

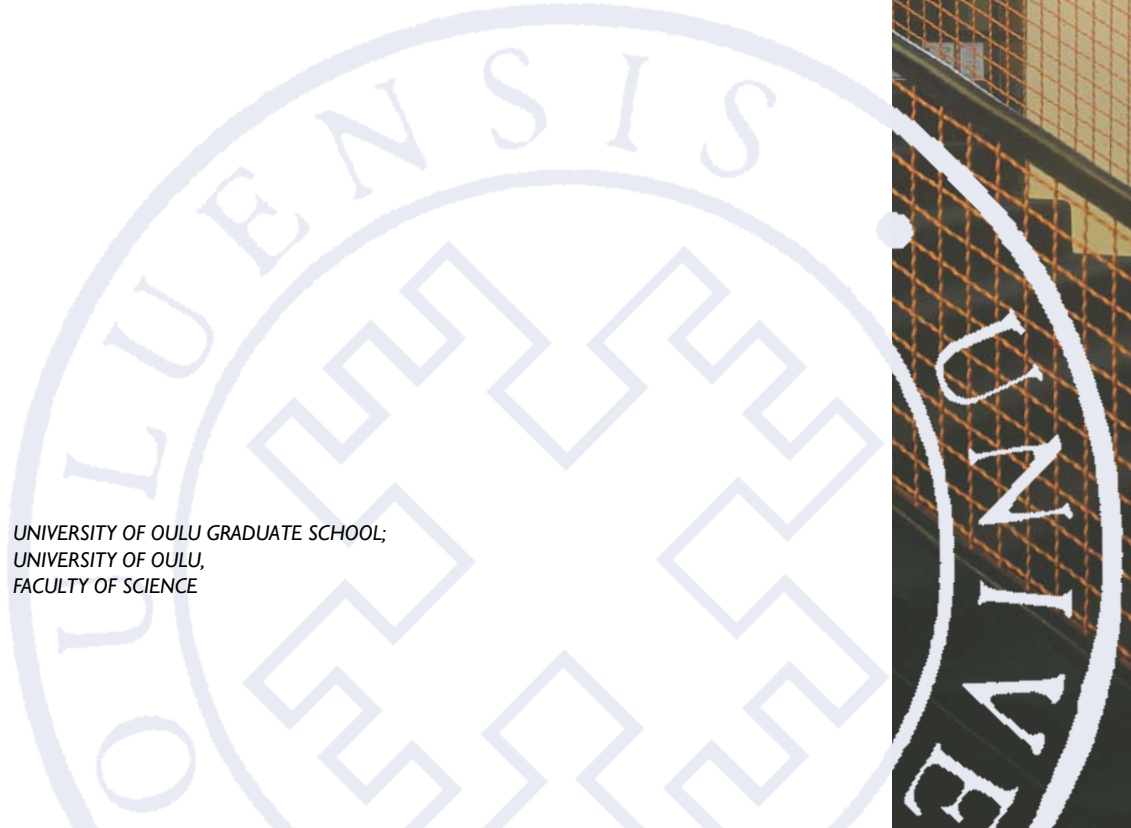
Kaisa-Leena Huttunen

BIODIVERSITY THROUGH
TIME: COHERENCE,
STABILITY AND SPECIES
TURNOVER IN BOREAL
STREAM COMMUNITIES

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COHERENCE, STABILITY AND
SPECIES TURNOVER IN BOREAL
STREAM COMMUNITIES**

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Abstract

Describing how and why species composition of ecological communities varies across spatial and temporal scales is a primary objective for ecological research. A key challenge is to distinguish changes in community composition resulting from external factors from the natural background variability. In this thesis I aimed to study: 1) the level of temporal variation in community composition of stream macroinvertebrates, 2) the role of different environmental factors to temporal variability, 3) the effect of temporal variability on bioassessment outcomes, and 4) comparability of different approaches to study community variability through time. A majority of the studied macroinvertebrate communities showed lower level of inter-annual variation, i.e. temporal turnover, than expected by chance. The observation of high community stability was further supported by the low level of inter-annual variation in taxonomic completeness (quotient of observed and expected number of species, O/E). Despite the low absolute variation in O/E, ecological status assessments varied annually. Thus the use of one year data may bias management decisions. Macroinvertebrate communities experienced similar dynamics across several spatial extents, from riffles within a stream to streams among regions, suggesting that large-scale extrinsic factors are the major driver of community dynamics. Especially climatically exceptional years may have a strong imprint on community variability. However, at the within-stream scale, coherence was lower than expected, indicating that community dynamics may be driven by different processes at different spatial extents. Stream macroinvertebrate community dynamics were strongly related to in-stream vegetation, temporal variability decreasing with increasing macrophyte cover. Importantly, the effect of in-stream vegetation on temporal turnover of macroinvertebrate communities was masked by the stochastic effect of habitat connectivity, suggesting that unless stochastic effects are controlled for, the role of deterministic processes may be obscured, thus affecting our ability to understand and predict community changes through time. In addition, different approaches to study temporal variability may disagree on estimates for the level of temporal turnover and factors explaining it – a fact that should be taken into account when planning and comparing studies.

