

Heikki Mykrä

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

FACULTY OF SCIENCE,
DEPARTMENT OF BIOLOGY,
UNIVERSITY OF OULU

A

SCIENTIAE RERUM
NATURALIUM



UNIVERSITY OF OULU

ACTA UNIVERSITATIS OULUENSIS
A Scientiae Rerum Naturalium 468

HEIKKI MYKRÄ

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

Academic Dissertation to be presented with the assent of
the Faculty of Science, University of Oulu, for public
discussion in Kuusamonsali (Auditorium YB210),
Linnanmaa, on September 23rd 2006, at 12 noon

OULUN YLIOPISTO, OULU 2006

Copyright © 2006
Acta Univ. Oul. A 468, 2006

Supervised by
Professor Timo Muotka
Doctor Jani Heino

Reviewed by
Doctor Russell Death
Doctor Leonard Sandin

ISBN 951-42-8181-0 (Paperback)
ISBN 951-42-8182-9 (PDF) <http://herkules.oulu.fi/isbn9514281829/>
ISSN 0355-3191 (Printed)
ISSN 1796-220X (Online) <http://herkules.oulu.fi/issn03553191/>

Cover design
Raimo Ahonen

OULU UNIVERSITY PRESS
OULU 2006

Mykrä, Heikki, Spatial and temporal variability of macroinvertebrate assemblages in boreal streams: implications for conservation and bioassessment

Faculty of Science, Department of Biology, University of Oulu, P.O.Box 3000, FI-90014 University of Oulu, Finland

Acta Univ. Oul. A 468, 2006

Oulu, Finland

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

Acknowledgements

First, I would like to express my gratitude to my supervisors Timo Muotka and Jani Heino. I am grateful to Timo for introducing me to the fascinating world of streams and guiding and supporting me during the years of this study. Jani is also a close friend and helped me in many ways in planning studies and constructing manuscripts, but in particular, I am grateful to him for many inspiring discussions we have had. Second, I would like to thank the members of our research group: Anna Astorga, Antti Haapala, Antti Juntunen, Irma Kananen, Saija Koljonen, Kai Korsu, Petri Liljaniemi, Kristian Meissner, Riku Paavola and Jukka Syrjänen. They were always helpful and good company during these years. I would also like to thank all my friends in the Department of Biological and Environmental Science at University of Jyväskylä. Discussions with Heikki Hämäläinen and Kari-Matti Vuori greatly improved my thinking about issues related to the bioassessment of streams and lakes. Special thanks to Jukka Aroviita for helping me with data preparation and statistics. John Loehr checked the language of this thesis. A major part of this study was carried out at the Department of Biological and Environmental Science of University of Jyväskylä. I am grateful to professors Pauli Bagge and Roger Jones for providing me working facilities in Jyväskylä. This thesis is a part of the Finnish Biodiversity Research Program (FIBRE), and has been funded by the Academy of Finland. Financial support was also provided by the Maj and Tor Nessling Foundation, Ministry of Agriculture and Forestry, and University of Oulu.

I would like to thank to my parents and sisters for their never-ending support during this work and years before that. I especially thank my little sister Tuija, who initially suggested me the idea to begin study biology. Above all, I would like to thank my wife Teija and our sons Vikke and Otto for their love and patience during these years.

List of original papers

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

- I Heino J, Muotka T, Mykrä H, Paavola R, Hämäläinen H & Koskenniemi E (2003) Defining macroinvertebrate assemblage types of headwater streams: implications for bioassessment and conservation. *Ecological Applications* 13: 842-852.
- II Mykrä H, Heino J & Muotka T (2004) Variability of lotic macroinvertebrate assemblages and stream habitat characteristics across hierarchical landscape classifications. *Environmental Management* 34: 341-352.
- III Heino J & Mykrä H (2006) Assessing physical surrogates for biodiversity: do tributary and stream type classifications reflect invertebrate assemblage diversity in running waters? *Biological Conservation* 129: 418-426.
- IV Mykrä H, Heino J & Muotka T (2006) Scale-related patterns in the spatial and environmental components of stream macroinvertebrate assemblage variation: large-scale gradients and neighbourhood effects. *Global Ecology and Biogeography*. In press.
- V Mykrä H, Heino J & Muotka T (2006) How general are patterns emerging from single-year biodiversity surveys? Temporal variability of assemblage classifications and assemblage-environment relationships in stream macroinvertebrates. (manuscript)

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 practises (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 constraints 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).

