among multiple taxonomic groups? *Journal of Biogeography* 28: 69-76.

1 INTRODUCTION

1.1 Biodiversity crisis and the stream biota

The degradation of natural habitats and consequent impoverishment of their biota is proceeding globally at a faster rate than ever before, and some have even called the present trend as the sixth mass extinction on the earth (Eldredge 1998). Mass extinction or not, a considerable proportion of biological diversity is being lost before we even knew what was lost, where it was located, or how the loss could have been prevented. In recent years, this crisis situation has been widely noticed by both the scientific community and the public, and considerable efforts are currently being devoted to revealing the patterns of biodiversity and identifying the imminent threats to its existence (Pimm et al. 1995, Gaston 2000, Purvis & Hector 2000, Sala et al. 2000). Acquiring such knowledge is indeed crucial if we are to find the means to conserve the most valuable components of natural variability and to reverse the prevailing trend of biodiversity loss. There is thus a great demand for biodiversity surveys across multiple spatial scales and ecosystems (Haila & Margules 1996).

Running waters are amongst the most threatened ecosystems (Allan & Flecker 1993, Dynesius & Nilsson 1994, Ricciardi & Rasmussen 1999). They are threatened by climate change, landscape alteration, degradation of in-stream habitat and water quality, and introduction of alien organisms (Allan 1995, Magnuson et al. 1997, Sala et al. 2000). Unfortunately, existing knowledge of the biodiversity of running water biota is heavily biased with regard to habitat types and taxonomic groups. For example, headwater streams have attained relatively little attention, yet headwaters harbour a highly diverse biota differing from those of larger rivers (Furse 2000, Malmqvist & Hoffsten 2000). Furthermore, contrary to the situation of large rivers, there are still pristine headwater streams left, although they are increasingly threatened by land-use changes, particularly forestry in boreal regions (e.g. Vuori & Joensuu 1996). Thus, pristine headwater streams may constitute important havens for threatened lotic biota, underscoring the importance of their conservation. While the preservation of wholesale biodiversity should be the foremost goal of

conservation, research activities are easily focused toward charismatic, large-sized organisms valued by the society. Undoubtedly, fish have attained this position in stream research, with the result that their biodiversity patterns are relatively well-known (e.g. Angermeier & Schlosser 1989, Oberdorff et al. 1995, Matthews 1998, Angermeier & Winston 1999), whereas the biodiversity exhibited by other stream organisms, e.g. micro-organisms, algae, bryophytes, and most invertebrates, remain less-well described.

Much of the biodiversity and ecosystem functioning in running waters are accounted for by benthic macroinvertebrates. Consisting of aquatic insects, worms, molluscs, and crustaceans, macroinvertebrate diversity in streams clearly exceeds that of fishes and macrophytes (Allan & Flecker 1993). Furthermore, benthic macroinvertebrates serve as important contributors to ecosystem functions, including detritus processing, animal-microbial interactions, herbivory, and energy transfer to the consumers at higher trophic levels (Allan 1995, Wallace & Webster 1996). Such functional versatility and ecological importance result from a multitude of adaptations that benthic invertebrates have evolved in response to the complex, spatially and temporally dynamic nature of running water habitats. Information on factors affecting the natural variability of macroinvertebrate assemblages is, therefore, not only vital for biodiversity conservation, but also as references for monitoring, restoring, and maintaining the quality of stream ecosystems (Rosenberg & Resh 1993, Palmer et al. 1997).

1.2 Spatial scale, environmental filters, and variability of lotic macroinvertebrate assemblages

A major aim of both community ecology and conservation biology is to reveal the factors determining the number, abundance, and identity of constituent species in biotic communities. This is not an easy task, considering that biotic communities are structured by a multitude of factors prevailing at various spatial and temporal scales (Wiens 1989, Menge & Olson 1990, Levin 1992). For instance, large-scale historical and climatic factors, including speciation and ice age glaciations, determine the composition of regional species pools (Ricklefs & Schluter 1993, Brown & Lomolino 1998). Regional species pool, in turn, sets the limits within which local communities are assembled (Ricklefs 1987, Tonn 1990, Cornell & Lawton 1992, Keddy 1992). Within regions, processes at the landscape-scale and within local systems eliminate species unable to pass the environmental constraints at different scales, eventually leading to the assembly of a local community. These considerations bear a close relationship to the relative importance of biotic versus abiotic control of community structure, and the degree to which local communities are random species combinations versus highly deterministic, locally-controlled subsets of species from the regional species pool (Gaston & Blackburn 2000, Godfray & Lawton 2001). Quantitative

information on the patterns and underlying processes of community assembly is, however, largely lacking for many ecosystems.

Streams are naturally hierarchical and extremely heterogeneous ecosystems across multiple spatial scales. The hierarchy of stream habitats consists of drainage systems, streams within drainage systems, pool-riffle sequences within streams, and small-scale microhabitats within riffles (Frissell et al. 1986). There is considerable variation in environmental factors at each spatial scale, ranging from differences in climate, geology, and vegetation among ecoregions and drainage systems to microhabitat configurations at the within-riffle scales. Viewing stream systems through such a hierarchy of environmental factors provides a highly applicable framework for assessing the assembly of stream communities. In this framework, environmental factors prevailing at hierarchical scales are regarded as screens that select subsets of species from the regional species pool to eventually coexist in a local assemblage (Tonn 1990, Poff 1997). Although the importance of multi-scale environmental control of local assemblage organization has been widely acknowledged, surprisingly few studies have simultaneously examined patterns and processes across spatial scales in streams (but see Crowl & Schnell 1990, Downes et al. 1993, Li et al. 2001). Furthermore, much of the traditional stream ecology has concentrated on complex phenomena at small spatial scales (Minshall 1988), while more generalized patterns are expected to emerge only across large spatial scales (Lawton 1999).

Understanding the geographical structuring of local assemblages yields important information for both basic ecological inquiry and environmental management. Considerable attention has thus recently been directed to classifying land areas into ecoregions (Wright et al. 1998, Abell et al. 2000), and testing whether patterns in stream biota correspond to such regional delineations (Whittier et al. 1988, Hawkins et al. 2000). A high ecoregion-assemblage correspondence would indicate that local assemblages are predominantly structured by large-scale factors, mediated either directly or indirectly through regional effects on stream habitats. Some studies have indeed found such correspondence between ecoregions and benthic assemblages, at least to a certain degree (Whittier et al. 1988, Harding et al. 1997, Sandin & Johnson 2000), but opposite findings are perhaps more prevalent (Quinn & Hickey 1990, Hawkins & Vinson 2000, Hawkins et al. 2000). However, a higher degree of correspondence could be expected among benthic assemblages and smaller regional units, i.e. subcoregions or drainage systems, simply because of the proximity effects (Van Sickle & Hughes 2000). Nevertheless, even studies reporting relatively high correspondence between regional delineations and benthic assemblages point out that variation within a region may be considerable, and that factors prevailing at smaller scales also need to be considered in order to explain variation in assemblage structure (e.g. Hawkins et al. 2000).

Within a drainage system, macroinvertebrate assemblages are shaped by stream size, physical habitat, and water chemistry (Hildrew & Giller 1994). A major pattern of assemblage structure follows the longitudinal gradient of lotic systems: species distributions, functional feeding group composition, and

diversity exhibit predictable changes from headwaters to large rivers downstream (Vannote et al. 1980, Ward 1998). For instance, taxonomically related species often show contrasting distributional patterns in relation to stream size (e.g. Edington & Hildrew 1990), longitudinal changes in the relative contribution of allochthonous and autochthonous production are paralleled by changes in functional feeding group composition (Vannote et al. 1980, Grubauch et al. 1996), and diversity peaks at the middle reaches of large rivers (Vannote et al. 1980, Minshall et al. 1985). However, although longitudinal changes have been documented for many river systems, the generality of such patterns have also been challenged (Winterbourn et al. 1981, Statzner & Higler 1985, Perry & Schaeffer 1987). Furthermore, even neighbouring headwater streams within a drainage system may exhibit contrasting water chemistry conditions and harbour widely differing macroinvertebrate assemblages (Townsend et al. 1983, Paavola et al. 2000). Thus, although streams do exhibit a continuum of biological variation, stream size is not the sole contributing factor, but just another actor in a far more complex play. A great challenge for stream ecology is to master such variability and to predict the influences of different factors on benthic assemblage structure.

High variability and complex relationships call for innovative approaches. One approach pertains to multivariate classification of assemblage types, and to testing of how well such classifications can be predicted using environmental variables (Wright et al. 1984, Ormerod & Edwards 1987). If effective and robust enough, biological classification would provide a highly useful reference system for bioassessment and conservation programs. However, classification systems are easily plagued by random factors, species-specific responses to the environment, and continuous variation of assemblage structure along environmental gradients (Chessman 1999, Hawkins & Vinson 2000). If assemblages were dividable into clearly discrete types, it would be straightforward to predict the structure and diversity of assemblage types in the landscape. Unfortunately, the opposite may often be the case. Therefore, other approaches should be, and have been, employed for community characterization, including testing of the correspondence of assemblage structure to landscape characteristics across spatial scales (e.g. Angermeier & Winston 1999, see also above), and combining regional stratification with biological characterizations (e.g. Johnson & Goedkoop 2000).

While considerable amounts of data have been accumulated on overall patterns of stream macroinvertebrate assemblage structure, surprisingly few multifactorial surveys have examined species richness patterns (Vinson & Hawkins 1998, Jacobsen 1999). However, because species richness is an important measure of biodiversity, in both basic and applied sense (Gaston 1996a, Currie et al. 1999), more attention should be directed to revealing spatial patterns of stream macroinvertebrate diversity. For instance, very little is known about regional-local richness relationships and latitudinal diversity patterns of stream macroinvertebrates (Vinson & Hawkins 1998, Jacobsen et al. 1997), although they have attracted considerable general interest both traditionally (e.g. Fisher 1960, MacArthur 1972) and recently (e.g. Karlson & Cornell 2002, Stevens & Willig 2002). Thus, acquiring such information for

stream macroinvertebrates would obviously facilitate comparisons of biodiversity patterns among different taxonomic groups, and among aquatic and terrestrial systems, thereby enhancing the effectiveness of conservation evaluation at global, regional, and landscape scales.

1.3 Aims of the thesis

This thesis focuses on the spatial patterns of macroinvertebrate assemblage structure and diversity across boreal stream ecosystems. The emphasis is on headwater streams, because their biodiversity remains generally poorly-known, yet they are sensitive to and severely threatened by landscape alteration and in-stream habitat changes. All subprojects were conducted at scales pertinent to the conservation, bioassessment, and management of freshwater ecosystems. The main objectives were to determine the correspondence of macroinvertebrate assemblages to regional delineations (I), to characterize assemblage types across large spatial scales (II), and to assess the utility of such classifications as the basis of stream conservation programs (I, II). I also tackled a more theoretical question about whether macroinvertebrate assemblages form clearly disjunct types or exhibit continuous variation along environmental gradients across a large spatial extent (II). Given the paucity of multifactor studies on stream macroinvertebrate diversity, I examined the correlates of macroinvertebrate richness at two spatial scales, i.e. across and within drainage systems, and specifically examined the relationship between regional (γ), turnover (β), and local (α) components of diversity (III). Furthermore, I tested for the congruence of diversity patterns among dominant stream insect groups (mayflies, stoneflies, caddisflies, chironomids) to determine if a single taxonomic group could be used as an indicator of wholesale lotic macroinvertebrate biodiversity (IV). Finally, I examined broad-scale concordance of species richness (V) and distribution patterns (VI) among five freshwater taxonomic groups (macrophytes, dragonflies, stoneflies, aquatic beetles, fish) to place the variation in stream macroinvertebrate assemblages to a bigger biogeographic picture.