Keywords: benthic macroinvertebrates, beta-diversity, bioassessment, climate, community composition, disturbance, habitat connectivity, in-stream vegetation, inter-annual variability, temporal dynamics

Huttunen, Kaisa-Leena, Biodiversiteetti ajassa: pohjaeläinyhteisöjen vuosien välinen vaihtelu pohjoisissa virtavesissä.

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Tiivistelmä

Yksi ekologisen tutkimuksen keskeisistä tavoitteista on kuvata, miten ja miksi eliöyhteisöjen koostumus muuttuu paikasta ja ajankohdasta toiseen. On tärkeää pystyä erottamaan erilaisten ulkoisten tekijöiden aiheuttamat muutokset luonnollisesta taustavaihtelusta. Väitöskirjani tavoitteena oli selvittää 1) miten paljon virtavesien pohjaeläinyhteisöissä tapahtuu ajallista vaihtelua 2) mitkä ympäristötekijät vaikuttavat yhteisöjen ajalliseen vaihteluun 3) miten ajallinen vaihtelu vaikuttaa ympäristön tilan arviointiin ja 4) kuinka vertailukelpoisia ovat eri lähestymistavat ajallista vaihtelua tutkittaessa. Valtaosa tutkituista pohjaeläinyhteisöistä vaihteli vuosien välillä vähemmän kuin olisi sattumalta odotettavissa osoittaen varsin suurta ajallista pysyvyyttä. Käsitystä yhteisöjen pysyvyydestä tuki myös vähäinen vuosittainen vaihtelu ekologista tilaa kuvaavassa taksonomisessa eheydessä (=havaitun ja odotetun lajiston suhde O/E). Huolimatta näennäisen pienestä vaihtelusta O/E suhteessa paikkakohtaiset tilaluokka-arviot saattoivat vaihtua vuodesta toiseen. Yhden vuoden aineistoon perustuvat tilan arvioinnit voivat siis johtaa virheellisiin johtopäätöksiin. Pohjaeläinyhteisöjen ajallinen vaihtelu oli samankaltaista eri mittakaavoilla niin peräkkäisten koskipaikkojen kuin eri alueilla sijaitsevien purojen välillä. Suuren mittakaavan ympäristötekijät näyttävät siis säätelevän eliöyhteisöjen ajallista vaihtelua. Erityisesti ilmastotekijöiltään poikkeukselliset vuodet säätelevät eliöyhteisöjä, ja niiden vaikutus voi näkyä vielä useiden vuosien kuluttua. Vaihtelun samankaltaisuus peräkkäisten koskipaikkojen välillä oli kuitenkin odotettua pienempää. Yhteisöjä voivat siis säädellä osittain eri tekijät eri mittakaavoilla. Tutkittujen pohjaeläinyhteisöjen ajallisen vaihtelun voimakkuus liittyi erityisesti vesikasvillisuuden määrään: vaihtelu väheni kasvillisuuden lisääntyessä. Kasvillisuuden määrän vaikutus peittyi kuitenkin satunnaisten tekijöiden alle. Jos satunnaisia tekijöitä ei huomioida, deterministiset syy-seuraussuhteet voivat jäädä huomaamatta heikentäen mahdollisuuksiamme ymmärtää ja ennustaa eliöyhteisöjen vaihtelua. Lisäksi eri lähestymistavat ajallista vaihtelua tutkittaessa voivat johtaa erilaisiin arvioihin vaihtelun suuruudesta ja siihen vaikuttavista tekijöistä, mikä tulisi ottaa huomioon tutkimuksia suunniteltaessa ja niiden tuloksia vertailtaessa.

