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SPATIAL AND TEMPORAL VARIABILITY OF MACROINVERTEBRATE ASSEMBLAGES IN BOREAL STREAMS: IMPLICATIONS FOR CONSERVATION AND BIOASSESSMENT
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Abstract

In this thesis, I studied spatial and temporal variability of macroinvertebrate assemblages of boreal streams. The main objectives were (i) to characterize macroinvertebrate assemblage types across large geographical extents, and to assess the utility of assemblage types and landscape and stream type classifications as the basis of stream bioassessment and conservation programs (ii, iii). I also examined the relative roles of large-scale spatial trends and local environmental conditions in structuring macroinvertebrate assemblages (iv). Finally, I assessed (v) if assemblage classifications produce temporally stable and predictable assemblage types.

Stream macroinvertebrate assemblage structure exhibited continuous variation instead of distinct assemblage types. Although ecoregions clearly accounted for a considerable amount of variation of macroinvertebrate assemblage characteristics, a combination of regional stratification and prediction from environmental factors would probably yield the most comprehensive framework for the characterizations of macroinvertebrate assemblages of boreal headwater streams. Differences in macroinvertebrate assemblage structure, as well as a group of effective indicator species for different stream types, suggest that landscape classifications could be used as a preliminary scheme for the conservation planning of running waters.

The strength of the relationship between assemblage structure and local environmental variables increased with decreasing extent, whereas assemblage variation related to spatially variables showed the opposite pattern. At the largest scale, spatial variation was related to latitudinal gradients, while spatial autocorrelation among neighbouring streams was the likely mechanism creating spatial structure within drainage systems. These results suggest that stream bioassessment should give due attention to spatial structuring of stream assemblage composition, considering that important assemblage gradients may not only be related to local environmental factors, but also to biogeographical constraints and neighbourhood dispersal processes.

The classification strengths of macroinvertebrate assemblages based on data of three years were overall rather weak, and more importantly, the compositions of the site groups varied considerably from year to year. Such wide and continuous variation was also mirrored by low and inconsistent predictability of classifications from environmental variables. The observed level of temporal variation in assemblage structure may not be a serious problem for predictive approaches frequently used in bioassessment of freshwater ecosystems. For conservation purposes, however, alternative approaches (e.g. physical surrogates of biodiversity) need to be considered.

Keywords: assemblage structure, benthic invertebrates, biomonitoring, environmental gradients, geographic extent, species richness, stability, stream conservation
To my family
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List of original papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:


Contents

Abstract
Acknowledgements
List of original papers
Contents

1 Introduction ................................................................................................................... 13
2 Aims of the thesis .......................................................................................................... 16
3 Materials and methods................................................................................................. 17

3.1 Study areas..............................................................................................................17
3.2 Field surveys...........................................................................................................17
3.3 Defining macroinvertebrate assemblage types .......................................................18
3.4 Variability of lotic macroinvertebrates across landscape classifications ..........19
3.5 Assessing physical surrogates for biodiversity ......................................................19
3.6 Spatial structure and environmental relationships of stream macroinvertebrate assemblages .............................................................................20

3.7 Temporal variation in assemblage classifications and assemblage-environment relationships .............................................................................21

4 Results and discussion................................................................................................. 23

4.1 Defining macroinvertebrate assemblage types .......................................................23
4.2 Variability of lotic macroinvertebrates across landscape classifications ..........24
4.3 Assessing physical surrogates of stream biodiversity ..........................................25
4.4 Scale-related variation in environmental relationships and spatial structures of stream macroinvertebrate assemblages .............................................27

4.5 Temporal variation in assemblage classifications and assemblage-environment relationships .............................................................................28

5 Implications for conservation and management ........................................................ 30
6 Suggestions for future research ..................................................................................... 32
References
Original papers
1 Introduction

Running waters are amongst the most threatened ecosystems in the world (Allan & Flecker 1993). River regulation, eutrophication and alteration of habitat structure have destroyed natural river systems in many parts of the world (Dynesius & Nilsson 1994, Malmqvist & Rundle 2002), and headwater streams are typically the only lotic ecosystems that remain in their close-to-natural state. However, even headwater streams are increasingly threatened by human activities, including habitat degradation (Zwick 1992) and, in boreal regions particularly, land use changes caused by forestry practices (Vuori et al. 1998). Headwater streams are highly variable environments that harbour diverse and unique biota (Malmqvist & Hoffsten 2000) and can therefore be defined as areas of high conservation value (Angermeier & Winston 1997). Furthermore, most of the drainage network is comprised of headwater streams, and ecological processes in the headwaters affect environmental conditions in the downstream sections of rivers (Saunders et al. 2001). However, many aspects of the biodiversity and ecological processes of headwater streams still remain poorly understood, hindering the implementation of effective conservation, assessment, and management programs.

A considerable part of the biodiversity of headwater streams is accounted for by benthic macroinvertebrates. Benthic macroinvertebrates have an important role in many ecosystem processes, including decomposition of allochthonous organic material, herbivory, and transport of energy from primary producers to secondary consumers (Allan 1995, Wallace & Webster 1996, Covich et al. 1999). Because of these and many other features, benthic macroinvertebrates have been widely used in stream bioassessment (Rosenberg & Resh 1993). Thus, information about the processes that structure macroinvertebrate assemblages is important not only from the perspective of biodiversity conservation, but also for the purposes of bioassessment, management, and restoration of stream ecosystems.

Streams are notoriously heterogeneous and naturally hierarchical environments, where habitat conditions at lower levels are constrained by higher-level factors (e.g., Frissell et al. 1986). At broad scales, geologic and climatic factors are the main determinants of stream habitat characteristics and species distributions, and broad-scale surveys have shown that stream assemblages often exhibit close correspondence to these factors (Whittier et al. 1988, Feminella 2000, Rabeni & Doisy 2000, Heino et al. 2002). On the other hand, differences in local, site-specific habitat characteristics (Richards et al. 1997,
Lammert & Allan 1999) and water chemistry (Townsend et al. 1983, Paavola et al. 2000) may create considerable variation in macroinvertebrate assemblage structure even among neighbouring streams.