2 MATERIALS AND METHODS

2.1 Study areas, spatial extent and regional delineations

The study areas ranged from Fennoscandia and Denmark (54°N to 71°N and 5°E to 32°E) (V, VI), through whole of Finland (60°N to 70°N and 20°E to 32°E) (I, II, III, IV), to single ecoregions and drainage systems (III, IV). Thus, the spatial extent varied from geographical ($>10^5$ km²), through regional (10^5 - 10^3 km²) to among-stream scale (10^3 - 10^2 km²). Ecoregions in papers I and IV were delineated according to Atlas of Finland (1988) and the Nordic Council of Ministers (1984). Finland was divided into five ecoregions, ranging from the hemiboreal region on the southern coast, through south boreal, middle boreal, and north boreal regions to the arctic-alpine region in the northernmost part of the country. The ecoregion delineations are based on climate, vegetation, geology, and land use, whereas subecoregion delineations in paper I were based on major watersheds and landscape characteristics, mainly following Atlas of Finland (1988). Regional delineations in paper III correspond to eight drainage systems, i.e. Kymijoki, Kyrönjoki, Kiiminkijoki, Oulujoki, Koutajoki, Muonionjoki, Kemijoki, and Tenojoki.

2.2 Field surveys and literature data

The subprojects of this thesis were based on two types of data. First, I analysed survey data from headwater streams, collected between 1992 and 2000 (I, II, III, IV). For these studies, only pristine and near-pristine headwater streams (base flow < 0.6 m³ s⁻¹, catchment area 1.0–60.0 km²) were sampled to diminish the potentially overriding effects of stream size. The data consisted of macroinvertebrate samples and simultaneous measurements of environmental characteristics. At each site, a two-minute kick-net sample was taken, aiming to cover most benthic microhabitats within a riffle-site of ca. 100 m². In practice, sampling effort was divided among differing current velocities, particle sizes,

and plant coverages. Environmental measurements incorporated riparian (tree composition, riparian integrity, and shading) and in-stream characteristics (current velocity, depth, particle size, and moss cover). Water samples were collected simultaneously to invertebrate samples, and they were analysed for pH, alkalinity, conductivity, total nitrogen, total phosphorus, iron, and colour by the regional environment centers of Finland. Data from a total of 156, 235, 120, and 110 streams were included in papers I, II, III, and IV, respectively.

Taxonomic resolution varied slightly among studies, but most taxa were generally identified to species or genus level. The most notable exceptions were chironomid and simuliid midges for which a family level identification was retained. In paper IV, however, chironomids were identified to species or genus level.

Second, I employed a macroecological approach (Brown 1995, Gaston & Blackburn 2000) and collected literature information for five freshwater taxa (macrophytes, stoneflies, dragonflies, aquatic beetles, and fish), and altitude and climatic characteristics, using the biogeographical provinces of Denmark, Sweden, Norway, and Finland as sampling units (V, VI). The data for stoneflies and aquatic beetles were already in provincial format, but for macrophytes, dragonflies, and fish, data were presented in distribution maps of variable resolution. For the latter three groups, the occurrence of each species was noted and the number of taxa in a province was thus obtained. I do not argue that all existing information on the distribution of these taxa was thus included, but rather I relied on the information given in easily-accessible sources to provide a broad picture of freshwater biodiversity patterns across the study area.

2.3 Specific methods

2.3.1 Regional delineations and stream macroinvertebrate assemblages (I)

Several types of multivariate techniques were employed to examine the correspondence between in-stream environmental variables, macroinvertebrate assemblages, and regional delineations (five ecoregions and 11 subcoregions).

Principal components analysis (PCA) was used to extract major gradients in stream environmental data. The principal components thus generated are uncorrelated composite variables, explaining most of the variation in the original data. A varimax rotation was used to maximize loadings of the original variables on each component to facilitate interpretation of the PCA (e.g. Legendre & Legendre 1998). Variables not conforming to normal distributions were log or arcsine-squareroot transformed prior to analysis. 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 is suitable for analysing ecological data sets for numerous reasons. NMDS performs well with data that are non-

normally distributed, are on arbitrary, discontinuous scales, or contain numerous zero values (McCune & Mefford 1999). Sorensen's coefficient based on $\log(x+1)$ transformed macroinvertebrate abundance data was used as the dissimilarity measure in NMDS. To diminish the chance of local optima (Legendre & Legendre 1998), several NMDS analyses were run, and the one with the lowest stress value was used as the starting configuration for the final analysis. Stress is a measure of departure from monotonicity in the relationship between distances in the original space and in the reduced ordination space (McCune & Mefford 1999). A three-dimensional solution of NMDS was used because the change in stress value was minor with further dimensions. Rare taxa were retained in the analysis because their omission may hinder the detection of meaningful ecological gradients in assemblage structure (Cao et al. 2001). Differences in the 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 the ecoregions and subcoregions the streams belonged to. Distances of stream sites to group (ecoregions or subcoregions) centers were calculated, and each site was allocated to the group it was closest to (Manly 1994). Logarithmic or arcsine-squareroot transformations of environmental variables were used, if necessary, 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 the assemblages belonged to. 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. In cross-validation, each site is removed in turn from the data set, the model is re-constructed, and the removed site is tested against the model.

The classification strength (CS) of the ecoregions and subcoregions was tested using a randomization method following Van Sickle (1997). The mean of all between-class similarities (B) and the within-class mean similarity (W) were first calculated using Sorensen similarity coefficients. The difference between these similarities, i.e. classification strength ($CS = W - B$), was then calculated. Values of CS range from 0 to 1, with values near 0 indicating that sites are randomly assigned to classes. Randomization tests, whereby the test statistic was recalculated for each of 1000 random reassignments of sites to groups, were used to examine if observed CSs differed from those obtained from randomized data sets (Van Sickle 1997).

Multi-response permutation procedure (MRPP) was performed to examine if there were differences among the ecoregions and subcoregions in the functional feeding group composition of macroinvertebrate assemblages. MRPP is a nonparametric method designed for testing differences in assemblage structure among a priori defined site groups (Zimmerman et al. 1985). The significance of the null hypothesis of no differences among groups was assessed by a Monte Carlo permutation procedure with 1000 permutations.

Indicator value method (INDVAL) (Dufrene & Legendre 1997) was used to detect significant indicator taxa for ecoregion delineations. This method is based on the comparison of relative abundances and frequencies of occurrence of taxa in different site groups, and it identifies indicator taxa that vary more between groups than would be expected by chance. The indicator value varies from 0 to 100, and it attains the maximum value when all individuals of a species occur at all sites of a single group. The significance of the indicator value for each species was tested using a Monte Carlo randomization test with 1000 permutations.

2.3.2 Definition of macroinvertebrate assemblage types (II)

Macroinvertebrate assemblage types of headwater streams were delineated using multivariate techniques to assess their utility for assemblage-level conservation. Furthermore, direct ordination analyses were performed to examine assemblage-environment relationships.

Two-way indicator species analysis (TWINSpan) was used to classify streams according to their species composition, i.e. to produce assemblage types. TWINSpan is a classification method based on reciprocal averaging (van Tongeren 1995). It has been criticized, because it assumes that a single gradient dominates the data, and because the rather arbitrary cutting of the major axis may lead to the separation of sites with relatively similar species composition (Belbin & McDonald 1993, Legendre & Legendre 1998). Despite its drawbacks, TWINSpan has been shown to perform even better than alternative clustering methods in classification of benthic macroinvertebrate assemblages (Moss et al. 1999). To validate the use of TWINSpan, I also analysed the same data set with an alternative clustering method, UPGMA, ending up with site groupings highly similar to those produced by TWINSpan.

The validity and strength of TWINSpan classifications were further examined using NMDS, MRPP, and INDVAL. A three-dimensional NMDS solution was run for the visual examination of whether TWINSpan groups represented truly discrete site groupings. Sites belonging to a single TWINSpan group were encircled by ellipses incorporating 90 percent of sites to examine the degree of among-group overlap. MRPP was used to test if sister groups at each TWINSpan division differed statistically from each other. Sorensen's coefficient was used as the distance measure in all MRPP analyses. In addition to statistical significance, the strength of among-group differences was assessed using MRPP's R statistic: R attains its maximum value 1 when all sites in a group are identical to each other, $R = 0$ when heterogeneity within groups equals that expected by chance, and $R < 0$ when heterogeneity within groups exceeds that expected by chance (McCune & Mefford 1999). Lastly, INDVAL was used to detect the best indicator taxa for each group at the first and fourth TWINSpan division levels.

Two methods were used for examining the relationships between assemblage structure and environmental factors. First, a stepwise DFA was

done to examine which environmental variables best discriminated among the site groups at the first and fourth TWINSpan division levels. DFA was also employed to examine how well environmental variables could predict the memberships of sites in each TWINSpan group. Second, canonical correspondence analysis (CCA) was performed to examine more closely the relationships among the environmental gradients, assemblage types, and their indicator species. CCA is a constrained ordination method that concomitantly analyses both species and environmental data by combining ordination and multiple regression (ter Braak 1995). A forward selection of environmental variables was used. At each step, the significance of the variable to be included in the model was tested using Monte Carlo randomization test with 1000 permutations.

2.3.3 Regional and local influences on macroinvertebrate diversity (III)

Relationships among different components of diversity, i.e. regional (γ), turnover (β) and local (α) diversity, were examined across and within eight drainage systems defined as regions.

Regression analysis was the main technique used for assessing the relationships between regional richness (RSR), local richness (LSR), and local environmental factors. Both linear and second-order polynomial regressions were used to examine whether mean LSR and RSR exhibited a linear or an asymptous relationship. For this purpose, the significance of the slopes of two competing regression models were examined following Griffiths (1999): if the second order term (bx^2) in the polynomial regression is non-significant, but the slope (bx) of the linear model significant and the intercept (a) non-significant, then LSR exhibits a linear relationship with RSR. Furthermore, forward stepwise regression analysis was used to examine the relative contributions of RSR and stream environmental variables to LSR. This analysis selects variables in order of importance: the first independent variable to enter the model explains most of variation in the dependent variable, the second one most of the remaining variation, and so forth. The analysis is terminated, when the next variable to enter does not account for a significant proportion of remaining variation (Sokal & Rolf 1995). Similar stepwise regressions were performed to explore which environmental factors best explain variation in macroinvertebrate richness within each of the eight regions studied.