Asiasanat: ajallinen dynamiikka, beta-diversiteetti, elinympäristöjen konnektiviteetti, häiriöt, ilmasto, lajien vaihdunta, tilan arviointi, vesikasvillisuus, vesiselkärangattomat, vuosien välinen vaihtelu, yhteisöjen koostumus

*We shall not cease from exploration, and the end of all
our exploring, will be to arrive where we started, and
know the place for the first time. (T.S. Eliot)*

Acknowledgements

When I started as a PhD student my thoughts about and expectations for the forthcoming job were somewhat different than they are now when this book is finally completed. To write four articles within four years and put them together with short introduction sounded like a piece of cake. Well, it was not. However, now it is done – although it took more than the given four years and the road to reach the destination has been a bit more winding than I could imagine on a day I started. But I do agree with Tommy Tabermann who wrote in his poem Roadmap that those who come along the straightest road arrive with empty pockets, whereas the ones who have roamed around all the tracks, arrive with their backpacks full of strange fruits. Similarly I feel that during the years I spend with this thesis project and partly overlapping teaching duties, I have learnt a lot; more than I expected, and still not enough.

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Kuusamo, March 2016

Kaisa-Leena Huttunen

List of original articles

This thesis is based on the following published papers or manuscripts, which are referred to in the text by their Roman numerals I-IV:

- I Huttunen K-L, Mykrä H & Muotka T (2012) Temporal variability in taxonomic completeness of stream macroinvertebrate assemblages. *Freshwater Science* 31(2): 423–441.
- II Huttunen K-L, Mykrä H, Huusko A, Mäki-Petäys A, Vehanen T & Muotka T (2014) Testing for temporal coherence across spatial extents: the roles of climate and local factors in regulating stream macroinvertebrate community dynamics. *Ecography* 37(6): 599–608.
- III Huttunen K-L, Mykrä H, Oksanen J, Astorga A, Paavola R & Muotka T (manuscript) Habitat connectivity and in-stream vegetation control temporal turnover of benthic invertebrate communities.
- IV Huttunen K-L, Mykrä H, Paavola R & Muotka T (manuscript) Comparing snapshot vs. trajectory approaches to the assessment of temporal turnover of benthic macroinvertebrate communities.

Own contribution

Original ideas for papers I, II and III were from my supervisors Timo Muotka and Heikki Mykrä. For all the papers, the final formulation of the research problems was done together with the supervisors. I contributed to the collection of field data especially in subprojects I, III and IV, and to the identification of benthic samples for all data sets. I have been mainly responsible for all data analyses: in paper I under the guidance of Heikki Mykrä for the use of predictive models and in paper III under the guidance of Jari Oksanen for the use of null models. I wrote the first drafts of all manuscripts which were then commented by the supervisors. All papers were finalized together with the co-authors.

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1 Introduction

All natural populations fluctuate through time, resulting in biological communities that are also dynamic, with variation occurring across several scales and at different magnitudes and forms depending on the system and type of organisms (Connell & Sousa 1983, Collins *et al.* 2000). Although everyone, scientists and men of the street alike, are aware of this temporal variability, spatial (i.e. among sites) variation has received traditionally much more scientific attention. For example, the concept of ‘beta diversity’ (describing variability in community composition) combined with either ‘spatial’ or ‘temporal’, received 1229 and 301 hits, respectively, in ISI Web of Science (as of March 31, 2015). In addition, replication across space seems to be far more common than replication through time. However, considering the potential for substantial variability in population numbers and species occurrences, the implicit assumption of a single sample in time providing comprehensive and accurate information about community patterns poses the risk of reporting results that are not truly representative of the system being studied (Wiens 1981).

Describing how species vary in their distribution and abundance across diverse spatial and temporal scales, and understanding the factors that control these patterns, are fundamental objectives of ecological research. A key challenge for researchers is to distinguish changes resulting from external factors, such as human-induced stress or an experimental treatment, from the natural background variability (Magurran *et al.* 2010). The separation between natural and human-induced variation in community organization is also important from an applied perspective, for example, to avoid false management decisions and biased predictions about biotic responses to environmental change. Today, the importance of long-term data for proper understanding of ecological phenomena is more important than ever before, yet long-term datasets are scarce in community ecology (Jackson & Füreder 2006, Magurran *et al.* 2010).