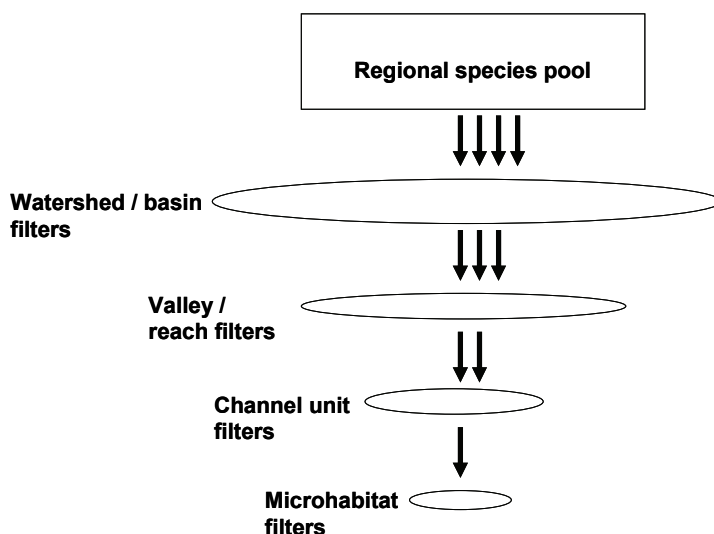


Fig. 1. Environmental filters selecting species with suitable traits at different scales. Modified from Poff (1997).

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 (Weatherley & 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, Wrigth *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 TWINSPAN 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. Classification 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., Magalhães *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

- Allan JD (1995) Stream Ecology. The Structure and Function of Stream Ecosystems. Chapman and Hall, London.
- Allan JD & Flecker AS (1993) Biodiversity conservation in running waters. *Bioscience* 43: 32-43.
- Angermeier PL & Schlosser IJ (1995) Conserving aquatic biodiversity: beyond species and populations. *American Fisheries Society Symposium* 17: 402-414.
- Angermeier PL & Winston MR (1997) Assessing conservation value of stream communities: a comparison of approaches on centres of density and species richness. *Freshwater Biology* 37: 699-710.
- Angermeier PL Winston MR (1999) Characterizing fish community diversity across Virginia landscapes: prerequisite for conservation. *Ecological Applications* 9: 335-349.
- Atlas of Finland (1988) Biogeography and nature conservation. Folio 141-143. National Board of Survey and Geographic Society of Finland, Helsinki.
- Bohonak AJ & Jenkins DG (2003) Ecological and evolutionary significance of dispersal by freshwater invertebrates. *Ecology Letters* 6: 783-796.
- Borcard D, Legendre P & Drapeau P (1992) Partialling out the spatial component of ecological variation. *Ecology* 73: 1045-1055.
- Chessman BC (1999) Predicting the macroinvertebrate faunas of rivers by multiple regression of biological and environmental differences. *Freshwater Biology* 41: 747-757.
- Cooper SD, Diehl S, Kratz K & Sarnelle O (1998) Implications of scale for patterns and processes in stream ecology. *Australian Journal of Ecology* 23: 27-40.
- Corkum L (1989) Patterns of benthic invertebrate assemblages in rivers of northwestern North America. *Freshwater Biology* 21: 191-205.
- Corkum L (1990) Intra-biome distributional patterns of lotic macroinvertebrate assemblages. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 2147-2157.
- Cottenie K, Michels E, Nuytten N & De Meester L (2003) Zooplankton metacommunity structure: regional vs. local processes in highly interconnected ponds. *Ecology* 84: 991-1000.
- Dangles O Malmqvist B & Laudon H (2004) Naturally acid freshwater ecosystems are diverse and functional: evidence from boreal streams. *Oikos* 104: 149-155.
- Declerck S, Vandekerkhove J, Johansson L, Muylaert K, Conde-Porcuna JM, Van Der Gucht K, Pérez-Martínez C, Lauridsen T, Shwenk K, Zwart G, Rommens W, López-Ramos J, Jeppesen E, Vyverman W, Brendonck L & De Meester L (2005) Multi-group biodiversity in shallow lakes along gradients of phosphorus and water plant cover. *Ecology* 86: 1905-1915.
- Digby PGN & Kempton RA (1987) Multivariate analysis of Ecological Communities. Chapman and Hall. New York.