The relationship between RSR and turnover diversity was assessed using Pearson correlation. A beta-diversity index was first calculated for each region using the formula of Harrison et al. (1992): $\beta_2 = [(S/\alpha_{\max} - 1)/(N - 1)] \times 100$, where S is the total number of taxa in a region, α_{\max} is the maximum number of taxa recorded at a single site, and N is the number of sites. Thus, β_2 ranges from 0 to 100, and measures the degree by which regional richness exceeds the maximum local richness. However, β_2 is directly dependent on the number of taxa in a data set, and thus can generate spurious correlations with RSR. Therefore, the average among-site dissimilarity in taxon composition was

calculated for each region to obtain an index of turnover that was mathematically independent of RSR. Sorensen's dissimilarities were calculated among all streams in a region using the formula: $\beta_{\text{Sor}} = 1 - 2W/(A + B)$, where W is the sum of shared taxon occurrences and A and B are the sums of taxa in individual sample units. Each pairwise dissimilarity and the average among-site dissimilarity for each region thus range from 0 to 1, with high values indicating high turnover among sites.

2.3.4 Single taxonomic groups as biodiversity indicators (IV)

The utility of a single stream insect group (mayflies, stoneflies, caddisflies, chironomids) in predicting the taxon richness, turnover, and assemblage composition of other groups was examined across and within four ecoregions.

Variability in the original insect and environmental matrices were reduced using ordination techniques. Detrended correspondence analysis (DCA) was run for each taxonomic group to obtain a measure of taxa turnover among sites. The gradient length of the first axis of DCA describes the degree of taxon turnover among sites: sites separated by a gradient length of more than 4 SD units have no species in common (Legendre & Legendre 1998). Due to the controversy surrounding the use of DCA (Peet et al. 1988, Jackson & Somers 1991), only the first axis was considered. PCA was used to extract major gradients in the original stream environmental data, and the site scores on the resulting components were subsequently used as independent variables, along with latitude and longitude, in regression analyses. Stepwise regression analysis was the main technique used to model variation in richness and turnover diversity (DCA axis 1 site scores) for each taxonomic group.

Concordance of diversity patterns among different insect groups was examined using Spearman rank correlations and Mantel tests. Pairwise correlations were calculated for taxon richness and turnover diversity. Mantel tests were done to examine if different insect groups showed congruent overall assemblage patterns. Mantel test evaluates the congruence between two distance matrices from the same set of sample units, without reducing the underlying species space (McCune & Mefford 1999). For this purpose, matrices based on Sorensen's coefficient were constructed from the original sites-by-taxa matrices for each insect group, and pairwise Mantel tests were subsequently performed. The resulting values of the statistic r_m are similar to those of Pearson correlation coefficient, varying from -1 to 1. The significance of the relationships between matrices for different taxonomic groups was tested using Monte Carlo randomization test. Spearman rank correlations and Mantel tests were performed for the whole data set, and separately for four ecoregions.

Three measures of β -diversity were calculated to elucidate which insect group showed most turnover across sites. First, the total inertia of the DCA was used as an index of overall variability for each data set (see Ohmann & Spies 1998). Second, the β -diversity index of Whittaker (1960) was calculated using the formula: $\beta_w = (S/\alpha) - 1$, where S is the total number of taxa in a data set, and

α is mean number of taxa recorded at a single site. Third, β_2 index (Harrison et al. 1992; see above) was also calculated for each taxonomic group.

2.3.5 Concordance of species richness patterns at large spatial scales (V)

Among-taxa concordance in species richness and richness-environment relationships of macrophytes, dragonflies, stoneflies, aquatic beetles, and fish were examined using simple correlation and regression techniques.

Prior to statistical analyses, species richness counts were corrected to equal province size following Lahti et al. (1988) and Kouki et al. (1994). Forward stepwise regression analysis was used to examine the relationships of provincial climate, altitude, and geographical location with the species richness of each taxonomic group. A Bonferroni correction (Sokal & Rolf 1995) was used for both entry and removal criteria for independent variables in the regression analysis: a conservative $P = 0.05/6$ was used because there were six independent variables. Among-taxa concordance was examined using Spearman rank correlation.

Because the data points in this type of analyses are spatially autocorrelated, traditional significance tests must be interpreted cautiously (Legendre 1993, Birks 1996, Carroll & Pearson 1998). Therefore, I emphasized the strength of the environment-richness and among-taxa relationships, i.e. coefficients of determination and correlation coefficients, respectively.

2.3.6 Biogeographic distribution patterns of freshwater organisms (VI)

Multivariate techniques were employed to examine congruence in the distribution patterns and provincial species composition of macrophytes, dragonflies, stoneflies, dytiscid beetles, and fish.

A TWINSPLAN with three division levels, resulting in eight province groups was done for each taxonomic group to facilitate the visual examination of among-taxa congruence. Mantel tests were performed among all taxa pairs to test for the significance of among-taxa congruence. For this purpose, dissimilarity matrices based on Sorensen's coefficient were constructed from the original species-by-province matrices, and pairwise Mantel tests were subsequently performed. The significance of each pairwise relationship was tested by Monte Carlo randomization procedure.

Canonical correspondence analysis (CCA) was used to examine the relationships of simple climate (mean July temperature, duration of snow cover, length of growing season) and geographical (altitude, latitude, longitude) variables with provincial species composition of each taxonomic group. Interset correlations of the variables with the first two CCA axes were used for this purpose. Furthermore, a series of four CCAs was run for each taxonomic group to examine the relative contribution of climate and geography to species distribution patterns (Borcard et al. 1992, Legendre & Legendre 1998): (i) CCA of species matrix constrained by climate variables; (ii) CCA of species matrix

constrained by geographical variables; *(iii)* CCA of species matrix constrained by climate variables, with geographical variables as covariables; and *(iv)* CCA of species matrix constrained by geographical variables, with climate variables as covariables. At each step, the sum of all canonical eigenvalues was divided by the total inertia (=variance) of species data to obtain the proportion of explained variation. Total amount of explained variation of species data was obtained by summing steps *(i)* and *(iv)*, or steps *(ii)* and *(iii)*. Variation in the provincial species composition of each taxonomic group was then partitioned into four fractions following Borcard et al. (1992): climatic (step *(iii)* above), shared climatic and geographical (step *(i)* - step *(iii)*, or step *(ii)* - step *(iv)*), geographical (step *(iv)*), and unexplained variation. Percentage unexplained variation equals to 100 - explained variation. Although widely applied for various purposes in recent years (e.g. Heikkinen & Birks 1996, Ohmann & Spies 1998, Paszkowski & Tonn 2000, Pozzi & Borcard 2001), the variance partitioning approach should be used with certain caution. Økland (1999) cautioned against using the total inertia as the basis of the partial CCAs and recommended that one should instead concentrate on examining the relative proportions of different predictor sets of the explained variance. While bearing this in mind, I partitioned variation into the four fractions as above, because one of my aims was to make among-taxa comparisons of the proportions of explained versus unexplained variation.

3 RESULTS AND DISCUSSION

3.1 Regional delineations and stream macroinvertebrate assemblages (I)

A relatively close match between ecoregions and stream environmental characteristics was observed, but macroinvertebrate assemblages exhibited a slightly lower degree of correspondence with ecoregion delineations. In general, for both environmental characteristics and macroinvertebrates, correct DFA classifications of streams decreased from the near-pristine arctic-alpine ecoregion to the more human-altered southern ecoregions, a pattern similar to that found previously for Swedish streams (Sandin & Johnson 2000). Compared with ecoregion level, stream classifications at the subcoregion level produced more variable results, which was likely related to the higher number of classes in this analysis. Nevertheless, significant regional differences were found for assemblage structure, functional feeding group composition, and taxon richness at both levels of consideration.

Regional differences in the prediction success of streams may be attributable to (i) natural or (ii) anthropogenic factors. For instance, hemiboreal streams showed a poor fidelity to their actual region both in terms of environmental characteristics and macroinvertebrate assemblages. In this ecoregion, the landscapes have been modified by forestry and agriculture for a longer time than in any of the other ecoregions. The conversion of natural vegetation into conifer-dominated forests may have modified the streams and their biotic communities to resemble those in the south boreal and middle boreal ecoregions. These patterns occurred regardless of the fact that we sampled only near-pristine streams, suggesting that regional-scale landscape alteration may modify stream faunas. By contrast, in the north boreal and arctic-alpine ecoregions, the variable relationships of stream macroinvertebrate assemblages to subcoregions were more likely driven by natural within-subregion variation in environmental conditions, paralleled by similar variation in macroinvertebrate assemblage structure. For instance, clear-water streams with riparian zones dominated by deciduous trees occur in each subregion of

the north boreal and arctic-alpine ecoregions, and these streams were highly similar in macroinvertebrate assemblage structure, regardless of their location.

The relative contribution of different functional feeding groups (FFGs) to lotic macroinvertebrate assemblages are typically connected with variation in stream size (Vannote et al. 1980, Grubauch et al. 1996), though abundances of FFGs may exhibit considerable variation even among similar-sized streams. In our study, the relative abundances of FFGs differed among ecoregions and subecoregions, reflecting among-region variation in stream characteristics. For instance, scrapers were generally abundant in the subecoregions 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). By contrast, brown-water streams in the middle boreal ecoregion were characterised by low numbers of scrapers and a high abundance of shredders, suggesting that shredders are unaffected by water colour, and respond more to riparian allochthonous inputs. Alternatively, given that the importance of the link between riparian characteristics and stream macroinvertebrates may be somewhat overestimated, variation in shredder versus scraper abundance may in fact reflect the acid-tolerance of macroinvertebrate taxa rather than any feeding categorization. For instance, stoneflies (mostly shredders) are known to be more tolerant of acidic waters than mayflies (mostly scrapers).

The predominance of filterers in the hemiboreal streams was probably related to lake connections, because streams in this region are typically short and connect a series of lakes to each other. Thus, they are continuously fed by lake-derived organic material, which forms an abundant and predictable resource base for filter-feeding invertebrates. Such patterns emerged regardless that we avoided true lake outlets (see Malmqvist & Eriksson 1995), suggesting long-distance influences of lakes on riffle-dwelling macroinvertebrates.

Despite obvious congruence among ecoregions and macroinvertebrate assemblage characteristics, the presence of wide within-region variability suggests that regional delineations do not alone provide a satisfactory background for stream management programs. Rather, a combination of regional delineations, landscape characterization, and in-stream environmental predictors would probably yield a better framework for the characterization of macroinvertebrate assemblages of boreal headwater streams. Similar arguments for a tiered bioassessment approach have been presented for streams (Hawkins et al. 2000, Sandin & Johnson 2000) and lakes (Johnson 2000, Johnson & Goedkoop 2000) elsewhere.

3.2 Definition of macroinvertebrate assemblage types (II)

Benthic macroinvertebrate assemblages of boreal headwater streams were not dividable into discrete types (II). Rather, our results demonstrated the continuous nature of macroinvertebrate assemblages, despite wide ranges in environmental conditions and relatively extensive geographical scope of the

study. It was obvious that the assemblage types generated by TWINSpan comprised just parts of the continuum of biological variation across the streams, as evidenced by the ordination analyses and MRPP. Furthermore, there were only a few good indicator species for any of the assemblage types, and even the best indicators did not occur at all sites of, or were not confined to, a given assemblage type. According to CCA, variation in assemblage structure was primarily related to geographical location, water acidity, and water colour, corroborating findings of former studies on macroinvertebrates of Fennoscandian streams (Malmqvist & Mäki 1994, Sandin & Johnson 2000, Paavola et al. 2000) and those elsewhere (Townsend et al. 1983, Wright et al. 1984, Reynoldson et al. 2001).