Streams provide a highly suitable environmental template for studies on temporal variability in community patterns because they are notoriously variable and disturbance-prone habitats, yet lotic communities often exhibit remarkable long-term stability (Lake 2000, Sponseller *et al.* 2010). Stream invertebrates form a species-rich group of organisms filling a variety of ecological niches. They are easy to sample and relatively easy to identify, if not to species, then at least to genus level. In addition, their rather short life-cycle enables rapid responses to environmental change and monitoring of several generations within a relatively short time scale (Rosenberg & Resh 1993).

Biological communities exhibit different degrees of persistence or stability, i.e. constancy in species occurrences or abundances, linked to several abiotic or biotic factors acting at diverse scales from microhabitats to continents. Results from existing studies on the persistence or stability of stream macroinvertebrate communities have been conflicting: some studies have reported assemblage composition to be relatively consistent from year to year (e.g. Scarsbrook 2002, Bêche & Resh 2007), whereas considerable temporal changes have been observed in others (e.g. Milner *et al.* 2006, Feio *et al.* 2010, MacDonald & Côte 2013). Changes in community composition from one time to another are inevitably reflected in other ecological variables or community measures; for example evenness or metrics of biotic integrity. On the other hand, aggregate measures ignoring species identity, such as species richness or total biomass, may show high constancy even when there is considerable variation in community composition (Micheli *et al.* 1999, Magurran & Henderson 2010).

Local extinction and colonization processes are among the major factors structuring communities. The composition of a biological community at any given site or time partly reflects these small-scale extinctions and colonizations resulting from either deterministic or stochastic forces, or most likely both. Deterministic perspectives emphasize interactions between species and their biotic and abiotic environment (Leibold *et al.* 2004), each species having its own niche. Due to differences among habitats, each site is advantageous for some species while disadvantageous for most others. Stochastic perspectives, by contrast, highlight the predominance of dispersal-assembled communities where, in the strictest sense, all species have equal requirements and probability of colonizing a site (Hubbell 2001, Rosindell *et al.* 2011). In the absence of niche control, this may then lead to high variation in community composition among sites and times.

Spatial community turnover (i.e. dissimilarity in community composition between sites), especially in terrestrial ecosystems, has been commonly related to productivity; the rate of community turnover increasing with increasing productivity, although contrasting results have also been reported (Chase 2010, Harrison *et al.* 2011 vs. Andrew *et al.* 2012, Stegen *et al.* 2013). Another widely supported explanation for spatial turnover is habitat heterogeneity, with communities in spatially heterogeneous environments being more dissimilar than those in more homogeneous landscapes (Veech & Crist 2007, Astorga *et al.* 2014). Temporal habitat heterogeneity in the same sense as in spatial studies would imply for differences in habitat through time. Indeed, a positive relationship has been frequently observed between temporal community turnover (i.e. dissimilarity in

community composition through time) and environmental variability (Death & Winterbourn 1994, Mykrä *et al.* 2008), suggesting that different species are favored at different times. Alternatively, an opposite relationship (Chase 2007, Lepori & Malmqvist 2009) may be observed if very high environmental variability, such as high disturbance frequency, acts as an environmental filter allowing only the most tolerant taxa to persist in frequently changing conditions. Spatial and temporal habitat variability may also interact, spatially heterogeneous (complex) habitats providing refugia for stream invertebrates during unfavorable conditions, and thus dampening variation in community composition resulting from environmental variability. This may lead to a negative relationship between within-habitat heterogeneity and temporal variability of stream macroinvertebrate communities (Brown 2003, Brown & Lawson 2010). Based at least partly on the same mechanisms, also abundant in-stream vegetation may stabilize benthic communities through time (Mykrä *et al.* 2011).

Stochastic processes may mask the influence of deterministic factors on community dynamics, potentially affecting our conclusions about the level of community turnover and hindering identification of the mechanisms generating turnover across space and time (Stegen *et al.* 2013). Here, 'stochastic process' is defined to be any process that gives rise to patterns of species diversity, abundance and community composition indistinguishable from random chance (Chase & Myers 2011). One important source of stochasticity in community patterns is sampling effect. Temporal turnover is dependent on the number of species at any particular year (temporal α -diversity), causing uncertainty as to the mechanism of observed turnover; that is, is it caused simply by random differences in α -diversity among samples (Chase *et al.* 2011). Similarly, sampling effect may also arise from differences in the total number of species across the study period (temporal γ -diversity) (Kraft *et al.* 2011; Stegen *et al.* 2013). Higher turnover may be expected at sites of high compared to low γ -diversity because, with an increasing number of species, the probability of observing some species only once or twice also increases. In addition to pure sampling effect, turnover may arise from stochastic ecological processes such as chance colonization and priority effect. For example, communities in isolated sites may exhibit a higher degree of stochastic variability than those in more connected sites (Chase & Ryberg 2004), high connectivity increasing the influx of immigrants and keeping the community more constant through time. Null models have proved to be a useful tool to test whether the observed level of temporal turnover differs from that expected by chance and to disentangle deterministic drivers of species turnover from stochastic factors (e.g.