- Dufrene M & Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 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.
- Feminella J (2000) Correspondence between stream macroinvertebrate assemblages and 4 ecoregions of the southeastern USA. *Journal of the North American Benthological Society* 19: 442-461.
- Ferrier S (2002) Mapping spatial patterns in biodiversity for regional conservation planning: where to from here? *Systematic Biology* 51: 331-363.
- Finn DS & Poff NL (2005) Variability and convergence in benthic communities along the longitudinal gradients of four physically similar Rocky Mountain streams. *Freshwater Biology* 50: 243-261.
- Frissell CA, Wiss WJ, Warren CE & Huxley MD (1986) A hierarchical framework for stream classification: viewing streams in watershed context. *Environmental Management* 10:199-214.
- Grenouillet G, Pont D & Hérissé C (2004) Within-basin fish assemblage structure: the relative influence of habitat versus stream spatial position on local species richness. *Canadian Journal of Fisheries and Aquatic Sciences* 61: 93-102.
- Hämäläinen H & Huttunen P (1990) Estimation of acidity in streams by means of benthic invertebrates: evaluation of two methods. In: Kauppi P, Anttila P & Kenttämies K. (eds.) *Acidification in Finland*. Springer, Berlin: 1051-1070.
- Hawkins CP, Norris RH, Gerritsen J, Hughes RM, Jackson SK, Johnson RK & Stevenson RJ (2000) Evaluation of the use of landscape classifications for the prediction of freshwater biota: synthesis and recommendations. *Journal of the North American Benthological Society* 19: 541-556.
- Hawkins CP & Vinson MR (2000) Weak correspondence between landscape classifications and stream invertebrate assemblages: implications for bioassessment. *Journal of the North American Benthological Society* 19: 501-517.
- Heino J (2005) Functional biodiversity of macroinvertebrate assemblages along major environmental gradients of boreal headwater streams. *Freshwater Biology* 50: 1578-1587.
- 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.
- Heino J, Muotka T Paavola R & Paasivirta L (2003). Among-taxon congruence in biodiversity patterns: can stream insect diversity be predicted using single taxonomic groups? *Canadian Journal of Fisheries and Aquatic Sciences* 60: 1039-1049.
- Heino J, Paavola R, Virtanen R & Muotka T (2005) Searching for biodiversity indicators in running waters: do bryophytes, macroinvertebrates, and fish show congruent diversity patterns? *Biodiversity and Conservation* 14: 415-428.
- Holomuzki JR & Biggs BJB (2000) Taxon-specific responses to high-flow disturbances in streams: implications for population persistence. *Journal of the North American Benthological Society* 19: 670-679.
- Hubbell SP (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton.
- Humphrey CL, Storey AW & Thurtell L (2000) AUSRIVAS: operator sample processing errors and temporal variability – implications for model sensitivity. In: Wright JF, Sutcliffe DW & Furse MT (eds) *Assessing the biological quality of fresh waters: RIVPACS and other techniques*. Freshwater Biological Association, Ambleside, UK.
- Johnson RK (2003) Development of a prediction system for lake stony-bottom littoral macroinvertebrate communities. *Archiv für Hydrobiologie* 158: 517-540.