The absence of discrete macroinvertebrate assemblage types in boreal headwater streams may be attributable to a number of reasons. For instance, benthic macroinvertebrates are known to have broad environmental tolerances (e.g. Malmqvist & Hoffsten 2000) and exhibit species-specific responses to environmental gradients (e.g. Hawkins & Vinson 2000). Consequently, only a few species are restricted to a similar range of conditions. Such species-environment relationships inevitably lead to non-disjunct assemblage types. Furthermore, if a system experiences high levels of unpredictable disturbances and its biota has a high capability of dispersal, assemblage structure should indeed be highly variable (Palmer et al. 1996). Boreal headwater streams are typically disturbed by unpredictable floods, droughts, and bottom freeze (Malmqvist & Hoffsten 2000), harbour species with widely differing dispersal capabilities (Malmqvist 2000), and are often relatively isolated from the nearest source of potential colonists compared with larger rivers. Therefore, random local extinctions and recolonizations might lead to assemblage structure different from that expected based on water chemistry and physical habitat at the time of sampling. Such stochastic events may be common in headwater streams, yet their existence and potential influence on assemblage structure may be difficult to quantify and predict. Obviously, studies determining the extent and predictability of short-term temporal and year-to-year variation in stream macroinvertebrate assemblages are badly needed. Before such knowledge is acquired, caution must be exercised when drawing conclusion from single-sample surveys of stream assemblages (see also Wiens 1981).

How should continuous and random variation in assemblage structure be controlled for in bioassessment and conservation programs? Given the major patterns of geographical variation in assemblage structure, a regional stratification might provide a useful background for the bioassessment and conservation of boreal headwater streams (I). For instance, regional stratification might allow mastering a part of the natural or sampling-based random variation in assemblage structure, based on the premise that headwater streams close to each other should harbour, on average, assemblages more similar to each other than to those far from them, and should respond similarly to environmental changes. A combination of regional delineations and assemblage prediction within an ecoregion might thus provide the most suitable framework available for stream bioassessment. Such a combination could, for instance, increase the robustness of predictive models, leading to

more parsimonious models than those generated for larger areas (e.g. Johnson & Goedkoop 2000). Moreover, within-region predictive models for headwater streams should preferably be based on approaches that do not rely too heavily on classification of sites (e.g. Chessman 1999). Finally, from the biodiversity perspective, a priori regional stratification would, by providing a physical surrogate of biological variation, guarantee that assemblages in different geographical regions acquire enough conservation attention.

3.3 Regional and local influences on stream macroinvertebrate diversity (III)

Macroinvertebrate richness (LSR) in headwater streams showed a linear relationship to regional richness (RSR), without any sign of curvilinearity. This finding thus suggests that regional-scale processes set the upper limit to LSR (Cornell & Lawton 1992, Srivastava 1999), at least within the observed range of RSR. Such a relationship between RSR and LSR of stream invertebrates comes as no big surprise, because they live in a frequently disturbed habitat and exhibit high degrees of dispersal by drifting or flying: these habitat or organismal characteristics should increase regional control of local communities (Palmer et al. 1996). Such characteristics are also typical of boreal headwater streams, which are disturbed by floods, droughts, and bottom freeze. Furthermore, many invertebrate taxa inhabiting boreal streams possess considerable dispersal ability, thereby facilitating rapid post-disturbance colonization of denuded stream areas. Therefore, an average site in a diverse region should, by chance, sample more taxa than one in a species-poor region. Furthermore, although competitive interactions among lotic macroinvertebrates may be strong at very small scales (e.g. McAuliffe 1984, Hemphill 1988), they rarely result in the exclusion of inferior competitors at the riffle scale (but see Kohler & Wiley 1997), suggesting that macroinvertebrate communities rarely attain saturation even in high-diversity regions.

Despite that RSR sets the upper limit to LSR, stream conditions eventually determine how large a portion of the regional pool exists in any local community. Considering that no two stream riffles are alike, and that within-region variation in local stream conditions may be considerable, strong effects of local factors on macroinvertebrate communities should be obvious. This was likely the reason for variable local richness patterns among streams in each region, and concurs with former studies showing that streams in close proximity to each other but differing in water chemistry may harbour macroinvertebrate assemblages differing widely in structure and taxonomic richness (Townsend et al. 1983, Hildrew & Giller 1994, Malmqvist & Mäki 1994, Paavola et al. 2000). Nevertheless, our results suggest that stream abiotic factors are secondary in importance to RSR in explaining LSR of stream macroinvertebrates.

Among-region differences in LSR and RSR could also portray regional differences in stream environmental conditions. Streams in some of the study regions drain landscapes dominated by peatlands, being thus acidic and humic, and harbouring communities with low species richness (I). Uniformly adverse stream conditions in these regions may lead to low local richness, and low species turnover among sites, eventually affecting the size of the regional species pool. Thus, these findings suggest that the determination of taxon richness of stream macroinvertebrates is not necessarily only from regional to local, but local factors may also have feedback effects on RSR (see Cornell 1993, Vinson & Hawkins 1998, Huston 1999). Alternatively, one may ask which factors are truly regional and which are truly local. Stream water chemistry reflects regional geology, being thus more a regional factor, but it also is in an intimate contact with the organisms at the local arenas, being thus a local factor. This leads to somewhat circular reasoning, and to the "chicken-and-egg" problem.

Different factors were related to variation in macroinvertebrate richness within each region. In general, factors most strongly correlated with taxon richness reflected either spatial heterogeneity, adverse local environmental conditions, or could be regarded as limiting the resource base for macroinvertebrates. Macroinvertebrate richness showed generally positive relationships to stream width, moss cover, and pH, all of which have been previously identified as important correlates of macroinvertebrate diversity (Hildrew & Giller 1994, Vinson & Hawkins 1998). Moreover, an interesting finding was the positive relationship of stream water nitrogen concentration with macroinvertebrate richness in the northernmost region (70°N) of this study. Nutrient concentrations in these subarctic streams ranged from very low to moderate, and they likely limit ecosystem productivity and biotic communities. Even slight increases in nutrient concentrations could increase algal productivity (Peterson et al. 1993, Perrin & Richardson 1996), and thus contribute indirectly to macroinvertebrate richness in subarctic streams. In contrast, no significant relationships between stream water nutrients and macroinvertebrate richness were found in the regions further south, implying that nutrients did not generally limit stream biodiversity.

Since RSR was the primary factor explaining LSR, future studies should also address the determinants of RSR of stream macroinvertebrates. Latitudinal gradients in climate, environmental productivity, and ice age history have often been proposed as probable explanations to differences in species richness among regions at large spatial scales (Currie 1991, Huston 1994, Rosenzweig 1995). However, studies on stream invertebrates have generated equivocal conclusions regarding among-region differences in species richness in general, and latitudinal species richness gradients in particular (Hildrew & Giller 1994, Jacobsen et al. 1997). This, however, does not mean that there are no among-region differences in stream macroinvertebrate diversity. Regional-scale differences do exist, but they may not always be detected by lumping all macroinvertebrate taxa together, and they do not necessarily follow any consistent latitudinal trends. For instance, the regional diversity of stoneflies increases with increasing latitude, whereas caddisflies exhibit an opposite

pattern across Finland, and these patterns are also weakly seen at the local scale (IV, V). Possible correlates for variation in RSR between regions in the present study include regional differences in altitudinal, geological, and vegetation heterogeneity, which could in turn affect regional stream riffle area and the variety of stream types within a region. These might affect regional-scale extinction probabilities and the degree of species turnover among sites within a region (Cornell & Lawton 1992). Although we did not find a statistically significant relationship between RSR and β -diversity, differences in within-region environmental heterogeneity could still potentially account for variation in RSR. Admittedly, the above reasoning remains speculative, but it should at least provide testable hypotheses for future studies utilizing more sophisticated multi-scale sampling designs and encompassing regions differing in areal extent and the size of the regional species pool.

3.4 Single taxonomic groups as biodiversity indicators (IV)

The utility of single taxonomic groups as overall biodiversity indicators has recently attracted increased attention (Prendergast et al. 1993, Gaston 1996b, Flather et al. 1997, McGeoch 1998), but such studies for stream organisms are lacking. To evaluate the utility of dominant lotic insect taxa for such purposes, the congruence of the biodiversity patterns among mayflies, stoneflies, caddisflies, and chironomid midges was examined across and within ecoregions. Different taxonomic groups exhibited slightly different relationships to environmental gradients, leading to low degrees of congruence. Although several among-taxa correlations for species richness, turnover, and assemblage composition were statistically significant, correlation coefficients remained variable and generally low ($r < 0.5$) both in the within-ecoregion and the combined data. Therefore, present results do not support the use of a single taxonomic group as a biodiversity indicator in boreal headwater streams, due to their limited predictive power (see Gaston 1996b, Flather et al. 1997).

Mechanisms generating congruence in diversity patterns among taxa can be divided into four general classes (Gaston & Williams 1996). High degrees of congruence may stem from (i) random draw of taxa from the surrounding regional species pool, (ii) similar responses of different taxa to the same environmental gradient; (iii) spatial covariance in environmental factors independently accounting for diversity variation in different taxa; or (iv) biotic interactions among taxa. Any of these mechanisms could potentially explain the covariation, or rather lack of it, in the diversity patterns of stream insect taxa. The present results, however, refer to the importance of among-taxa differences in (i) and (ii).

Contrasting regional-local richness patterns may lead to low degrees of among-taxa congruence when local stream systems are compared. This may indeed be one of the reasons why the congruence in species richness among the studied stream insect groups was low. For instance, stoneflies attain high regional species richness in the northernmost regions of the study area, unlike

many other groups of freshwater organisms (V). This was also suggested by the present findings that the local richness of stoneflies was positively related to latitude, whereas that of caddisflies exhibited an opposite latitudinal trend. Even if the relationship among regional and local richness of stream insects has not been widely examined (Vinson & Hawkins 1998), the present results and evidence from other studies (III) suggest that the determination of lotic insect diversity constitutes a complex series of processes, and that no single pattern applies to all taxonomic groups.

The lack of strong congruence may also be due to differential responses by each insect group to local environmental gradients. Such patterns were indeed seen in the environmental determinants of species richness and assemblage turnover. For instance, species richness and turnover in mayflies were negatively related to gradients in water acidity and humic content, and the same was largely true for chironomid midges. By contrast, the diversity of stoneflies and caddisflies showed more complex relationships to geographical location and local environmental gradients. However, the amount of variation explained was very low for stoneflies and chironomids, implying that factors not measured here were probably affecting these taxa. Therefore, it appears that the environmental gradients captured by these four taxa are simply too different to allow a single group to be used for modelling variation in the diversity of the other groups.