Chase *et al.* 2011, Kraft *et al.* 2011, Stegen *et al.* 2013). However, although the use of null models is an emerging practice in studies on spatial turnover of biological communities (e.g. Chase 2010; Astorga *et al.* 2014; Hawkins *et al.* 2015), it is still rarely used for assessing temporal turnover.

Studies on temporal coherence (i.e. the tendency of populations, communities or ecosystem dynamics to behave similarly among locations over time) may yield valuable information about whether results from a site and time can be extrapolated to other sites and spatial scales. Also the spatial extent of temporal coherence may be used to define whether regional- or local-scale factors are the major drivers regulating the systems: low coherence between geographically distinct locations points to the importance of local-scale intrinsic factors, whereas high coherence indicates the primacy of large-scale extrinsic factors (Rusak *et al.* 1999). Coherence in biological variables often decreases with geographical distance, i.e. nearby sites are more likely to exhibit synchronous variation than sites further apart (Koenig 2002), reflecting the ‘Moran effect’ where spatially correlated environmental variables cause concurrent ups and downs of populations and communities at geographically distinct sites (Moran 1953, Koenig 2002, Rusak *et al.* 2008). Large-scale climatic phenomena, such as North Atlantic Oscillation and El Niño Southern Oscillation, may synchronize dynamics of individual taxa, or even whole communities, as well as their food-web interactions (Bradley & Ormerod 2001, Straile 2002, Rusak *et al.* 2008). Similarly, changes in large-scale climatic factors have been reported to affect the long-term trends of stream macroinvertebrate assemblages (e.g., Chessman 2009, Webb & King 2009).

Community stability may be seen as a basic assumption in environmental assessment (Bunn & Davies 2000, Robinson *et al.* 2000). Bioassessment programs are based on the comparison of potentially disturbed sites with sites minimally disturbed by human actions (the reference condition approach). In this approach, variation among communities at reference sites represents the range of acceptable conditions, and the degree of deviation of a test site from that range quantifies the magnitude of degradation of a site (Reynoldson *et al.* 1997, Stoddard *et al.* 2006). The reference condition is typically defined using data from single sampling events from several sites, and these data are then used to predict the expected community composition at other sites (test sites). Data from test sites are likely to be collected in a different year than data for the reference condition, and status assessment is often based on a snapshot survey, with the implicit assumption that the fauna observed in any one year is representative of the local assemblage of a site. Temporal variation either in reference conditions or at test sites may jeopardize the

assessment outcomes by obscuring human-induced changes in local communities or, alternatively, indicating an impact when an exceptional event represents natural community variability (Wiens 1981, Magurran *et al.* 2010). Such a concern about the representativeness of single-year data is not limited to bioassessment; more generally, snapshot studies can yield a biased view of the variability of natural populations and thus affect our understanding of the patterns observed (Eby *et al.* 2003, Vaughn & Young 2010).

There are two major approaches to the study of temporal variability: the “trajectory approach” and the “snapshot approach”. In the trajectory approach, sites are monitored across several consecutive years, whereas in the snapshot approach, monitoring is conducted on only a few (often just two) occasions several years apart. The trajectory data are thought to be temporally more representative but, being often based on just a few sites, the results may not be easily extrapolated elsewhere (‘too few replicates in space’; Hildrew & Giller 1994). By contrast, the snapshot approach typically is more representative spatially, but the results may depend strongly on the environmental conditions of the particular years included (‘too few replicates in time’; Hildrew & Giller 1994) and thus study outcomes might be unrepresentative of real temporal trends. The two approaches provide different kinds of information about community variability, yet there have been no studies comparing the results of these differing approaches about community turnover through time. Also the comparability of results from studies of differing duration is a central issue to the study of temporal community variation. This is obvious when studies distributed across days or months are compared to those that last for years or decades (Jackson & Füreder 2006), but the same may hold true for more comparable time scales as well. For example, Bengtsson *et al.* (1997) reported temporal variability of woodland bird communities to increase the longer (from two to 22 years) the communities were observed.