Such a multi-scale hierarchical structure can be related to the concept of environmental filters that assemble local stream communities from the regional species pool (Poff 1997). In this framework, historical and climatic factors shape the composition of the regional species pool from which species are screened by different environmental constrains at each successive scale. Thus, each species has to pass a series of environmental filters at different scales, and only a subset of species from the regional species pool may eventually coexist in a local community (Tonn 1990, Keddy 1992, Poff 1997, Zobel 1997) (Fig. 1). It has indeed been suggested that environmental filters for stream macroinvertebrates are highly effective, resulting in locally-controlled, predictable assemblage types (Hawkins et al. 2000). However, although it has been widely recognized that multi-scale studies are needed to disentangle the relative roles of multi-scale drivers of assemblage structure (Wiens 1989, Menge & Olson 1990, Poff 1997, Cooper et al. 1998), studies examining community patterns in streams by systematically changing the study extent are still rare (but see Angermeier and Winston 1999, Magalhães et al. 2002).

Fig. 1. Environmental filters selecting species with suitable traits at different scales. Modified from Poff (1997).

Understanding the geographical structuring of assemblages yields important information for the bioassessment of stream ecosystems. During the last two decades, most bioassessment programs have adopted a regional approach which requires that the natural variability of stream habitat characteristics and biotic assemblages can be effectively stratified with some classification scheme (Reynoldson 1997). Considerable attention has been directed to testing whether the structure of stream assemblages corresponds to
terrestrial landscape-classifications such as ecoregions (Hawkins et al. 2000). A number of studies have found a close correspondence between ecoregions and benthic assemblages (Whittier 1988, Feminella 2000), while others have shown that catchment-scale characteristics are more useful than regional factors in predicting stream macroinvertebrate assemblage structure (Corkum 1990). In general, the strength of classifications has been weak, and it has therefore been suggested that regional-scale classifications should be accompanied by stratification through habitat type, and predictive modelling should be targeted on these smaller spatial units (Hawkins & Vinson 2000, Heino et al. 2002). The few studies that have examined the variability of stream assemblages across multiple landscape scales have indeed shown that despite regional differences in assemblage structure, variability at smaller scales may strongly influence the patterns observed (Li et al. 2001, Snelder et al. 2004). However, studies comparing the effectiveness of different landscape and stream-type classifications in characterizing variation in stream macroinvertebrate assemblages are still surprisingly rare (but see Snelder et al. 2004). Furthermore, although landscape classifications are increasingly being used in conservation planning and biodiversity management, no study to date has rigorously examined the utility of different stream type classes as physical surrogates for stream biodiversity.

The structure of local communities is not determined only by factors acting at different spatial, but also at different temporal scales. The results from studies addressing temporal variation of stream macroinvertebrate assemblages have been controversial thus far; some studies have shown that the composition of assemblages may be relatively persistent (Wheatherley & Ormerod 1990, Robinson et al. 2000, Scarsbrook 2002), while others have reported considerable changes in assemblage composition over time (Townsend et al. 1987, Humphrey et al. 2000). In general, assemblage structure has been found to be more stable at sites where local environmental conditions do not vary appreciably over time (Townsend 1987, Robinson et al. 2000, but see Scarsbrook 2002).

Temporal variation in assemblage structure has also important implications for the conservation and bioassessment of stream environments. Many biodiversity surveys produce data on the distribution of species across sites, as well as a set of simultaneously measured environmental variables. The biotic and environmental data are subsequently used to model assemblage-environment relationships with the primary aim to predict biodiversity patterns at a particular area and beyond (e.g., Ferrier 2002). Such predictive approaches have been increasingly used in stream bioassessment (RIVPACS and its variants, e.g., Marchant et al. 1997, Wricht et al.1998, Hawkins et al. 2000, Reynoldson et al. 2001, Johnson 2003). A notable pitfall of such approaches is temporal variation in the patterns of interest. Thus, if there is high year-to-year variation, predictions of species distributions and assemblage-environment relationships obtained in a single year can not be effectively used in other years, leading to questionable extrapolations in conservation and bioassessment programs. To date, however, only few studies have assessed the influences of temporal variability on the performance of predictive models (but see Weatherley & Ormerod 1990, Humphrey et al. 2000).
2 Aims of the thesis

This thesis concentrates on the spatial and temporal variability of macroinvertebrate assemblage structure in boreal headwater streams. The main objectives were to characterize macroinvertebrate assemblage types across large geographical extents (I), to examine the variability of assemblage characteristics across different landscape and stream type classifications (II, III), and to assess the utility of such classifications as the basis of stream conservation and bioassessment programs (I, II, III). I also examined the relative roles of large-scale spatial trends and local environmental conditions in structuring macroinvertebrate assemblages, and whether the contributions of these factors exhibit scale- and context-related patterns (IV). I also explored less studied aspects of temporal variation in stream macroinvertebrate assemblages (V). I examined whether assemblage classifications produce temporally stable assemblage types, and how well these assemblage types can be predicted using environmental variables. The influence of taxonomic coverage on the temporal stability of assemblage classifications and assemblage-environment relationships was also assessed.
3 Materials and methods

3.1 Study areas

The study area ranged from all of Finland (I) (60°N to 70°N and 20°E to 32°E) through ecoregions (II, III) to a single drainage system (IV, V). A total of 235, 72, 78, streams were included in papers I, II, III, and 148 and 34 for papers IV and V, respectively. The data sets for papers II and IV were subsets of the data set of paper I. Finland is delineated into five ecoregions, two of which, Middle boreal and North boreal ecoregion, were included in papers II and III. Ecoregional delineations are based on climate, vegetation, geology, and land use (Atlas of the Finland 1988, Nordic Council of Ministers 1984). In papers II and IV, ecoregions were further divided into major drainage systems. Streams in papers III and V, were sampled from the three main tributaries (River Oulankajoki, River Kitkajoki, and River Kuusinkijoki) of the Koutajoki drainage system.