- Johnson RK, Goedkoop W & Sandin L (2004) Spatial scale and ecological relationships between the macroinvertebrate communities of stony habitats of streams and lakes. *Freshwater Biology* 49: 1179-1194.
- Joy MK & Death RG (2002) Predictive modelling of freshwater fish as a biomonitoring tool in New Zealand. *Freshwater Biology* 47: 2261-2275.
- Karr JR & Chu EW (1999) Restoring life in running waters: better biological monitoring. Island Press, Covelo.
- Keddy PA (1992) Assembly response rules: two goals for predictive community ecology. *Journal of Vegetation Science* 3: 157-164.
- Knapp, RA, Hawkins CP, Ladau J & McClory JG (2005) Fauna of the national park lakes has low resistance but high resilience to fish introductions. *Ecological Applications* 15: 835-847.
- Lammert M & Allan JD (1999) Assessing biotic integrity of streams: effects of scale in measuring the influence of land use/cover and habitat structure on fish and macroinvertebrates. *Environmental Management* 23: 257-270.
- Lamouroux N, Dolédec S & Gyraud S (2004) Biological traits of stream macroinvertebrate communities: effects of microhabitat, reach, and basin filters. *Journal of the North American Benthological Society* 23: 449-466.
- Legendre P & Legendre L (1998) *Numerical Ecology*. Developments in Environmental Modeling 20. Elsevier, Amsterdam.
- Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt, RD, Shurin JB, Law R, Tilman D, Loreau M & Gonzales A (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, 7: 601-613.
- Li J, Herlihy A, Gerth W, Kaufman P, Gregory S, Urquhart S & Larsen DP (2001) Variability in stream macroinvertebrates at multiple spatial scales. *Freshwater Biology* 46: 87-97.
- Linke S & Norris R (2003) Biodiversity: bridging the gap between condition and conservation. *Hydrobiologia* 500: 203-211.
- Linke S, Norris RH, Faith DP & Stockwell D (2005) ANNA: A new prediction method for bioassessment programs. *Freshwater Biology* 50: 147-158.
- Magalhães MF, Batalha DC, Collares-Perreira MJ (2002) Gradients in stream fish assemblages across a Mediterranean landscape: contributions of environmental factors and spatial structure. *Freshwater Biology* 47: 1015-1031.
- Malmqvist B (2002) Aquatic invertebrates in riverine landscapes. *Freshwater Biology* 47: 679-694.
- Malmqvist B & Mäki M (1994) Benthic macroinvertebrate assemblages in north Swedish streams: environmental relationships. *Ecography* 17: 9-16.
- Malmqvist B & Hoffsten PO (2000) Macroinvertebrate taxonomic richness, community structure and nestedness in Swedish streams. *Archiv für Hydrobiologie* 150: 29-54.
- Malmqvist B & Rundle S (2002) Threats to running water ecosystems of the world. *Environmental Conservation* 29: 134-153.
- Marchant R, Hirst A, Norris RH, Butcher R, Metzeling L & Tiller D (1997) Classification and prediction of macroinvertebrate assemblages from running waters in Victoria, Australia. *Journal of the North American Benthological Society* 16: 664-681.
- Mazor RD, Reynoldson TB, Rosenberg DM & Resh VH (2006) Effects of biotic assemblage, classification and assessment method on bioassessment performance. *Canadian Journal of Fisheries and Aquatic Sciences* 63: 394-411.
- McCune B & Mefford MJ (1999) *PC-Ord. Multivariate Analysis of Ecological Data*. Version 4.0. MjM Software, Glenden Beach, Oregon.
- McCune B & Grace JB (2002) *Analysis of Ecological Communities*. MJM Software, Oregon.
- Menge BA & Olson AM (1990) Role of scale and environmental factors in regulation of community structure. *Trends in Ecology and Evolution* 5: 52-57.