2 Aims of the study

The main objective of this thesis was to study temporal variation in community composition and to explore the role of different environmental factors behind such variability. The thesis aims to produce basic information about the temporal variation of natural communities applicable to, for example stream bioassessment. The study has four main themes. First, I aimed to explore the stability or, conversely, the level of natural temporal turnover, of macroinvertebrate communities in near-pristine streams, and to find out which environmental variables best explain differences in community stability among study sites. I was specifically interested in whether the key environmental drivers suggested to determine spatial β -diversity also explain temporal turnover even after controlling for stochastic factors. The second aim was to assess whether, and under which circumstances, temporal variation in macroinvertebrate community composition has consequences on bioassessment outcomes. The key question then being: are communities stable enough for bioassessment programs to be based on single-year surveys? Third, I aimed to study the degree to which temporal variation in community composition is synchronous among spatially distinct locations at different spatial extents, i.e. how similarly benthic communities behave at different locations through time. In addition, I was interested in determining the contribution of local versus regional factors to similarity in community dynamics across sites. Fourth, I aimed to assess the comparability of studies on temporal community variability using different approaches or different study duration, i.e. to what degree the level of temporal turnover in community composition, and the factors driving it, depends on the approach used (snapshot vs. trajectory approach) or on study duration.

2.1 Expected results

I predicted that there is (1) a negative relationship between connectivity and temporal turnover, and (2) a positive relationship between γ -diversity and community turnover, both of which would weaken or disappear once stochastic factors are controlled for (paper III). Also, I predicted that, after controlling for stochastic effects, turnover patterns will be best explained (3) by in-stream disturbance, posing an environmental filter that allows only the most tolerant taxa to persist at a site, or (4) by within-site heterogeneity and/or in-stream vegetation, providing refugia for stream invertebrates during adverse conditions; therefore,

community turnover through time should decrease with increasing disturbance and/or within-stream heterogeneity and in-stream vegetation.

For temporal variation in taxonomic completeness of stream invertebrates (paper I), I predicted that unmodified near-pristine sites would be better buffered against disturbances than modified test sites due to their higher species diversity ('insurance hypothesis'). Thus it was expected that at reference-like sites there would be only little inter-annual variability in community structure and, consequently, in taxonomic completeness and status assessment, whereas sites exposed to human disturbance were expected to show more erratic variation among years.

For the level of temporal coherence, i.e. similarity in behavior of benthic communities at different locations through time (paper II), coherence was predicted to decrease with increasing spatial extent. Specifically, I expected to detect a Moran effect, with coherence being high if climatic variables are strongly synchronized across spatial extents. The view of regional control of community dynamics was expected to be further supported by a hydrologically exceptional year enhancing synchrony among locations.

For the comparability of studies using different approaches to temporal variability, and spanning different durations (paper IV), deviation in study outcomes for different approaches (describing partly different views of temporal turnover) were expected to occur, especially in the estimates of temporal turnover, but also in the key variables explaining the patterns. Similarly, studies spanning different durations were expected to produce different outcomes. These results were expected to highlight the importance of considering the comparability of results from studies using different approaches or having a difference in study duration.

3 Materials & Methods

3.1 Study areas and data sets

The papers in this thesis are based on analyses of five separate sets of biological and environmental data, four of which are long-term data sets ranging from five to fourteen years. The longest data set is from the Oulanka area in northeastern Finland (Koutajoki drainage basin; Fig. 1B), where macroinvertebrate samples from 24 pristine or near-pristine stream sites have been collected from the year 2000 onwards. Many of these sites are located within a nature conservation reserve, Oulanka National Park, which represents the westernmost remnants of pristine taiga forests (Malmqvist *et al.* 2009). This data set was used in papers I, III and IV. In paper I, also a one-year (2001) data set from 51 independent reference streams in the same area was used to build a predictive model. Long-term monitoring streams were used for model validation and as unmodified test sites. In addition, a set of inter-annual data (2006–2010) from ten streams from a neighboring catchment (Iijoki drainage area) was used as additional (modified) test sites to study temporal variation in taxonomic completeness (see chapter 3.4.1 for more details). All of these streams are first-to-fourth, mainly first-to-second, order forest streams, draining mixed forests, bogs and fens with minimal anthropogenic impact, except the ten forestry-impacted streams in the Iijoki drainage basin.