3.2 Field surveys

Stream macroinvertebrates were sampled between 1992 -2000 in papers I, II, and IV while sampling for paper III was conducted in 2001 and for paper V during three (2001-2003) consecutive years. Invertebrate sampling was conducted between early September and late October in each study. A two-minute kick-sample (consisting of four subsamples) was taken at each site, aiming to cover most benthic microhabitats available in a riffle section of approximately 100 m². This sampling effort typically yields >70 % of species present at a site in a given season (Mykrä et al. 2006). At each site, a set of environmental characteristics were measured, including both riparian (tree species composition, riparian integrity, and shading) and in-stream habitat variables (stream width, depth, current velocity, moss cover and particle size). Water samples were collected simultaneously with benthic sampling, and they were analysed for pH, alkalinity, conductivity, water colour, iron, total nitrogen, and total phosphorus using Finnish national standards.
Macroinvertebrates were identified to species or genus level, with the exception of chironomid midges for which family level identification was retained. Since chironomids form a heterogeneous group with varying responses to environmental conditions, they were excluded from further analyses. However, in paper V, chironomids were identified to species or genus level, and were retained in all analyses of that paper.

3.3 Defining macroinvertebrate assemblage types

Macroinvertebrate assemblage types were defined to evaluate their utility for assemblage-level conservation and bioassessment programs. The relationships between assemblage structure and environmental gradients were also assessed.

Two-way-Indicator-Species-Analysis (TWINSPAN) was used to cluster sites to assemblage types according to their species composition. TWINSPAN is a classification method based on reciprocal averaging and, although it has been criticised (mainly because of the arbitrary cutting of the main axis, e.g., Legendre & Legendre 1998), it is a widely used method that has been shown to perform well in classification of benthic macroinvertebrates (e.g. Moss et al. 1999).

TWINSPAN classifications were further visualised using Nonmetric Multi-Dimensional Scaling (NMDS). NMDS is an ordination method based on ranked distances, and it is suitable for analysing ecological data sets for numerous reasons. NMDS does not require normally distributed data and it performs well with data that contain numerous zero values (McCune & Mefford 1999). Sorensen’s coefficient based on log(x+1) transformed macroinvertebrate data was used as the distance measure in the ordinations. NMDS was run on an autopilot mode, in which the program chooses the solution with the lowest stress value from 100 separate runs of real data (McCune & Mefford 1999). A three dimensional solution of NMDS was used because change in stress value with further dimensions was minor.

The strengths of the TWINSPAN classifications were examined using Multi Response Permutation Procedure (MRPP) and Indicator value Method (IndVal). 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 the TWINSPAN groups was assessed by a Monte Carlo permutation procedure with 1000 permutations. Indicator Value Analysis (IndVal) was used to detect significant indicator taxa for the TWINSPAN site groupings. IndVal is based on the comparison of relative abundances and frequencies of occurrence of taxa in different site groups, and it identifies taxa that differ more between groups than would be expected by chance (Dufrene & Legendre 1997). The indicator value varies between 0 and 100, and it attains its maximum value when all individuals of a species occur at all sites of a single group, and not in the other groups.

Two methods were used for examining assemblage-environment relationships. First, Discriminant Function Analysis (DFA) was used to examine which environmental variables best discriminated among the TWINSPAN site groups. DFA was also used to examine how well the environmental variables could predict the group membership of the sites in each TWINSPAN group. A stepwise selection of variables was used. Finally,
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 widely used direct ordination method that analyses simultaneously both environmental and species data by combining ordination and multiple regression techniques (Ter Braak 1995). Forward selection of environmental variables was used. At each step, the significance of the variable to be included in the ordination was tested using Monte Carlo permutation procedure with 1000 permutations.

### 3.4 Variability of lotic macroinvertebrates across landscape classifications

Nested analysis of variance and multivariate techniques were used to examine variability in stream macroinvertebrate assemblage characteristics and environmental variables at three hierarchical landscape scales (ecoregions, drainage systems, streams). Furthermore, the influence of stream size to assemblage variability was also assessed.

First, eight macroinvertebrate metrics were calculated for each stream, and a partially nested mixed-model ANOVA was then used to examine variability in macroinvertebrate metrics among ecoregions, drainage systems, and stream size classes. A three-factor model was constructed: ecoregions and drainage systems were random factors, and size class was a fixed factor. There were thus three main effects (ecoregion, drainage systems(ecoregion) and size class) and two interaction terms (ecoregion*size class and drainage systems(ecoregion)*size class), resulting in five terms in the model. Variance components for the random factors and residual terms were also calculated, and their contribution to total variance was measured (see e.g., Morrisey et al. 1992, Underwood 1997).

Variation in environmental characteristics among the regional delineations and stream size classes also was analysed using nested ANOVAs. For this purpose, the dimensionality of the environmental data was first reduced using principal component analysis (PCA), and ANOVAs were then conducted on the PCA site scores. Only components with eigenvalues > 1.0 were included in the analysis.

Lastly, NMDS was used to examine patterns of variation in macroinvertebrate assemblage structure among sites. Differences in macroinvertebrate assemblage structure among the landscape classifications were further examined using MRPP. The significance of the null hypotheses of no differences among groups was assessed by a Monte Carlo permutation procedure with 1000 permutations.

### 3.5 Assessing physical surrogates for biodiversity

In this study, we assessed the utility of tributary and stream type classifications in reflecting invertebrate biodiversity in a boreal drainage system. We specifically examined how strong a priori landscape classifications are in accounting for the variability of
invertebrate biodiversity, and if these classifications could be used as physical surrogates in conservation planning.

The study sites were divided among the three tributary systems (Kitkajoki, Kuusinkijoki, Oulankajoki) and among four stream types (small streams, medium-sized stream, large streams, and lake outlets). MRPP and NMDS were used to examine variability of macroinvertebrate assemblage structure (presence-absence and abundance data) among classifications. Classification strengths (CS) of the classifications were assessed using the mean similarity approach (van Sickle & Hughes 2000). CS is calculated as the difference between mean of all within-group similarities (W) and mean between-group similarity (B) (CS = W – B). Large values of CS thus indicate a strong classification (high within-group and low among-group similarity). Classification strengths were also calculated for TWINSPAN cluster classification (two division levels and four groups) for comparison between the a priori physical classifications and the best biological classification, where within-group similarities were maximised and between-group similarities minimised. MSA, MRPP and TWINSPAN were run for the whole data for tributary and stream type comparisons, and separately for stream type comparisons within each tributary. Two-dimensional NMDS ordinations were run to visualize the variability and differences in macroinvertebrate assemblage structure among the stream types within each tributary.