What are the implications of these results for biodiversity inventories? The results suggest that no single group of stream insects can be used as a reliable indicator of diversity variation in other taxa in boreal streams. This finding is somewhat discouraging regarding cost-effective biodiversity inventories, and suggests that a reliable picture of stream insect biodiversity can only be obtained by examining all taxonomic groups. This is not an easy task, considering that a high proportion of insect diversity in lotic systems is comprised of taxonomically and ecologically poorly-known groups such as chironomid midges. Nevertheless, assessment and prediction of lotic biodiversity require that such difficult taxa are given increased attention.

3.5 Biogeographic background and among-taxa congruence (V and VI)

Large-scale variation in species richness and distribution patterns were highly concordant among macrophytes, dragonflies, beetles, and fish (V, VI). Such concordance likely resulted from common responses of different taxonomic groups to large-scale climatic factors. Species richness in these groups decreased with increasing latitude and altitude, and most of the variation was accounted for by mean July temperature. By contrast, stoneflies showed weaker negative relationships with the other taxonomic groups, and their species richness correlated positively, albeit weakly, with province altitude. Nevertheless, the combined species richness of all five taxonomic groups showed a strong

positive relationship with mean July temperature (V). However, most of the variation in provincial species composition remained unexplained, suggesting that other factors were also affecting these taxa (VI). Although seemingly trivial, documentation of such patterns for freshwater taxa has important implications for revealing global patterns of diversity, understanding the organization of local communities, and for conserving regional biodiversity.

Climatically-controlled species richness gradients in macrophytes, dragonflies, beetles, and fish generally concurred with those found for various plant and animal groups globally (Adams & Woodward 1989, Currie 1991, Huston 1994, Brown & Lomolino 1998) and across the present study area (Pedersen 1990, Väisänen & Heliövaara 1994). Such patterns are to be expected for freshwater taxa, given that the distributions of ectothermic organisms are largely governed by temperature (Vannote & Sweeney 1980, Ward & Stanford 1982). However, it is difficult to fully disentangle the effects of climate, vegetation, and history as determinants of geographical species richness gradients in freshwater taxa. For instance, climatic patterns are paralleled by the zonation of terrestrial vegetation, and terrestrial-aquatic linkages are known to affect the distribution of freshwater taxa. Further, historical influences in terms of ice age glaciations may modify the distribution patterns of freshwater taxa by affecting regional extinction and subsequent recolonization of denuded areas (Pielou 1991). However, considering that taxa with presumably low dispersal capability, e.g. stoneflies, show considerable diversity in the high latitude and altitude areas of Fennoscandia that have had the least time to recuperate from the latest glaciation, history does not seem to be the only major determinant of species richness gradients of the taxa studied (V, see also Birks 1996). Although historical factors contribute to the distribution of individual species (VI), it appears that most freshwater taxa as groups have attained their distributional limits to correspond to present-day climate, vegetation characteristics, and local habitat availability across the study area.

Despite revealing important patterns, this kind of macroecological studies are not without problems (see Gaston & Blackburn 1999, Ricketts et al. 1999). For instance, all areas are never surveyed with a similar effort, the quality of data may differ among taxa, and the literature data used for a study may not cover all existing information. Undoubtedly, the present studies were plagued by such facts, the degree of which is difficult to evaluate. However, even if more accurate distributional data for freshwater taxa accumulates, the main patterns likely remain the same: most freshwater taxa do show congruent biodiversity patterns at large spatial scales across the study area. Nevertheless, finding a pattern does not mean an end to the inquiry of the determinants of freshwater biodiversity in an area, but rather only a crude starting point for more detailed analyses. More detailed distribution data (e.g. 50 km x 50 km grid) could help us answer more explicit questions about the relationships among climate, landscape characteristics, and freshwater biota, with important repercussions for the conservation of biodiversity in the study area.

4 IMPLICATIONS FOR CONSERVATION AND BIOASSESSMENT OF BOREAL STREAMS

A major challenge for ecology lies in determining how many assemblage types there are, where they are located, and what factors determine their characteristics. Such definitions are also becoming increasingly urgent for conservation biologists, given the notion that conservation of single species and populations do not provide a necessary basis for effective biodiversity conservation (Franklin 1993, Angermeier & Schlosser 1995). Therefore, increasing interest has recently arisen in the typification of assemblages and landscapes within which they are embedded. Similarly, considerable attention has been directed to assemblage classification for the assessment of water quality impairment (Wright et al. 1998, Reynoldson et al. 1997, Hawkins et al. 2000). Thus, stream macroinvertebrates, for instance, are regarded as either biodiversity indicators or environmental indicators (cf. McGeoch 1998). Although these two avenues of research have developed somewhat independently, their basic goals are the same: to predict what kind of assemblages are there in natural systems and how anthropogenic influences may modify their structure. Because of the largely shared needs of biodiversity conservation and bioassessment, a general framework could be applied for both.

What should such a framework incorporate? Considering macroinvertebrate assemblages in boreal lotic systems, such a scheme could be based on three phases: 1) regional stratification, 2) habitat type stratification, and 3) biological characterization of assemblage types and evaluation of conservation value. Stratification by region and habitat type would likely guarantee that biological characterizations of stream assemblages are conducted within ecologically meaningful units. For instance, ecoregions provide the biogeographical context for local assemblages in terms of climate, terrestrial-aquatic linkages, and the species pool from which local communities are assembled, and stratification by habitat type (i.e. drainage characteristics) further specify these relationships. Such stratifications are supported by a large body of evidence showing that ecological communities in general (Tonn 1990, Cornell 1999, Huston 1999), and stream assemblages in particular (Minshall

1988, Poff 1997, Cooper et al. 1998, III), are structured by factors prevailing at multiple spatial scales, and that local assemblage organization cannot be understood without regard to large-scale processes (Ricklefs & Schluter 1993, Gaston & Blackburn 2000).

For bioassessment, stratification by ecoregion and habitat type could provide a suitable background for a preliminary partitioning of variation in assemblage structure (Hawkins et al. 2000, Sandin & Johnson 2000, I). Such a basis for bioassessment would guarantee that regional predictive models are robust, incorporate only a parsimonious set of explanatory variables, and are not overwhelmingly ruled by geographical location. Without ecoregion stratification, geographical location, rather than environmental variables, would almost certainly emerge as the major correlate of macroinvertebrate assemblage structure (II). Similarly, the well-known differences in macroinvertebrate assemblage structure among headwater streams, large rivers, and lake outlets (Malmqvist & Mäki 1994, Malmqvist & Eriksson 1995, Furse 2000, Paavola et al. 2000), would obscure the relationships between assemblage structure and smaller-scale physicochemical factors. Water chemistry and local habitat characteristics would, however, tell us much about species-environment relationships, thus yielding important information for defining the reference conditions.

A priori regional and habitat stratifications could also form a suitable background for lotic biodiversity conservation by providing preliminary physical surrogates for biological variation. The final task of conservation evaluation would incorporate more detailed biodiversity inventories in different habitat types in each ecoregion. These inventories should provide necessary information for detecting sites with an unusually high conservation value, i.e. high species richness, numerous rare species, and unusual species combinations, as well as to predict the occurrence of such invaluable assemblages using landscape, riparian, and in-stream characteristics. These evaluations should preferably be based on multiple taxonomic groups because basing conclusions on just a few macroinvertebrate groups, for example, may be of little value for the conservation of the whole benthic fauna (IV).

Any framework for community characterization and biodiversity conservation should be sufficiently adjustable to accommodate new research findings (Angermeier & Schlosser 1995, Haila & Margules 1996). For instance, it might be necessary to add levels above (e.g. bioregions; Illies 1966) and below ecoregions (e.g. drainage systems) in the hierarchy (see Abell et al. 2000). These additional levels would likely increase our capability to a priori predict variation in lotic assemblages. It must be stressed, however, that the utility of the proposed framework for stream conservation programs should not be tested using a single organism group alone. Rather, such programs should be based on knowledge from multiple organism groups, e.g. algae, bryophytes, invertebrates, and fish (e.g. Omernik 1987, Whittier et al. 1988). This is especially true for conservation evaluation. However, if we knew that major taxa do exhibit congruent biogeographic regionalization and biodiversity patterns across environmental gradients, then single organism groups could be employed for such purposes. Although some groups of freshwater organisms

do exhibit highly congruent biogeographic distribution and diversity patterns (V, VI), the scale-dependent variability of natural phenomena suggests that such patterns may not hold at the local scale. Thus, future research should clearly demonstrate that strong among-taxa congruence also exist at the local scale, i.e. variation in assemblage structure, species richness, and rarity among different lotic plant and animal taxa can be reliably predicted using information from a single organism group. Should this not be the case, then we will face a formidable task of enumerating the multitude of other plant and animal taxa in streams to effectively conserve the biodiversity of these rapidly degrading ecosystems.

5 CONCLUDING REMARKS

As always, the research conducted for a thesis generates more questions than yields answers. In this sense, the present thesis is all but an exception: each single study propagated several ideas, hypotheses, and problems to be tested in future studies. For instance, it would be important to understand more fully (i) how patterns and processes at different spatial scales are intertwined; (ii) how spatial variation is linked to temporal variation; and (iii) how persistent benthic assemblages are across different temporal scales. The last question is particularly important, because little is known about year-to-year variation in macroinvertebrate assemblages of boreal streams. If there is a high degree of temporal turnover in assemblage structure, then one must seriously consider the utility of any management program relying on limited single-year sampling and biological classification.

Future challenges for the study of lotic ecosystems obviously require a blend of innovative approaches and sophisticated methodology. A fruitful avenue might be to view benthic assemblages in a metacommunity context. To this end, more attention should be directed to the assembly of stream communities from the regional species pool, as well as to assessing their degree of nestedness and the distribution dynamics of single species at the landscape-scale (for theoretical frameworks, see Weiher & Keddy 1999, Hubbell 2001). In practice, this will require increasing use of hierarchical sampling designs and geostatistics in studies of stream macroinvertebrate assemblages. An important aspect for both basic and applied research is to assess the degree to which other stream-dwelling organisms exhibit biodiversity patterns similar to those of benthic macroinvertebrates. Finally, a step further is to compare and contrast patterns of stream biodiversity with those of other aquatic and riparian ecosystems to provide a broader basis for conservation decisions at the regional and landscape-scales.

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YHTEENVETO

Pohjaeläinyhteisöjen monimuotoisuuden spatiaalinen vaihtelu pohjoisissa virtavesissä - eliömaantieteellinen yhteys sekä merkitys jokivesien suojelulle

Biologisen monimuotoisuuden köyhtyminen on saavuttanut maailmanlaajuisesti ennennäkemättömät mittasuhteet, ja viime vuosina myös makeiden vesien eliöstön nopeaan yksipuolistumiseen on kiinnitetty yhä enemmän huomiota. Järviä ja jokia uhkaavat pääasiassa elinympäristön laadun heikentyminen, ilmastomuutokset sekä vieraiden lajien vaikutukset kotoperäiseen eliöstöön. Jokivesien osalta tilanne on erityisen huolestuttava, koska niitä on monin tavoin muokattu jo satoja vuosia, ja enää harvat jokivesistöt virtaavat luonnontilaisina. Tästä syystä luonnontilaisten tai lähes luonnontilaisten jokivesien eliöyhteisöjen monimuotoisuuden vaihtelun tuntemus on tärkeää, jotta perusta tuleville suojelu- ja kunnostusohjelmille olisi riittävä. Tämä pätee myös Suomen jokivesiin, joista erityisesti latvapurojen eliöyhteisöt ovat vaarantuneita ja jääneet varsin vähäiselle huomiolle.