Paper II was based on a data set from 11 second-to-third order forest streams monitored three times a year from early summer 1999 to autumn 2006. These streams are located in two drainage basins, the Kymijoki drainage basin in southern Finland and Oulujoki drainage basin in northeastern Finland (Fig. 1A). One riffle in each of five study streams was monitored in southern Finland from 2001 to 2006, whereas in northeastern Finland, three consecutive riffles, separated by slow-flowing pool sections, were monitored in each of six streams (Fig. 1A2). One riffle in each of these NE Finland streams was monitored from 1999 to 2006 and the two others from 1999 to 2004.

3.2 Species data

We collected macroinvertebrate samples usually in the autumn (September–October) when most species are in their larval stage, except for paper II where samples were collected three times a year (June, August, October), thus comprising

both seasonal and inter-annual time scales. At each site, we collected either a 2-min kick-sample (net mesh size 0.3 mm) or a set of surber samples (0.04 m² each, net mesh size 0.3 mm). In kick-net sampling (papers I, III, IV), we aimed to cover most benthic microhabitats present within an about 100 m² riffle section. Such a sample covers ~1.3 m² of the stream bed and captures about 75% of invertebrate species present at a site, missing mainly species that occur only sporadically in streams (Mykrä *et al.* 2006). In surber sampling (II), eight to ten subsamples were taken at each site on each occasion; these subsamples were later pooled to yield one sample covering a total of ~0.40 m² of the stream bed.

All macroinvertebrate samples were preserved in the field with ethanol. In the laboratory, samples were sorted and all individuals were identified and counted. Identification was done to the lowest feasible level: mainly to species (papers I, III and IV) or genus level (II). Chironomids were identified to family level only and were not counted every year; therefore they were omitted from all analyses.

3.3 Environmental data

Depending on the study, a variety of environmental variables, acting either at regional or local scale, were measured at each study site. These variables were then used as potential explanatory factors for the observed patterns of stream macroinvertebrate communities, or as candidate predictors of taxon occurrence.

Climate data were obtained either from i) regional precipitation data from the closest monitoring station (paper I), ii) catchment-specific interpolated climate data (precipitation and air temperature) from Finnish Meteorological Institute (II), or (iii) data loggers installed at each site to monitor water depth, water temperature and air temperature (III and IV). Water samples were collected simultaneously with benthic samples. Depending on the study, some or all of the following variables were analyzed: conductivity, pH, water color, total P and total N. For paper II, water samples were collected at every sampling occasion, i.e. three times a year, thus enabling calculation of temporal coherence also for water chemistry variables.