Indicator species analysis (IndVal) was employed to search for significant indicator species discriminating the stream types within each tributary. Only species abundance data were used. Finally, we used analysis of variance (ANOVA) to test for differences in taxonomic richness between tributaries and stream types. One-way ANOVA with Tukey test for pairwise comparisons was also used to examine differences in taxonomic richness between stream types within each tributary.

### 3.6 Spatial structure and environmental relationships of stream macroinvertebrate assemblages

In this study, the contributions of spatial structure and environmental factors to stream macroinvertebrate assemblage structure were examined. The geographical extent of the data was varied using hierarchically-occurring, natural geographical units: bioregion, ecoregions, and drainage systems. The regional context in environmental conditions and their effects on assemblage-environment relationships were also examined.

Canonical correspondence analysis (CCA) was used as the primary analytical method to examine the relationship between macroinvertebrate assemblage structure and the explanatory variables. Following Borcard et al. (1992), a series of partial CCAs were performed to quantify the relative contributions of environmental and spatial variables to explained variation in macroinvertebrate assemblage structure at the three successive spatial extents. In partial CCA, variables of no direct interest are included as covariables and the effects of these variables to variation in species data are partialled out (Legendre & Legendre 1998). Based on these analyses, total variation in macroinvertebrate community structure was partitioned into four independent fractions: pure environmental, pure spatial, spatially structured environmental and unexplained variation. Prior to
analysis, the matrix of spatial variables (geographic coordinates) was completed by calculating all terms of a cubic trend surface regression, and all nine terms from the regression were used as independent variables in further analysis. To avoid artificially inflating explained variation, forward selection of environmental and spatial variables was used. At each step, only variables significant at $\alpha = 0.10$ (Monte Carlo permutation test with 100 permutations) were included in the partial constrained ordinations.

To separate the influence of spatial extent from the larger sample size at the bioregion and ecoregion levels, “randomized bioregions” with 75 streams and “randomized ecoregions” with 25 streams (i.e., sample size of the successively smaller spatial extent) were constructed. Twenty random subsets of 75 streams spanning evenly across all drainage systems were constructed, thus retaining the original spatial structure of the complete data set. Similarly, at the ecoregion level, 20 subsets of 25 streams were constructed. Partial CCAs were then run as above.

### 3.7 Temporal variation in assemblage classifications and assemblage-environment relationships

Several different types of multivariate techniques were used to assess the reliability of assemblage classifications derived from single-year sampling of streams in northeastern Finland. The influence of taxonomic coverage on assemblage classifications and assemblage-environment relationships was also examined using three different taxonomic data sets: (i) data with all macroinvertebrates, (ii) chironomid midges excluded, and (iii) only chironomids included. Lastly, we examined the degree of concordance in assemblage patterns among different years for each of the three taxonomic data sets.

Flexible beta clustering (with Sørensen’s dissimilarity coefficient, beta-value set at $-0.5$; see Moss et al. 1999) was first used for each taxonomic data set to classify the sites into four groups in each year based on their macroinvertebrate assemblages. Classification strengths (CS) for each assemblage classification were assessed using the mean similarity approach (MSA). Classification strengths were also assessed using classifications from 2001, 2002, 2003 and species data from each of the other two years to examine how year-to-year variation in assemblage structure affected classification strengths. Furthermore, to examine the influence of taxonomic coverage on classification strength, we compared how well the classifications based on different taxonomic data sets discriminated groups when classifications of each data set were assessed against the species data from each of the other two data sets.

Discriminant function analysis (DFA) with stepwise selection was used to examine which environmental variables were most important in discriminating the site groups (flexible beta linkage) for each taxonomic data set in each year. DFA was also used to predict the group membership of each site according to environmental variables. The robustness of the DFA models for different taxonomic data sets for each year was further tested with discriminant functions from the other two years.

Finally, Procrustes rotation analysis was used to examine the degree of year-to-year concordance of assemblage patterns for each taxonomic data set. Procrustes analysis works by scaling, rotating, and dilating one ordination solution and then superimposing it
on a second ordination, maximizing the fit between corresponding observations of the
two ordination configurations. The most commonly used method for Procrustean fitting is
based on least-squares criterion, minimizing the sum of the squared residuals ($m^2$)
between the two configurations. The $m^2$ is then used as a measure of the degree of
association between the two ordinations (Digby & Kempton 1987). Low values of $m^2$
indicate strong concordance, and vice versa. Prior to Procrustes analysis, NMDS
ordination (based on Sorensen’s distance) was used to summarize the variability in
assemblage structure (separately for each taxonomic data set) in each year. A three-
dimensional solution of NMDS was used in all ordinations. To examine the degree of
temporal concordance, ProTest with 9999 permutations was used for pairwise (among-
year) comparisons of the NMDS ordinations for each data set. ProTest was further used to
examine the degree of concordance between the ordinations and environmental variables
for each year. For this purpose, principal component analysis (PCA) was first used to
reduce the dimensionality of the environmental data into a few components, representing
the major environmental gradients in the data.