Jokivesien eliöyhteisöjen rakenteeseen vaikuttavat lukuisat tekijät laaja-alaisista ilmasto-olosuhteista kosken sisäiseen habitaattirakenteen vaihteluun. Monien ympäristötekijöiden yhteisvaikutus ilmenee luonnontilaisissa jokivesissä huomattavana monimuotoisuuden, lajikoostumuksen ja yksilörunsauden purojen välisenä ja purojen sisäisenä vaihteluna. Ihmistoiminnan vaikutusten erottamiseksi onkin välttämätöntä tuntea luonnollisen taustavaihtelun suuruus ja tyypittää eliöyhteisöjä luonnontilaisissa jokivesissä viitekehukseksi ympäristön tilan seurannalle. Tällaiset tyypitykset voivat perustua alueellisiin kriteereihin, biologiseen eliöyhteisöjen luokitteluun tai edellisten yhdistelmään. Tämän väitöskirjan päätavoitteena oli selvittää boreaalisten virtavesien pohjaeläinyhteisöjen rakenteen vaihtelua suhteessa maantieteelliseen sijaintiin ja paikallisiin ympäristötekijöihin, sekä arvioida ekoregiojakojen ja eliöyhteisöjen biologisen luokittelun soveltuvuutta jokivesien tilan suojelu- ja seurantaohjelmien perustaksi (I, II). Tässä suhteessa on myös tärkeää ymmärtää eliöyhteisöjen jatkuvuus-epäjatkuvuus ympäristögradienteilla (II), sekä pohjaeläimistöön taksonimäärien vaihteluun vaikuttavat tekijät (III). Lisäksi pyrin arvioimaan, vastaavatko yksittäisten puroissa elävien vesihyönteisryhmien monimuotoisuuden (IV) ja toisaalta useiden vesieliöryhmien lajimäärän ja levinneisyyden laaja-alainen maantieteellinen vaihtelu toisiaan (V, VI).

Latvapurojen pohjaeläinyhteisöjen rakenteessa oli havaittavissa selvä etelä-pohjoissuuntainen vaihtuma, mikä pääasiassa selitti myös verraten hyvän ekoregiorajausten ja pohjaeläinyhteisöjen välisen yhteisvaihtelun. Selvimmin muista erottuivat pohjoisimman Suomen arktis-alpiinisen ja pohjoisboreaalisen ekoregion purot eteläisemmistä puroista. Maantieteellisen sijainnin ja ilmastotekijöiden lisäksi pohjaeläimistöön vaihtelu oli selvimmin yhteydessä vesikemian eroihin pohjoisten ja eteläisten purojen välillä: arktis-alpiinisen ja pohjoisboreaalisen alueen purot olivat keskimäärin kirkasvetisempiä, vähäravinteisempia ja emäksisempiä kuin eteläisten (keskiboreaalinen,

eteläboreaalin ja hemiboreaalin) ekoregioiden purot. Huolimatta yhteisö-rakenteen etelä-pohjoissuuntaisesta vaihtelusta, paikallisissa taksonimäärissä ei ollut havaittavissa selvää leveyspiirin mukaista vaihtelua, vaan ekoregioiden sisällä purojen välinen taksonimäärän vaihtelu oli huomattavaa. Keskimäärin alhaisimmat paikalliset taksonimäärät havaittiin keskiboreaalin ekoregion ja korkeimmat eteläboreaalin ekoregion puroissa.

Huolimatta pitkistä ympäristögradien-teista, latvapurojen pohjaeläin-yhteisöjen rakenteessa ei ollut havaittavissa selvää epäjatkuvuutta, eli yhteisötyypit eivät muodostaneet selvärajaisia, erillisiä kokonaisuuksia. Tästä oli osoituksena myös se, että TWINSPAN-analyysin rajaamille yhteisötyypeille ei löytynyt montaakaan erityisen hyvää indikaattorilajia INDVAL-analyyseissä. Samoin päällekkäisyys yhteisötyyppien välillä oli ordinaatioanalyyseissä hyvin suurta. Nämä havainnot viittaavat siihen, että monet pohjaeläintaksonit pystyvät esiintymään varsin monenlaisissa ympäristöolosuhteissa sekä reagoivat hieman eri tavoin paikallisiin ympäristötekijöihin. Tärkein yhteisöjen koostumusta selittävä tekijä oli sen sijaan puron maantieteellinen sijainti, mikä viittaa laaja-alaisten ilmasto- ja kasvillisuusolosuhteiden merkittävään suoraan tai epäsuoraan merkitykseen latvapurojen pohjaeläinyhteisöjen rakenteen säätelyssä tällä maantieteellisellä laajuudella.

Pohjaeläinyhteisöjen paikallinen taksonimäärä oli positiivisessa suhteessa alueellisen taksonimäärän kanssa. Tästä huolimatta paikallisen taksonimäärän vaihtelu oli kuitenkin huomattavaa alueiden sisällä, ja purojen ympäristöolosuhteet selittivätkin huomattavan osan taksonimäärän vaihtelusta. Merkittävää oli myös se, että alueiden sisäisissä tarkasteluissa eri muuttujat nousivat tärkeään asemaan taksonimäärän vaihtelun selittämisessä. Yleisesti ottaen puron koko, veden happamuus ja veden ravinnepitoisuus olivat tärkeimpiä taksonimäärän kanssa korreloivia muuttujia. Työn tulokset viittaavat monimutkaisiin vuorovaikutussuhteisiin alueellisten ja paikallisten tekijöiden välillä purojen pohjaeläinyhteisöjen monimuotoisuuden säätelyssä.

Eri eliöryhmien monimuotoisuuden yhteisvaihtelu on viime vuosina saavuttanut tärkeän osan luonnonsuojelubiologisessa ja eliömaantieteellisessä tutkimuksessa. Soveltavassa mielessä olisikin tärkeää selvittää yhteisvaihtelun taso ja sitä kautta arvioida, voidaanko yksittäistä taksonomista ryhmää käyttää ennustamaan monimuotoisuuden vaihtelua myös toisissa eliöryhmissä. Laajan latvapuroaineiston perusteella päivänkorentojen, koskikorentojen, vesiperhosten ja surviaissääskien välinen yhteisvaihtelu taksonimäärässä ja -koostumuksessa oli verraten heikkoa, vaikka osa parittaisista riippuvuussuhteista olikin tilastollisesti merkitseviä. Yhteisvaihtelua aiheutti lähinnä eri ryhmien reagoiminen samaan vesikemiagradien-teihin, mutta yleisesti ottaen tärkeimmät taksonimäärää ja -koostumusta selittävät muuttujat vaihtelivat hyönteisryhmien välillä. Työn tuloksien perusteella ei yksittäisiä hyönteisryhmiä voida suositella käytettäväksi ennustamaan hyönteislajiston monimuotoisuutta latvapuroissa, vaan tutkimusten tulisi huomioida mahdollisuuksien mukaan mahdollisimman monia taksonomisia ryhmiä.

Ekologiset ilmiöt ovat mittakaavariippuvaisia, mikä havaittiin myös tarkasteltaessa eri eliöryhmien monimuotoisuuden yhteisvaihtelua. Vaikka paikallisen monimuotoisuuden yhteisvaihtelu vesihyönteisryhmien välillä oli

heikkoa, alueellisen lajimäärän vaihtelu vesikasvien, sudenkorentojen, koskikorentojen, vesikovakuoriaisten ja kalojen välillä oli tilastollisesti merkitsevää ja vahvaa. Näiden ryhmien lajimäärä korreloi negatiivisesti leveyspiirin ja positiivisesti heinäkuun keskilämpötilan kanssa. Koskikorennoilla riippuvuussuhteet olivat päinvastaisia, ja lajimäärä korreloi positiivisesti myös alueen keskimääräisen korkeuden kanssa. Nämä tulokset vahvistavat lukuisia aiempia tutkimuksia ilmastotekijöiden tärkeästä roolista lajien levinneisyyden ja leveyspiirien mukaisen lajimäärävaihtelun säätelyssä, mutta osoittavat myös, ettei lajimäärä kaikissa taksonomisissa ryhmissä välttämättä vähene yhdenmukaisesti etelästä pohjoiseen, vaan voi noudattaa jopa päinvastaista riippuvuussuhdetta.

Tämän väitöskirjan päätulosten perusteella alueellista stratifikaatiota voidaan suositella käytettäväksi alustavana pohjana jokivesien suojele- ja seurantaohjelmille. Perusteluna kyseiselle stratifikaatiolle voidaan pitää purojen ympäristöolosuhteiden ja pohjayhteisöjen rakenteen verraten hyvää vastaavuutta ekoregiojakojen kanssa sekä useiden eliöryhmien levinneisyyden ja monimuotoisuuden vastaavuutta laaja-alaisten ilmastotekijöiden kanssa. Lisäksi on oletettavaa, että ekoregioiden sisäiset yhteisörakennetta ja monimuotoisuutta kuvaavat mallit olisivat tarkempia kuin laajempia maantieteellisiä alueita kattavat mallit.

REFERENCES

- Abell, R. A., Olson, D. M., Dinerstein, E., Hurley, P. T., Diggs, J. T., Eichbaum, W., Walters, S., Wettengel, W., Allnut, T., Loucks, C. J. & Hedao, P. 2000. Freshwater ecoregions of North America. A conservation assessment. Island Press, Washington.
- Adams, J. M. & Woodward, F. I. 1989. Patterns in tree species richness as a test of the glacial extinction hypothesis. *Science* 339: 699-701.
- Allan, J. D. 1995. Stream ecology. The structure and function of running waters. Chapman and Hall, London.
- Allan, J. D. & Flecker, A. S. 1993. Biodiversity conservation in running waters. *BioScience* 43: 32-43.
- Angermeier, P. L. & Schosser, I. J. 1989. Species-area relationships for stream fishes. *Ecology* 70: 1450-1462.
- Angermeier, P. L. & Schlosser, I. J. 1995. Conserving aquatic biodiversity: beyond species and populations. *Am. Fish. Soc. Symp.* 17: 402-414.
- Angermeier, P. L. & Winston, M. R. 1999. Characterizing fish community diversity across Virginia landscapes: prerequisite for conservation. *Ecol. Appl.* 9: 335-349.
- Atlas of Finland. 1988. Biogeography and nature conservation. Folio 141-143. National Board of Survey and Geographical Society of Finland, Helsinki.
- Belbin, L. & McDonald, C. 1993. Comparing three classification strategies for use in ecology. *J. Veg. Sci.* 4: 341-348.
- Birks, H. J. B. 1996. Statistical approaches to interpreting diversity patterns in the Norwegian mountain flora. *Ecography* 19: 332-340.
- Borcard, D., Legendre, P. & Drapeau, P. 1992. Partialling out the spatial component of ecological variation. *Ecology* 73: 1045-1055.
- Brown, J. H. 1995. Macroecology. University of Chicago Press, Chicago.
- Brown, J. H. & Lomolino, M. 1998. Biogeography. Sinauer, Sunderland.
- Cao, Y., D. P. Larsen, and R. St-J. Thorne. 2001. Rare species in multivariate analysis for bioassessment: some considerations. *J. N. Am. Benthol. Soc.* 20:144-153.
- Carroll, S. S. & Pearson, D. L. 1998. Spatial modeling of butterfly species richness using tiger beetles (Cicindelidae) as a bioindicator taxon. *Ecol. Appl.* 8: 531-543.
- Chessman, B. C. 1999. Predicting the macroinvertebrate faunas of rivers by multiple regression of biological and environmental differences. *Freshwat. Biol.* 41: 747-757.
- Cooper, S. D., Diehl, S., Kratz, K. & Sarnelle, O. 1998. Implications of scale for patterns and processes in stream ecology. *Aust. J. Ecol.* 23: 27-40.
- Cornell, H. V. 1993. Unsaturated patterns in species assemblages: the role of regional processes in setting local species richness. In Ricklefs, R. E. & Schluter, D. (eds), *Species diversity in ecological communities. Historical and geographical perspectives*: 243-252 University of Chicago Press, Chicago.