- Morrisey DJ, Howitt L, Underwood AJ & Stark JS (1992) Spatial variation in soft-sediment benthos. *Marine Ecology Progress Series* 81: 197-204.
- Moss D, Wright JF, Furse MT & Clarke RT (1999) A comparison of alternative techniques for prediction of the fauna of running waters in Great Britain. *Freshwater Biology* 41: 167-181.
- Mykrä H, Muotka T & Ruokonen T (2006) The effect of sample duration on the efficiency of kick-sampling in two streams with contrasting substratum heterogeneity. *Verhandlungen der internationalen Vereinigung für theoretische und angewandte Limnologie*: 29:1351-1355.
- Nordic Council of Ministers (1984) *Naturgeografisk regionindelning av Norden*. Nordiska Ministerrådet, Oslo, Norway.
- Olden JD, Jackson DA & Peres-Neto PR (2001) Spatial isolation and fish communities in drainage lakes. *Oecologia* 127:572-585.
- Oliver I, Holmes A, Dangerfield JM, Gillings M, Pik AJ, Britton DR, Holley M, Montgomery ME, Raison M, Logan V, Pressey RL & Beattie A (2004) Land systems as surrogates for biodiversity in conservation planning. *Ecological Applications* 14: 485-503.
- Orians GH (1993) Endangered at what level? *Ecological Applications* 3: 206-208.
- Otto C & Svensson B (1983) Properties of acid brown water streams in South Sweden. *Archiv für Hydrobiologie* 99:15-36.
- Paavola R, Muotka T & Tikkanen P (2000) Macroinvertebrate community structure and species diversity in humic streams of Finnish Lapland. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie* 27: 2550-2555.
- Paavola R, Muotka T, Virtanen R, Heino J, Jackson D, & Mäki-Petäys A (2006) Spatial scale affects community concordance among fishes, benthic macroinvertebrates and bryophytes in streams. *Ecological Applications* 16: 368-379.
- Palmer MA, Allan JD & Butman CA (1996) Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. *Trends in Ecology and Evolution* 11: 322-326.
- Poff NL (1997) Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* 16: 391-409.
- Pont D, Huguency B, Beier U, Goffaux D, Melcher A, Noble R, Rogers C, Roset N & Schmutz S (2006) Assessing river biotic condition at a continental scale: a European approach using functional metrics and fish assemblages. *Journal of Applied Ecology* 43: 70-80.
- Pulliam HR (1988) Sources, sinks, and population regulation. *American Naturalist* 132: 652-661.
- Rabeni CF & Doisy KE (2000) Correspondence of stream benthic invertebrate assemblages to regional classification schemes in Missouri. *Journal of the North American Benthological Society* 19: 419-428.
- Reynoldson TB, Norris RH, Resh VH, Day KE & Rosenberg DM (1997) The reference condition: a comparison of multimetric and multivariate approaches to assess water-quality impairment using benthic macroinvertebrates. *Journal of the North American Benthological Society* 16: 833-852
- Reynoldson TB, Rosenberg DM, & Resh VH (2001) Comparison of models predicting invertebrate assemblages for biomonitoring in the Fraser River catchment, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1395-1410.
- Richards C, Haro RJ, Johnson LB & Host GE (1996) Landscape-scale influences on stream habitats and biota. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 295-311.
- Richards C, Haro RJ, Johnson LB & Host GE (1997) Catchment and reach-scale properties as indicators of macroinvertebrate species traits. *Freshwater Biology* 37: 219-230.
- Robinson CT, Misnhall GW & Royer TV (2000) Inter-annual patterns in macroinvertebrate communities of wilderness streams in Idaho U.S.A. *Hydrobiologia* 421: 187-198.
- Rosenberg DM & Resh VH (1993) *Freshwater biomonitoring and benthic macroinvertebrates*. Chapman and Hall, New York.