The length of the vector residual for each sample provided by ProTest can be used as a
means of investigating the deviation in the positions of individual samples between the
superimposed ordinations (Olden et al. 2001). Vector residuals from the among-year
comparisons were used to examine whether temporal concordance in assemblage patterns
was related to temporal variation in physical and chemical conditions. We first
standardized the environmental variables by their maximum values. Changes in
environmental conditions from year-to-year were estimated for each site by calculating
the Euclidean distances separately for the combined in-stream variables and water
chemistry variables. Spearman rank correlations were then calculated between the
average vector residuals for each data set and the Euclidean distances of environmental
conditions. Spearman correlations were also calculated between the average vector
residuals and means of individual environmental variables to find out which
environmental variables were most strongly related to the temporal concordance of
assemblage structure for each data set.
4 Results and discussion

4.1 Defining macroinvertebrate assemblage types

Stream macroinvertebrate assemblage structure exhibited continuous variation instead of distinct assemblage types. As indicated by the ordination analyses and MRPP, there was wide variation among sites within TWINSPLAN groupings, as well as high degrees of overlap among different groups. Furthermore, the number of effective indicator taxa was rather low, also indicating continuous variation in assemblage structure. According to CCA, variation in assemblage structure was mainly related to geographic location, water pH, and stream size, factors formerly related to major gradients in macroinvertebrate assemblage structure in Fennoscandian streams (Malmqvist & Mäki 1994, Sandin & Johnsson 2000, Paavola et al. 2000, Sandin 2003) and elsewhere (Townsend et al. 1983, Wright et al. 1984).

The absence of discrete assemblage types in boreal headwater streams may stem from a number of reasons. Benthic macroinvertebrates in these streams have wide environmental tolerances and geographic distributions (Malmqvist & Hoffsten 2000), and they may exhibit species-specific responses to environmental conditions (Hawkins & Vinson 2000). Thus, although gradients in environmental conditions and assemblage-environment relationships were quite strong, only few species were generally restricted to similar environmental conditions. Furthermore, if a system experiences frequent and unpredictable disturbances and if its biota show a high dispersal capacity, it should be controlled mostly by regional factors (Palmer et al. 1996). In general, flying stream macroinvertebrates possess a high capacity for colonization via aerial dispersal (Malmqvist 2002, Bohonak & Jenkins 2003). Therefore, although no site within a drainage system is truly beyond the range of any species, some sites will be slower to recover after temporary extinctions. Thus, regional dispersal processes may cause assemblage structure to differ from that predicted by local environmental factors, resulting in relatively low predictability of macroinvertebrate assemblage structure in boreal streams.

Given the strong patterns of geographical variation in assemblage structure, a regional stratification might provide a useful framework for the conservation evaluation and
bioassessment of boreal streams. A combination of regional delineations and predictive modelling might thus provide the best framework for the assessment of boreal headwater streams. Because macroinvertebrate assemblages exhibit continuous variation along major environmental gradients, it is likely that predictive models that do not rely on distinct site groupings might be better able to incorporate variation in reference conditions than models based on assemblage classifications (e.g., Chessman 1999, Linke et al. 2005). From the biodiversity perspective, a priori regional stratification might provide a physical surrogate of biological variation, guaranteeing that assemblages in different geographical regions acquire sufficient conservation attention.

4.2 Variability of lotic macroinvertebrates across landscape classifications

Significant among and within-region differences were observed for most of the macroinvertebrate metrics and in-stream habitat characteristics studied. For most metrics, ecoregions accounted for more variation than did drainage systems. However, a considerable portion of total variation was attributable to residuals, suggesting high among-stream variation in macroinvertebrate assemblage composition. For the principal components associated with water chemistry, regional delineations explained most of the variation, with ecoregions being clearly more influential than drainage systems. By contrast, variation in physical habitat characteristics did not show any clear regional patterns. Distinct differences attributable to stream size were observed for several metrics, especially total number of taxa and abundance of algae-scraping invertebrates.

Among-ecoregion differences in taxonomic composition were paralleled by variation in the functional composition of the benthic fauna. This is hardly surprising since pH and water colour (the water chemistry variables that were strongly related to among-ecoregion differences) are among the most important factors controlling macroinvertebrate assemblages in boreal streams (Malmqvist & Mäki 1994, Paavola et al. 2000). Among-ecoregion variation may originate from differences in acid-tolerance of functional groups such as scrapers and shredders (Hämäläinen & Huttunen 1990, Dangles et al. 2004). Alternatively, these differences may stem from regional differences in water colour, which may indirectly control algal resources available to scrapers, thereby affecting their distribution (Otto & Svensson 1983, Vuori & Muotka 1999). However, functional composition also varied considerably among streams within drainage systems, suggesting that local-scale factors related to in-stream habitat structure also had a strong role in controlling the distributions of functional feeding groups.

Despite the relatively narrow gradient in stream size (1st to 3rd order streams), surprisingly distinct differences attributable to stream size were observed for several macroinvertebrate metrics. Longitudinal shifts in assemblage structure is one of basic tenets of the River Continuum Concept (Vannote et al. 1980), and it has been shown repeatedly that stream size is indeed a major factor influencing the taxonomic composition of macroinvertebrate assemblages, with distinctly different communities in, for example, headwaters vs. mid-sized streams (Malmqvist & Mäki 1994, Wiberg-Larsen et al. 2000). However, since all the streams studied were headwater streams, it seems that
even within a relatively narrow size range, the influence of the riparian zone on macroinvertebrate assemblage composition decreases rapidly with increasing stream size. Because ecoregions do not always partition variation in assemblage structure, it has been suggested that they should only be used for initial spatial stratification, accompanied by reach-scale environmental predictors of macroinvertebrate assemblage composition (Hawkins et al. 2000, Sandin & Johnson 2000, Heino et al. 2002). The present results support these conclusions, since among-stream variation was the most important source of variation for most of the metrics studied. Furthermore, macroinvertebrate metrics commonly used in stream bioassessment were strongly affected by scale-dependent variation in macroinvertebrate distributions. Thus, although ecoregions accounted for a considerable amount of variation for many metrics, high within-region variation suggests that regional delineations do not provide a satisfactory background for stream bioassessment. A three-tiered classification system, that is, stratification through ecoregion or some other regional delineation and habitat type (e.g., headwaters vs. large rivers), and assemblage prediction within such ecologically meaningful and spatially restricted units, will likely provide the most effective basis for the bioassessment of boreal running waters.