- Cornell, H. V. 1999. Unsaturation and regional influences on species richness: a review of the evidence. *Ecoscience* 6: 303-315.
- Cornell, H. V. & Lawton, J. H. 1992. Species interactions, local and regional processes, and limits to the richness of local communities: a theoretical perspective. *J. Anim. Ecol.* 61: 1-12.
- Crowl, T. A. & Schnell, G. A. 1990. Factors determining population density and size distribution of a freshwater snail in streams: effects of spatial scale. *Oikos* 59: 359-367.
- Currie, D. J. 1991. Energy and large-scale patterns of animal and plant species richness. *Am. Nat.* 137: 27-49.
- Currie, D. J., Francis, A. P. & Kerr, J. T. 1999. Some general propositions about the study of spatial patterns of species richness. *Ecoscience* 6: 392-399.
- Downes, B. J., Lake, P. S. & Schreiber, E. S. G. 1993. Spatial variation in the distribution of stream invertebrates: implications of patchiness for models of community organization. *Freshwat. Biol.* 30: 119-132.
- Dufrene, M. & Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* 67: 345-366.
- Dynesius, M. & Nilsson, C. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. *Science* 266: 753-761.
- Edington, J. M. & Hildrew, A. G. 1995. Caseless caddis larvae of the British Isles. *Freshwat. Biol. Ass. Sci. Publ.* 53: 1-134.
- Eldredge, N. 1998. *Life in the Balance. Humanity and the biodiversity crisis.* Princeton University Press, Princeton.
- Fischer, A. G. 1960. Latitudinal variation of organic diversity. *Evolution* 14: 64-81.
- Flather, C. F., Wilson, K. R., Dean, D. J. & McComb, W. C. 1997. Identifying gaps in conservation networks: of indicators and uncertainty in geographic-based analyses. *Ecol. Appl.* 7: 531-542.
- Franklin, J. F. 1993. Preserving biodiversity: species, ecosystems, or landscapes? *Ecol. Appl.* 3: 202-205.
- Frissell, C. A., Wiss, W. J., Warren, C. E. & Huxley, M. D. 1986. A hierarchical framework for stream classification: viewing streams in a watershed context. *Env. Manag.* 10: 199-214.
- Furse, M. T. 2000. The application of RIVPACS procedures in headwater streams – an extensive and important national resource. In: Wright, J. F., Sutcliffe, D. W. & Furse, M. T. (eds), *Assessing the Biological Quality of Fresh Waters: 79-92.* Freshwater Biological Association, Ambleside.
- Gaston, K. J. 1996a. Species richness: measure and measurement. In: Gaston, K. J. (ed.), *Biodiversity. A biology of numbers and difference: 77-113.* Blackwell Science, Oxford.
- Gaston, K. J. 1996b. Biodiversity -congruence. *Prog. Phys. Geogr.* 20: 105-112.
- Gaston, K. J. 2000. Global patterns in biodiversity. *Nature* 405: 220-227.
- Gaston, K. J. & Blackburn, T. M. 1999. A critique for macroecology. *Oikos* 84: 353-368.
- Gaston, K. J. & Blackburn, T. M. 2000. *Pattern and process in macroecology.* Blackwell Science, Oxford.

- Gaston, K. J. & Williams, P. H. 1996. Spatial patterns in taxonomic diversity. In: Gaston, K. J. (ed.), *Biodiversity. A biology of numbers and difference*: 202-229. Blackwell Science, Oxford.
- Gauch, H. G. 1982. *Multivariate analysis in community ecology*. Cambridge University Press, Cambridge.
- Godfray, C. H. J. & Lawton, J. H. 2001. Scale and species numbers. *TREE* 16: 400-404.
- Griffiths, D. 1999. On investigating local-regional species richness relationships. *J. Anim. Ecol.* 68: 1051-1055.
- Grubauch, J. W., Wallace, J. B. & Houston, E. S. 1996. Longitudinal changes of macroinvertebrate communities along an Appalachian stream continuum. *Can. J. Fish. Aquat. Sci.* 53: 896-909.
- Haila, Y. & Margules, C. R. 1996. Survey research in conservation biology. *Ecography* 19: 323-331.
- Harding, J. S., Winterbourn, M. J. & McDiffet, W. F. 1997. Stream faunas and ecoregions in South Island, New Zealand: do they correspond? *Arch. Hydrobiol.* 140: 289-307.
- Harrison, S., Ross, S. J., & Lawton, J. H. 1992. Beta diversity on geographic gradients in Britain. *J. Anim. Ecol.* 61: 151-158.
- Hawkins, C. P. & Vinson, M. R. 2000. Weak correspondence between landscape classifications and stream invertebrate assemblages: implications for bioassessment. *J. N. Am. Benthol. Soc.* 19: 501-517.
- Hawkins, C. P., Norris, R. H., Gerritsen, J., Hughes, R. M., Jackson, S. K., Johnson, R. K. & Stevenson, R. J. 2000. Evaluation of the use of landscape classifications for the prediction of freshwater biota: synthesis and recommendations. *J. N. Am. Benthol. Soc.* 19: 541-556.
- Heikkinen, R. K. & Birks, H. J. B. 1996. Spatial and environmental components of variation in the distribution patterns of subarctic plant species at Kevo, north Finland – a case study at the meso-scale level. *Ecography* 19: 341-351.
- Hemphill, N. 1988. Competition between two stream dwelling filter-feeders, *Hydropsyche oslari* and *Simulium virgatum*. *Oecologia* 77: 73-80.
- Hildrew, A. G. & Giller, P. S. 1994. Patchiness, species interactions and disturbance in the stream benthos. In: Giller, P. S. Hildrew, A. G. & Raffaelli D. (eds), *Aquatic ecology. Scale, pattern and process*: 21-62. Blackwell Science, Oxford.
- Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton.
- Huston, M. A. 1994. *Biological diversity. The coexistence of species on changing landscapes*. Cambridge University Press, Cambridge.
- Huston, M. A. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos* 86: 393-401.
- Illies, J. 1966. Die Verbreitung der Süßwasserfauna Europas. *Verh. int. Verein. Limnol.* 16: 287-296.
- Jackson, D. A. & Somers, K. A. 1991. Putting things in order: the ups and downs of detrended correspondence analysis. *Am. Nat.* 137: 704-712.

- Jacobsen, D. 1999. Patterns of macroinvertebrate species richness in streams: a review. In: Friberg, N. & Carl, J. D. (eds), Biodiversity in benthic ecology: 29-38. NERI Technical Report, No. 266.
- Jacobsen, D., Schultz, R. & Encalada, A. 1997. Structure and diversity of stream invertebrate assemblages: the influence of temperature with altitude and latitude. *Freshwat. Biol.* 38: 247-261.
- Johnson, R. K. 2000. Spatial congruence between ecoregions and littoral macroinvertebrate assemblages. *J. N. Am. Benthol. Soc.* 19: 475-468.
- Johnson, R. K. & Goedkoop, W. 2000. The use of biogeographical regions for partitioning variance of littoral macroinvertebrate communities. *Verh. int. Verein. Limnol.* 27: 333-339.
- Karlson, R. H. & Cornell, H. V. 2002. Species richness of coral assemblages: detecting regional influences at local spatial scales. *Ecology* 83: 452-463.
- Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. *J. Veg. Sci.* 3: 157-164.
- Kohler, S. L., & Wiley, M. J. 1997. Pathogen outbreaks reveal large-scale effects of competition in stream communities. *Ecology* 78: 2164-2176.
- Kouki, J., Niemelä, P. & Viitasaari, M. 1994. Reversed latitudinal gradient in species richness of sawflies (Hymenoptera, Symphyta). *Ann. Zool. Fennici* 31: 83-88.
- Lahti, T., Kurtto, A. & Väisänen, R. 1988. Floristic composition and regional species richness of vascular plants in Finland. *Ann. Bot. Fennici* 25: 281-291.
- Lawton, J. H. 1999. Are there general laws in ecology? *Oikos* 84: 177-192.
- Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74: 1659-1673.
- Legendre, P. & Legendre, L. 1998. Numerical ecology. Second edition. Elsevier, Amsterdam.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943-1967.
- Li, J., Herlihy, A., Gerth, W., Kaufmann, P., Gregory, S., Urquhart, S. & Larsen, D. P. 2001. Variability of stream macroinvertebrates at multiple spatial scales. *Freshwat. Biol.* 46: 87-97.
- MacArthur, R. H. 1972. Geographical ecology. Patterns in the distribution of species. Harper & Row, New York.
- Malmqvist, B. 2000. How does wing length relate to distribution patterns of stoneflies (Plecoptera) and mayflies (Ephemeroptera)? *Biol. Cons.* 93: 271-276.
- Malmqvist, B. & Eriksson, Å. 1995. Benthic insects in Swedish lake-outlet streams: patterns in species richness and assemblage structure. *Freshwat. Biol.* 34: 285-296.
- Malmqvist, B. & Hoffsten, P. O. 2000. Macroinvertebrate taxonomic richness, community structure and nestedness in Swedish streams. *Arch. Hydrobiol.* 150: 29-54.
- Malmqvist, B. & Mäki, M. 1994. Benthic macroinvertebrate assemblages in north Swedish streams: environmental relationships. *Ecography* 17: 9-16.