- Sandin L (2003) Benthic macroinvertebrates in Swedish streams; community structure, taxonomic richness, and environmental relations. *Ecography* 26: 269-282.
- Sandin L & Johnson RK (2000) Ecoregions and benthic macroinvertebrate assemblages of Swedish streams. *Journal of the North American Benthological Society* 19: 462-474.
- Saunders DL, Meeiwig JJ & Vincent ACJ (2001) Freshwater protected areas: strategies for conservation. *Conservation Biology* 16: 30-41.
- Scarsbrook MR (2002) Persistence and stability of lotic invertebrate communities in New Zealand. *Freshwater Biology* 47: 417-431.
- Snelder, TH, Cattaneo F, Suren A M & Biggs BJ (2004) Is the river environment classification an improved landscape-scale classification of rivers? *Journal of the North American Benthological Society* 23: 580-598.
- Statzner B, Bis B, Dolédec & Usseglio-Polatera P (2001) Perspectives for biomonitoring at large spatial scales: a unified measure for the functional composition of invertebrate communities in European running waters. *Basic and Applied Ecology* 2: 73-85.
- Stazner B, Dolédec S & Hugueny B (2004) Biological trait composition of European stream invertebrate communities: assessing the effects of various trait filter types. *Ecography* 27: 470-488.
- Suren AM & Winterbourn MJ (1992) The influence of periphyton, detritus and shelter on invertebrate colonisation of aquatic bryophytes. *Freshwater Biology* 27: 327-339.
- Ter Braak CJF (1995) Ordination. In: Jongman RHG, ter Braak CJF & van Tongeren OFR (eds) *Data analysis in community and landscape ecology*. Cambridge University Press, Cambridge, UK.
- Tonn WM (1990) Climate change and fish communities: a conceptual approach. *Transactions of the American Fisheries Society* 119: 337-352.
- Townsend CR, Hildrew AG & Francis J (1983) Community structure in some southern English streams: the influence of physicochemical factors. *Freshwater biology* 13: 521-544.
- Townsend CR, Hildrew AG & Schofield K (1987) Persistence of stream invertebrate communities in relation to environmental variability. *Journal of Animal Ecology* 56: 597-613.
- Townsend CR, Dolédec S, Norris R, Peacock K, Arbuttle C (2003) The influence of scale and geography on relationships between stream community composition and landscape variables: description and prediction. *Freshwater Biology* 48: 768-785.
- Underwood AJ (1997) *Experiments in Ecology*. Cambridge University Press, Cambridge.
- Vannote RL, Minshall GW, Cummins KW, Sedell JR & Cushing CE (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37:130-137
- Van Sickle J & Hughes RM (2000) Classification strengths of ecoregions, catchments, and geographic clusters for aquatic vertebrates in Oregon. *Journal of the North American Benthological Society* 19: 370-384.
- Van Sickle J, Huff DD & Hawkins CP (2006) Selecting discriminant function models for predicting the expected richness of aquatic macroinvertebrates. *Freshwater Biology* 51: 359-372.
- Vuori KM, Joensuu I, Latvala J, Jutila E & Ahvonen A (1998) Forest drainage: a threat to benthic biodiversity of boreal headwater streams? *Aquatic Conservation Marine and Freshwater Ecosystems* 8: 745-759.
- Vuori KM & Muotka T (1999) Benthic communities in humic streams. In: Keskkitalo J & Eloranta P (eds.) *Limnology of humic waters*. Backhuys, Leiden, The Netherlands: 193-207.
- Wallace JB & Webster JR (1996) The role of macroinvertebrates in stream ecosystem functioning. *Annual Review of Entomology* 41: 115-139.
- Weatherley NS & Ormerod SJ (1990) The constancy of invertebrate assemblages in soft-water streams: implications for the prediction and detection of environmental change. *Journal of Applied Ecology* 27: 952-964.

- Whittier T, Hughes RM, & Larsen DP (1988) Correspondence between ecoregions and spatial patterns in stream ecosystems in Oregon. *Canadian Journal of Fisheries and Aquatic Sciences* 45: 1264–1278.
- Wiberg-Larsen P, Brodersen KP, Birgholm S, Gron PN, & Skriver J (2000) Species richness and assemblage structure of Trichoptera in Danish streams. *Freshwater Biology* 43: 633-647.
- Wiens J (1989) Spatial scaling in ecology. *Functional Ecology* 3: 385-397.
- Wright JF (2000) An introduction to RIVPACS. In: Wright JF, Sutcliffe DW & Furse MT (eds) *Assessing the biological quality of fresh waters: RIVPACS and other techniques*. Freshwater Biological Association, Ambleside, UK.
- Wright JF, Furse MT & Mielke PW (1998) River classification using invertebrates: RIVPACS application. *Aquatic Conservation Marine and Freshwater Ecosystems* 8: 617-631.
- Wright JF, Armitage PD & Furse MT (1984) A preliminary classification of running water sites in Great Britain based on macroinvertebrate species and the prediction of community types using environmental variables. *Freshwater Biology* 14: 1518-1527.
- Zwick P (1992) Stream habitat fragmentation – a threat to biodiversity. *Biodiversity and Conservation* 1: 80-97.
- Zimmerman GM, Goetz H & Mielke PW Jr, (1985) Use of improved statistical method for grouping comparisons to study effects of prairie fire. *Ecology* 66: 606-611.
- Zobel M (1997) The relative roles of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends in Ecology and Evolution* 12: 266-269.