4.3 Assessing physical surrogates of stream biodiversity

There were weak but significant differences in assemblage structure between the tributaries of Koutajoki drainage system based on abundance data, but no significant differences were found when analyses were based on presence-absence data. Classification strengths were very low. Significant differences and higher classification strengths were found in stream type comparisons. Classifications strengths were, however, only marginally higher for cluster classifications than stream type classifications. Despite low classification strengths, stream types differed significantly in assemblage structure in each tributary based on MRPP. These differences were rather weak, however, as evidenced by both low values of MRPP’s A statistic and the fact that there was wide variation within and considerable overlap between the stream types in assemblage structure in the NMDS ordinations. Overall, lake outlets showed the clearest separation from the other stream types in each tributary. Only a few taxa were strong indicators of a single stream type. By contrast, several species were either common to all stream types or occurred on a couple of sites only, and were thus of limited value in discriminating between the stream types.

Taxonomic richness varied significantly between both tributaries and stream types. Pairwise comparison indicated that the taxonomic richness in the streams of the Kitkajoki tributary differed from those of the other two tributaries, and that small streams differed from the mid-sized and large streams. However, there were no differences in taxonomic richness between outlets, mid-sized streams and large streams. In within tributary comparisons of stream types, there was a general trend for increasing diversity from small to large streams, with lake outlets having intermediate taxonomic richness.

To be effective in practice, landscape classifications or physical surrogates should follow easily distinguishable landscape classes, classes should be few in number, and
they should reflect ecologically important factors for the biota (Orians 1993, Angermeier & Schlosser 1995, Karr & Chu 1999). In this respect, our a priori tributary and stream type classifications surely fill these expectations. While our tributary classifications might portray spatial proximity effects and dispersal, our stream type classifications reflected stream size, riparian shading, and productivity base (e.g., Allan 1995), thereby being potentially important contributors to the characteristics of invertebrate biodiversity. Our findings, however, showed that only weak, though significant, differences existed between the a priori classifications regarding assemblage structure, number of indicator species, and taxonomic richness.

Low classification strengths reflected the relatively low within-group similarity and surprisingly low between-group heterogeneity. These patterns likely resulted from the facts that most stream macroinvertebrate taxa show individualistic responses to environmental gradients, thereby leading to continuous variability of assemblage structure. Many taxa also occur either across all stream types or only sporadically in a given stream type, and only a few species show high fidelity to a given stream type. Overall, these patterns suggest that stream macroinvertebrate assemblages are dominated by taxa that are widely distributed across the stream types. This finding is somewhat similar to that found recently for terrestrial plant, invertebrate and microbial biodiversity (Oliver et al. 2004).

The weak classification patterns and barely significant differences in taxonomic richness between the surrogate classes may also reflect a relatively poor match between stream type classifications and local environmental factors, because macroinvertebrates respond strongly to a more localised variation in water chemistry and in-stream variables (e.g., Malmqvist & Hoffsten 2000, II). Although several key environmental factors follow our stream type classifications (e.g., stream width, discharge), others (e.g., moss cover, particle size) are likely to vary considerably within each stream type. Predicting assemblage structure and biodiversity (e.g., Linke & Norris 2003) would thus benefit from using continuous variables instead of stream type classes. However, for the purpose of conservation planning, physical surrogate classes are probably more heuristic than continuous environmental variables, thereby justifying their limitations in capturing the continuous variability of assemblage structure, species distributions, and taxonomic richness.

Landscape classifications thus provide at least a preliminary approach for the conservation planning of running water biodiversity. The use of such surrogates is supported by the fact that stream size can shape the assemblage structure and biodiversity of widely varying taxa (Angermeier & Winston 1999, Malmqvist & Hoffsten 2000, Grenouillet et al. 2004, Heino et al. 2005), although no single group is likely to show a perfect match to any landscape classification. This match could be increased, however, by incorporating more detailed landscape classifications in biodiversity surrogate schemes. A future modification of our stream type classification will incorporate, for example, the division of each stream type into wetland-influenced and non-wetland influenced, as wetlands strongly characterise boreal catchments. Such additional divisions will also help one to combine terrestrial landscape characteristics and associated patterns of biodiversity to those of stream biodiversity, leading to a more balanced approach for conservation planning at the watershed level.
4.4 Scale-related variation in environmental relationships and spatial structures of stream macroinvertebrate assemblages

The strength of the relationship between assemblage structure and local environmental variables increased with decreasing scale, whereas assemblage variation related to spatial variables and spatially structured environmental variation showed the opposite pattern. At the largest scale, spatial variation was related to latitudinal gradients, whereas spatial autocorrelation among neighbouring streams was the likely mechanism creating spatial structure within drainage systems.

Many large-scale surveys have suggested that variation in stream macroinvertebrate assemblages may show stronger correspondence to large-scale regional factors than to local habitat conditions (e.g., Corkum 1989, Richards et al. 1996). The geographical extent of this study was relatively large and although the importance of geographical gradients was evident, local environmental conditions appeared more influential in structuring macroinvertebrate assemblages, even at the largest study scale. However, the present results also suggested that the influence of geographical extent may not only be related to species distribution patterns, but also to spatial structuring of environmental conditions. There was also a relatively strong spatial component of variation that was unrelated to environmental conditions even within drainage systems.

Spatial autocorrelation among neighbouring streams may result from extinction-recolonisation dynamics (e.g., Magahães et al. 2002, Cottenie et al. 2003). Many flying stream macroinvertebrates possess a high capacity for dispersal (Malmqvist 2002), and it has been suggested that, within a drainage system, the distributions of stream insects capable of aerial dispersal should not be strongly affected by geographical location (Townsend et al. 2003). In our study, however, spatial structure was relatively strong within some drainage systems, suggesting that not only poor disperses, but also a wider array of species may have been affected by spatial location. Therefore, it is probable, that regional dispersal processes may result in assemblage structure differing from that predicted by environmental variables, and they may therefore be responsible for the weak predictability of assemblage types in boreal headwater streams (I).

Only stream size and acidity appeared consistently important in explaining assemblage structure at all spatial extents, while the influence of in-stream characteristics and other water chemistry variables was more context-specific. Furthermore, there was a positive relationship between the explanatory power of variables significant in CCA and their ranges of variation, indicating that the importance of local environmental variables depends on the regional context.