- Magnuson, J. J., Webster, K. E., Assel, R. A., Bowser, C. J., Dillon, P. J., Eaton, J. G., Evans, H. E., Fee, E. J., Hall, R. I., Mortsch, L. R., Schindler, D. W. & Quinn, F. H. Potential effects of climate changes on aquatic systems: Laurentian Great Lakes and Precambrian Shield Region. *Hydrol. Proc.* 11: 825-871.
- Manly, B. F. J. 1994. *Multivariate statistical methods. A primer.* Second edition. Chapman and Hall, London.
- Matthews, W. J. 1998. *Patterns in freshwater fish ecology.* Chapman and Hall, New York.
- McAuliffe, J. R. 1984. Resource depression by a stream herbivore: effects on the distributions and abundances of other grazers. *Oikos* 42: 327-333.
- McCune, B. & Mefford, M. J. 1999. *PC-ORD. Multivariate analysis of ecological data.* MjM Software Design, Gleneden Beach, Oregon.
- McGeoch, M. 1998. The selection, testing and application of terrestrial insects as bioindicators. *Biol. Rev.* 73: 181-201.
- Menge, B. A. & Olson, A. M. 1990. Role of scale and environmental factors in regulation of community structure. *TREE* 5: 52-57.
- Minshall, G. W. 1988. Stream ecosystem theory: a global perspective. *J. N. Am. Benthol. Soc.* 7: 263-288.
- Minshall, G. W., Petersen, R. C. & Nimz, C. F. 1985. Species richness in streams of different size from the same drainage basin. *Am. Nat.* 125: 16-38.
- Moss, D., Wright, J. F., Furse, M. T. & Clarke, R. T. 1999. A comparison of alternative techniques for prediction of the fauna of running water-sites in Great Britain. *Freshwat. Biol.* 41: 167-181.
- Nordic Council of Ministers. 1984. *Naturgeografisk regionindelning av Norden.* Nordiska Ministerrådet, Oslo.
- Oberdorff, T., Guegan, J. F. & Hugueny, B. 1995. Global patterns of fish species richness in rivers. *Ecography* 18: 345-352.
- Ohmann, J. L. & T. A. Spies. 1998. Regional gradient analysis and spatial pattern of woody plant communities of Oregon forests. *Ecol. Monogr.* 68: 151-182.
- Økland, R. H. 1999. On the variation explained by ordination axes and constrained ordination axes. *J. Veg. Sci.* 10: 131-136.
- Omernik, J. M. 1987. Ecoregions of the conterminous United States. *Ann. Ass. Am. Geogr.* 77: 118-125.
- Ormerod, S. J. & Edwards, R. W. 1987. The ordination and classification of macroinvertebrate assemblages in the catchment of the River Wye in relation to environmental factors. *Freshwat. Biol.* 17: 533-546.
- Otto, C. & Svensson, B. 1983. Properties of acid brown water streams in South Sweden. *Arch. Hydrobiol.* 99: 15-36.
- Paavola, R., Muotka, T. & Tikkanen, P. 2000. Macroinvertebrate community structure and species diversity in humic streams of Finnish Lapland. *Verh. int. Verein. Limnol.* 27: 2550-2555.
- Palmer, M. A., Allan, J. D. & Butman, C. A. 1996. Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. *TREE* 11: 322-326.
- Palmer, M. A., Ambrose, R. F. & Poff, N. L. 1997. Ecological theory and community restoration ecology. *Rest. Ecol.* 5: 291-300.

- Paszkowski, C. A. & Tonn, W. M. 2000. Community concordance between the fish and aquatic birds of lakes in northern Alberta, Canada: the relative importance of environmental and biotic factors. *Freshwat. Biol.* 43: 421-437.
- Pedersen, B. 1990. Distributional patterns of vascular plants in Fennoscandia: a numerical approach. *Nord. J. Bot.* 10: 163-189.
- Peet, R. K., Knox, R. G., Case, J. S. & Allen, R. B. 1988. Putting things in order: the advantages of detrended correspondence analysis. *Am. Nat.* 131: 924-934.
- Perry, J. A. & Schaeffer, D. J. 1987. The longitudinal distribution of riverine benthos: a river dis-continuum? *Hydrobiologia* 148: 257-268.
- Pielou, E. C. 1991. *After the ice age*. University of Chicago Press, Chicago.
- Pimm, S. L., Russell, G. J., Gittleman, J. L. & Brooks, T. M. 1995. The future of biodiversity. *Science* 269: 347-350.
- Poff, N. L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *J. N. Am. Benthol. Soc.* 16: 391-409.
- Pozzi, S. & Borcard, D. 2001. Effects of dry grassland management on spider (Arachnida: Araneae) communities on the Swiss occidental plateau. *Ecoscience* 8: 32-44.
- Prendergast, J. R., Quinn, R. M., Lawton, J. H., Eversham, B. C. & Williams, P. H. 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* 365: 335-337.
- Purvis, A. & Hector, A. 2000. Getting the measure of biodiversity. *Nature* 405: 212-219.
- Quinn, J. M. & Hickey, C. W. 1990. Characterization and classification of benthic invertebrate communities in 88 New Zealand rivers in relation to environmental factors. *N. Z. J. Mar. Freshwat. Res.* 24: 387-409.
- Reynoldson, T. B., Norris, R. H., Resh, V. H., Day, K. E. & Rosenberg, D. M. 1997. The reference condition: a comparison of multimetric and multivariate approaches to assess water-quality impairment using benthic macroinvertebrates. *J. N. Am. Benthol. Soc.* 16: 833-852.
- Reynoldson, T. B., Rosenberg, D. M. & Resh, V. H. 2001. Comparison of models predicting invertebrate assemblages for biomonitoring in the Fraser River catchment, British Columbia. *Can. J. Fish. Aquat. Sci.* 58: 1395-1410.
- Ricciardi, A. & Rasmussen, J. B. 1999. Extinction rates of North American freshwater fauna. *Cons. Biol.* 13: 1220-1222.
- Ricketts, T. H., Dinerstein, E., Olson, D. M. & Loucks, C. 1999. Who's where in North America? Patterns of species richness and the utility of indicator taxa for conservation. *BioScience* 49: 369-381.
- Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. *Science* 235: 167-171.
- Ricklefs, R. E. & Schluter, D. 1993. *Species diversity in ecological communities. Historical and geographical perspectives*. Chicago University Press, Chicago.
- Rosenberg, D. M. & Resh, V. H. 1993. *Freshwater biomonitoring and benthic macroinvertebrates*. Chapman and Hall, New York.

- Rosenzweig, M. L. 1995. Species diversity in space and time. Oxford University Press, Oxford.
- Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M.T., Walker, B. H., Walker, M. & Wall, D. H. 2000. Global biodiversity scenarios for the year 2100. *Science* 287: 1770-1774.
- Sandin, L. & Johnson, R. K. 2000. Ecoregions and benthic macroinvertebrate assemblages of Swedish streams. *J. N. Am. Benthol. Soc.* 19: 462-474.
- Sokal, R. R. & Rolf, F. J. 1995. Biometry. Third edition. W. H. Freeman, New York.
- Stevens, R. D. & Willig, M. R. 2002. Geographical ecology at the community level: perspectives on the diversity of new world bats. *Ecology* 83: 545-560.
- Statzner, B. & Higler, B. 1985. Questions and comments on the river continuum concept. *Can. J. Fish. Aquat. Sci.* 42: 1038-1044.
- Ter Braak, C. J. F. 1995. Ordination. In: Jongman, R. H. G., ter Braak, C. J. F. & van Tongeren, O. F. R. (eds), *Data analysis in community and landscape ecology*: 91-173. Cambridge University Press, Cambridge.
- Tonn, W. M. 1990. Climate change and fish communities: a conceptual approach. *Trans. Am. Fish. Soc.* 119: 337-352.
- Townsend, C. R., Hildrew, A. G. & Francis, J. 1983. Community structure in some southern English streams: the influence of physicochemical factors. *Freshwat. Biol.* 13: 521-544.
- Väisänen, R. & Heliövaara, K. 1994. Hot-spots of insect diversity in northern Europe. *Ann. Zool. Fennici* 31: 71-81.
- Vannote, R. L. & Sweeney, B. W. 1980. Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *Am. Nat.* 115: 667-695.
- Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R. & Cushman, C. E. 1980. The river continuum concept. *Can. J. Fish. Aquat. Sci.* 37: 130-137.
- Van Sickle, J. 1997. Using mean similarity dendrograms to evaluate classifications. *J. Agr. Biol. Env. Stat.* 2:370-384.
- Van Sickle, J. & Hughes, R. M. 2000. Classification strengths of ecoregions, catchments, and geographic clusters for aquatic vertebrates in Oregon. *J. N. Am. Benthol. Soc.* 19: 370-384.
- Van Tongeren, O. F. R. 1995. Cluster analysis. In: Jongman, R. H. G., ter Braak, C. J. F. & van Tongeren, O. F. R. (eds), *Data analysis in community and landscape ecology*: 174-212. Cambridge University Press, Cambridge.
- Vinson, M. R. & Hawkins, C. P. 1998. Biodiversity of stream insects: Variation at local, basin and regional scales. *Ann. Rev. Entomol.* 43: 271-293.
- Vuori, K.-M. & Muotka, T. 1999. Benthic communities in humic streams. In: Keskkitalo, J. & Eloranta, P. (eds), *Limnology of humic waters*: 193-207. Backhyus, Leiden.
- Wallace, J. B. & Webster, J. R. 1996. The role of macroinvertebrates in stream ecosystem function. *Ann. Rev. Entomol.* 41: 115-139.

- Ward, J. V. 1998. Riverine landscapes. Biodiversity patterns, disturbance regimes, and aquatic conservation. *Biol. Cons.* 83: 269-278.
- Ward, J. V. & Stanford, J. A. 1982. Thermal responses in the evolutionary ecology of aquatic insects. *Ann. Rev. Entomol.* 27: 97-117.
- Weiher, E. & Keddy, P. 1999. Ecological assembly rules. Perspectives, advances, and retreats. Cambridge University Press, Cambridge.
- Whittaker, R. M. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.* 30: 279-338.
- Whittier, T. R., Hughes, R. M. & Larsen, D. P. 1988. Correspondence between ecoregions and spatial patterns in stream ecosystems in Oregon. *Can. J. Fish. Aquat. Sci.* 45: 1264-1278.
- Wiens, J. A. 1981. Single-sample surveys of communities: are the revealed patterns real? *Am. Nat.* 117: 90-98.
- Wiens, J. 1989. Spatial scaling in ecology. *Funct. Ecol.* 3: 385-397.
- Winterbourn, M. J., Rounick, J. S. & Cowie, B. 1981. Are New Zealand stream ecosystems really different? *N. Z. J. Mar. Freshwat. Res.* 15: 321-328.
- Wright, J. F., Armitage, P. D. & Furse, M. T. 1984. A preliminary classification of running water sites in Great Britain based on macroinvertebrate species and the prediction of community types using environmental variables. *Freshwat. Biol.* 14: 221-256.
- Wright, J. F., Furse, M. T. & Moss, D. 1998. River classification using invertebrates: RIVPACS applications. *Aquat. Cons. Mar. Freshwat. Ecosyst.* 8: 617-631.
- Wright, R. G., Murray, M. P. & Merrill, T. 1998. Ecoregions as a level of ecological analyses. *Biol. Cons.* 86: 207-213.
- Zimmerman, G. M., Goetz, H. & Mielke, P. W. 1985. Use of an improved statistical method for group comparisons to study effects of prairie fire. *Ecology* 66: 606-611.

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