Original papers

- I Heino J, Muotka T, Mykrä H, Paavola R, Hämäläinen H & Koskenniemi E (2003) Defining macroinvertebrate assemblage types of headwater streams: implications for bioassessment and conservation. *Ecological Applications* 13: 842-852.
- II Mykrä H, Heino J & Muotka T (2004) Variability of lotic macroinvertebrate assemblages and stream habitat characteristics across hierarchical landscape classifications. *Environmental Management* 34: 341-352. Reprinted with kind permission of Springer Science and Business Media.
- III Heino J & Mykrä H (2006) Assessing physical surrogates for biodiversity: do tributary and stream type classifications reflect invertebrate assemblage diversity in running waters? *Biological Conservation* 129: 418-426. Reprinted with permission of Elsevier.
- IV Mykrä H, Heino J & Muotka T (2006) Scale-related patterns in the spatial and environmental components of stream macroinvertebrate assemblage variation: large-scale gradients and neighbourhood effects. *Global Ecology and Biogeography*. In press.
- V Mykrä H, Heino J & Muotka T (2006) How general are patterns emerging from single-year biodiversity surveys? Temporal variability of assemblage classifications and assemblage-environment relationships in stream macroinvertebrates. (manuscript)

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

ACTA UNIVERSITATIS OULUENSIS
SERIES A SCIENTIAE RERUM NATURALIUM

453. Rautiainen, Pirjo (2006) Population biology of the *Primula sibirica* group species inhabiting frequently disturbed seashore meadows: implications for management
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
456. Thomson, Robert L. (2006) Breeding habitat selection and its consequences in boreal passerines. Using the spatial dispersion of predators and heterospecifics as a source of information
457. Iivari, Netta (2006) Discourses on 'culture' and 'usability work' in software product development
458. Vähöja, Pekka (2006) Oil analysis in machine diagnostics
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
461. Korkalo, Tuomo (2006) Gold and copper deposits in Central Lapland, Northern Finland, with special reference to their exploration and exploitation
462. Pahnla, Seppo (2006) Assessing the usage of personalized web information systems
463. Puhakainen, Petri (2006) A design theory for information security awareness
464. Rytönen, Anna (2006) The role of human replicative DNA polymerases in DNA repair and replication
465. Rönkä, Antti (2006) Dynamics, genetic structure and viability of a small and declining Temminck's stint (*Calidris temminckii*) population
466. Wäli, Piippa (2006) Environment and genetic background affecting endophyte-grass symbiosis
467. Broggi, Juli (2006) Patterns of variation in energy management in wintering tits (*Paridae*)

Book orders:
OULU UNIVERSITY PRESS
P.O. Box 8200, FI-90014
University of Oulu, Finland

Distributed by
OULU UNIVERSITY LIBRARY
P.O. Box 7500, FI-90014
University of Oulu, Finland

S E R I E S E D I T O R S

A
SCIENTIAE RERUM NATURALIUM
Professor Mikko Siponen

B
HUMANIORA
Professor Harri Mantila

C
TECHNICA
Professor Juha Kostamovaara

D
MEDICA
Professor Olli Vuolteenaho

E
SCIENTIAE RERUM SOCIALIUM
Senior Assistant Timo Latomaa

F
SCRIPTA ACADEMICA
Communications Officer Elna Stjerna

G
OECONOMICA
Senior Lecturer Seppo Eriksson

EDITOR IN CHIEF
Professor Olli Vuolteenaho

EDITORIAL SECRETARY
Publication Editor Kirsti Nurkkala

ISBN 951-42-8181-0 (Paperback)

ISBN 951-42-8182-9 (PDF)

ISSN 0355-3191 (Print)

ISSN 1796-220X (Online)