Spatial structure in stream assemblages should be considered in applied research, considering that important assemblage gradients may not only be related to local environmental factors, but also to biogeographical constraints and neighbourhood dispersal processes, and more importantly, to spatial structuring in local environmental conditions. If not accounted for, such within-ecoregion and within-drainage system variation may pose a serious risk to comparisons between reference and impacted sites in assessments that rely on regional reference conditions. Furthermore, many important environmental variables may be context-dependent, such that their importance varies among regions and drainage systems, and very few environmental variables are thus
likely to be universally important contributors to assemblage structure. Finally, our findings suggest that models of assemblage structure that utilize environmental variables are likely to be more successful when devised for drainage systems as opposed to larger geographical regions, where biogeographical factors and dispersal limitation may have more pronounced roles.

4.5 Temporal variation in assemblage classifications and assemblage-environment relationships

The classification strengths of macroinvertebrate assemblages based on three-years of data from the Koutajoki river system were overall rather weak, and more importantly, the composition of the site groups was not stable, but varied considerably from year to year. Such wide and continuous variation was also mirrored by low consistency and predictability of classifications. The relative importance of discriminating environmental variables also varied widely among data sets and study years, thus providing only weak support for generalizations about the relationships between assemblage types and environmental conditions.

Increased temporal variation in assemblage structure was related to increased temporal variation in physical environmental conditions and decreasing cover of aquatic macrophytes, although these relationships were not evident for chironomids. The positive relationship between temporal stability of non-chironomid macroinvertebrates and macrophyte cover may be related to increased habitat complexity, a factor related to the stability of stream macroinvertebrate assemblage structure (Suren & Winterbourn 1992, Holomuzki & Biggs 2000).

The site groupings differed considerably between chironomids and non-chironomid invertebrates. Similar low congruence between the diversity of chironomid midges and other major lotic insect groups were also found by Heino et al. (2003), who suggested that the environmental responses of these groups are too different to allow any predictions of variation in other taxonomic groups to be made. The predictability of classifications and the temporal concordance of assemblage patterns were also lower for chironomids in comparison to other taxonomic data sets, suggesting that a random component of variation in assemblage-environment relationships may be larger for chironomid midges than for other macroinvertebrate taxa.

A high sensitivity of assemblage classifications to temporal variation may not pose a serious risk to predictive approaches typically used in the bioassessment of benthic assemblages (RIVPAC-type approaches), since these generally include some probability threshold for species occurrence in comparisons between reference and potentially impacted sites (see e.g., Marchant et al. 1997). From the conservation perspective, however, *a posteriori* cluster classifications are rather problematic if there is considerable temporal variability in assemblage structure and assemblage-environment relationships. Landscape classifications might provide an alternative strategy to partition variation in macroinvertebrate assemblages for the purposes of conservation planning. Furthermore, in the face of temporal stability of assemblage classifications, landscape classifications have clear benefits, because the composition of the site groups remains the same over the
years. Therefore, although stream macroinvertebrates are unlikely to show a perfect match to any classification, landscape surrogates might provide at least a preliminary framework for the conservation planning of headwater streams.
5 Implications for conservation and management

Freshwater biodiversity is rapidly declining globally. Thus, it is not surprising that the reasons for this decline, e.g., decrease in the quality of freshwater environments, have gained increased attention (Allan & Flecker 1993, Malmqvist & Rundle 2002). Nevertheless, there is still a paucity of studies that have rigorously examined the state of freshwater biodiversity in near-pristine ecosystems; yet this is a prerequisite for the implementation of effective management programs. The main objective of this thesis was to examine the utility of biological and landscape classifications as the basis of stream bioassessment and conservation programs. An important finding was that a combination of regional stratification and predictive models based on stream environmental conditions seems to provide the most comprehensive framework for the characterization of macroinvertebrate assemblages in boreal streams. Indeed, given the strong influence of regional factors and spatial structuring of environmental conditions at the level of ecoregions (IV), it is likely that predictive models are more efficient when devised at smaller-scale geographical units, such as single drainage systems. Smaller-scale geographical units would also increase the predictability of assemblage-environment relationships, leading to more parsimonious models with higher overall performance (see Van Sickle et al. 2006).

Predictive models typically used in freshwater bioassessment (e.g., RIVPACS-type models) should be based on landscape-level predictors that are not influenced by anthropogenic activities (e.g., catchment size, underlying geology). The efficiency of any predictive model depends on its ability to characterize the factors that control the distribution of the organisms concerned, and this may bear a close relationship to the degree of environmental variation across the suite of sites studied. Thus, it is possible that landscape variables may not vary sufficiently to allow discrimination of sites within relatively restricted areas such as drainage systems. Some studies have shown, however, that landscape variables may have relatively high explanatory power even within a single catchment (Townsend et al. 2003), indicating their potential use in predictive approaches at smaller scales than are typically used in bioassessment programs. Because the landscape variables do not vary over time, their use would obviously increase the temporal stability of the models, although temporal variation in assemblage structure could still be problematic. Thus, if there is considerable temporal variability, it might be
necessary to consider alternative approaches such as predictive models that do not rely on groupings of reference sites (e.g., Linke et al. 2005) or the use of landscape and stream type classifications (III).

Given that inclusion of higher order streams into a stream classification framework would almost certainly result in a predominantly size-related gradient (e.g., Malmqvist and Mäki 1994, Angermeier and Winston 1999), it is not surprising that classification strengths in Koutajoki drainage system were only marginally higher for cluster classifications than stream type classifications (III). Such strong influence of stream size could, however, obscure the detection of other biologically relevant trends that could be important in explaining variation within stream types in this classification framework. Thus, when the purpose is conservation planning of streams within a single stream type (e.g., headwater streams) more detailed biodiversity inventories should be incorporated into classification framework to allow detection of sites with high conservation value. This could include sites with high species diversity, high number of rare species or unusual species combinations. Furthermore, it would be important that the utility of a classification framework was tested using multiple organism groups (e.g., Whittier et al. 1988).

The importance of assessing environmental changes using multiple organism groups has gained increased attention, and the multi-taxon approach has recently become an official policy in the European Union Water Framework Directive. Recent studies have shown, however, that the degree of concordance between different freshwater organism groups is typically rather low, mainly because of deviating environmental responses of different groups (Heino et al. 2003, Declerck et al. 2005, Paavola et al. 2006). Such deviating environmental responses could also indicate that landscape classifications, or any other a priori classification, may not partition assemblage variation effectively for multiple organism groups (Mazor et al. 2006). By contrast, in predictive modelling, the predictions for each taxonomic group are modelled separately and are not related to the typologies of reference sites of the other organism groups. Predictions from these models are thus directly linked to environmental gradients important to each organism group. Predictive models have been shown to perform relatively well also for other groups than benthic macroinvertebrates (Joy & Death 2002, Mazor et al. 2006), and they could thus provide a more suitable framework for the multi-taxon assessment than a priori landscape classifications that may not necessarily represent environmental gradients of equal importance to multiple organism groups (see also Knapp et al. 2005). Furthermore, it has been suggested that predictive models could also be used to detect sites with exceptionally high species richness, i.e., sites of potentially high conservation value (Wright 2000, Linke & Norris 2003). This application of predictive modelling remains to be assessed rigorously, but the detection of such exceptionally diverse sites using multiple organism groups would provide an interesting alternative to more traditional ways of examining biodiversity patterns in freshwater ecosystems.
6 Suggestions for future research

Not surprisingly, the research conducted for this thesis raised several questions for future studies. For example, spatial structuring within drainage systems (IV) as well as differences in community stability among sites (V) may indicate strong influence of regional processes (e.g., dispersal, climate forcing) in structuring local communities and potential existence of metacommunity dynamics among streams. In a metacommunity context, sites with stable conditions and stable assemblages may act as sources for other sites (“sinks”) that harbour less stable communities (Pulliam 1988, Leibold et al. 2004). Metacommunity dynamics remain, however, poorly understood for most organism groups, including stream macroinvertebrates.

Spatial structure can arise either from the homogenizing effect of dispersal or dispersal limitation (Hubbell 2001, Cottenie et al. 2003). The potential influence of dispersal in structuring assemblages could thus be related to the dispersal ability of species, with poor dispersers showing strongly spatially structured communities, whereas strong dispersers should be more or less uniformly distributed across a suite of sites. Clarifying variation in metacommunity dynamics among stream macroinvertebrates with differing capabilities of dispersal could provide more comprehensive understanding of the relative roles of local and regional drivers in structuring stream communities, thus representing a fruitful area for future research in stream systems.

Examination of the functional organization of stream macroinvertebrate assemblages provides an alternative way to study the structuring of stream assemblages. While taxonomic structure is likely to be strongly affected by the regional species pool, thus reflecting biogeographical processes, functional structure of stream assemblages is probably more closely associated with local habitat conditions (Poff 1997, but see Lamouroux et al. 2004). The weak influence of regional filters on functional structure has indeed been shown in a number of studies that have examined large-scale patterns in the trait structure of stream macroinvertebrate assemblages (e.g., Stazner et al. 2001, 2004). These studies have been conducted in large rivers, however, and it is unclear whether the observed patterns could be extrapolated to headwater streams, where functional structure can exhibit strong geographical patterns (Heino et al. 2002, Heino 2005, II). Furthermore, the findings from the few studies that have simultaneously compared assemblage patterns using both taxonomic and functional structure have been somewhat mixed. Some studies
have suggested that both taxonomic and functional trait structure vary similarly along the same environmental gradients (Finn and Poff 2005), while others have shown that the relative importance of ecological gradients varies between taxonomic and functional structure (Johnson et al. 2004). More work is thus needed to clarify the relative importance of different ecological filters in shaping taxonomic structure versus functional structure of stream assemblages.

The use of functional structure in the context of bioassessment has also gained increased attention. Recently, Pont et al. (2006) introduced a novel approach for assessing biotic conditions using fish-based functional metrics at the continental scale across a wide variety of stream types. In this approach, the influence of natural environmental characteristics on different functional metrics was accounted for by regressions using only a few stream type-specific and region-specific variables. Subsequently, residuals were used to model the response of the developed functional index to a gradient of human disturbance. The constructed index was highly sensitive to this gradient, and the authors suggested that the principles of their method could be applied to a wide variety of organism groups. Diagnostic properties are almost entirely lacking from the toolbox typically used in freshwater bioassessment. However, it would be highly important that the magnitude of changes in local biotic conditions could be directly related to the level of anthropogenic disturbance. The ideas of Pont et al. (2006) seem highly promising in this regard, and future studies should assess whether such an approach could be applied to predict the expected composition of stream assemblages at specific levels of anthropogenic disturbance. While not arguing against the need to develop continent-wide assessment methods, it seems clearly more important to model the relationships between assemblages and anthropogenic disturbances at the level of catchments, because this is the scale at which impacted streams are eventually restored and monitored. The development of such diagnostic approaches is undoubtedly among the most important future tasks in freshwater bioassessment.
References


Original papers


Original publications are not included in the electronic version of the dissertation.

454. Taskinen, Jukka (2006) Protein crystallographic studies of CoA-dependent proteins: new insight into the binding mode and exchange mechanism of acyl-CoA

455. Molin-Juustila, Tonja (2006) Cross-functional interaction during the early phases of user-centered software new product development: reconsidering the common area of interest


459. Mutanen, Marko (2006) Genital variation in moths—evolutionary and systematic perspectives

460. Bhaumik, Prasenjit (2006) Protein crystallographic studies to understand the reaction mechanism of enzymes: α-methylacyl-CoA racemase and argininosuccinate lyase


464. Rönkä, Antti (2006) Dynamics, genetic structure and viability of a small and declining Temminck’s stint (Calidris temminckii) population


Heikki Mykrä

SPATIAL AND TEMPORAL VARIABILITY OF MACROINVERTEBRATE ASSEMBLAGES IN BOREAL STREAMS: IMPLICATIONS FOR CONSERVATION AND BIOASSESSMENT