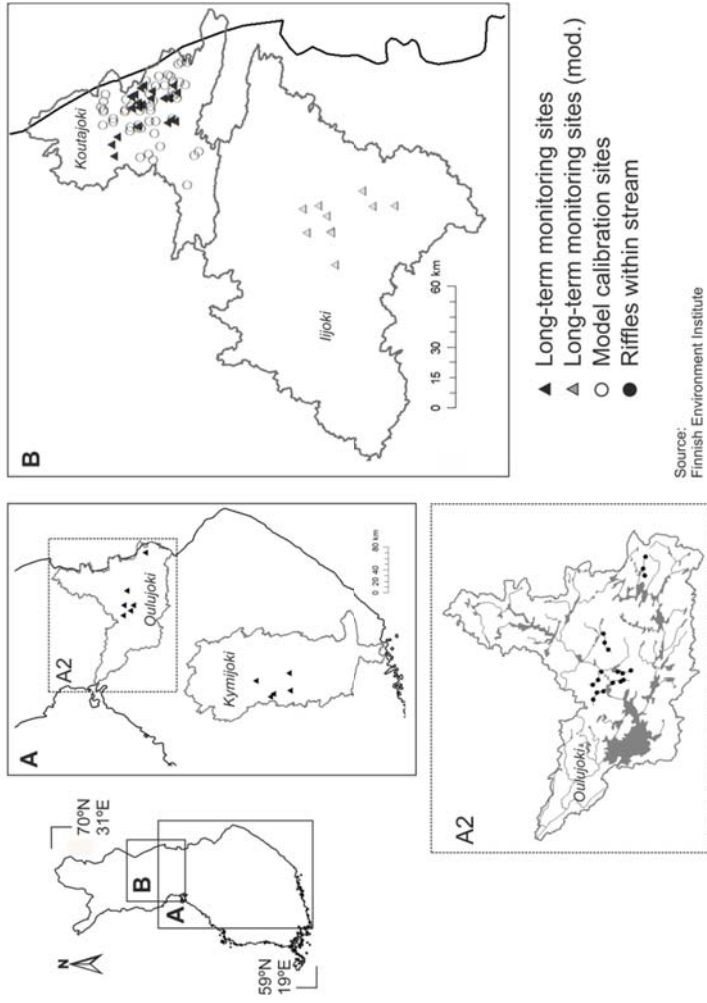


Fig. 1. Location of study sites used in papers II (A & A2) and I, III and IV (B). Distances between riffles within a stream (A2) are on an arbitrary scale. mod = modified.

At long-term monitoring sites in the Oulanka area, NE Finland, environmental stability was measured as bed disturbance intensity/frequency by monitoring the movement of individual stones (papers III and IV). In spring 2005, marked stones were arranged in 12 transects within a reach, each transect consisting of three stones – small, intermediate and large – in a random order. Stone movement was then monitored for five successive years, twice a year (spring and autumn), until autumn 2009. Bed movement intensity (BMI) was calculated following Townsend *et al.* (1997) as the mean percentage of stones moved across the whole study period.

Within-site habitat heterogeneity was measured as substratum diversity. Particle size distribution was determined for ten randomly placed quadrats using a modified Wentworth scale with ten size classes from fine sediments or organic matter to large boulder and bed rock. Particle size distribution was then used to calculate an index of substratum heterogeneity: Simpson's Diversity (1/D). The amount of in-stream vegetation was measured as percentage cover of macrophytes, estimated visually at 20–30 randomly placed quadrats at each site. For paper II, macrophyte cover was measured at every sampling occasion, thus enabling calculation of temporal coherence.

For papers III and IV, connectivity was measured as the relative isolation of a site by estimating, based on site visits, the surface area of riffle habitat available for stream invertebrates within a 500 m buffer in both upstream and downstream direction of the study site. In addition, for paper I, a variety of catchment-scale GIS variables was acquired and used as candidate variables in the construction of the predictive model. This information was obtained using data from the National Land Survey of Finland (NLS) and the Finnish Environment Institute (SYKE).

3.4 Statistical analysis

3.4.1 Temporal variation in taxonomic completeness (paper I)

Methodology and statistical procedures described in detail by, for example, Moss *et al.* (1987), Wright (2000) and Clarke *et al.* (2003) were used to construct and implement a predictive model to assess taxonomic completeness of study sites. River InVertebrate Prediction and Classification System (RIVPACS) -type model is basically a multi-taxon species distribution model, the idea of which is, based on a set of natural reference sites to provide an estimation for the number of taxa expected (E) at a site with certain environmental characteristics. By relating the

number of predicted and observed taxa (O) to the expected number of taxa, one obtains the value for taxonomic completeness (O/E) describing biotic integrity, and thus an indication of the potential biological degradation of the site. In this study, O/E values were calculated separately for each site in each year. Inter-annual variability in O/E was then assessed by calculating standard deviation of O/E values across years, separately for the unmodified and modified test sites. Repeated measures analysis of variance (ANOVA) was used to test for differences between the a priori defined site types (unmodified vs. modified sites) and among-year variation in O/E across the overlapping 5-yr study period (2006 to 2010). We also calculated variance components for both random and fixed factors and measured their contribution to total variance.

The influence of temporal variation in O/E on bioassessment outcomes was assessed by examining the inter-annual variability in the biological status of each test site. Status classes were defined by first setting the boundary between high and good quality class, as defined by the European Union Water Framework Directive (WFD), based on the 10th percentile of the O/E distribution at model calibration sites and then placing the following status classes (good, moderate, poor, bad) evenly along the O/E range of the calibration sites from the 10th percentile to 0. In addition of defining the boundary between high and good quality classes based on model calibration sites, the critical boundary was set also based on the unmodified test sites separately for each year (2000–2010) to assess how the threshold of 10th percentile varied through time.

3.4.2 Temporal coherence (paper II)

The level of coherence was assessed for several biological variables characterizing different aspects of benthic macroinvertebrate communities, i.e. the total number of individuals, total number of taxa, community evenness and the number of individuals of key macroinvertebrate taxa. In addition, to examine whether changes in community composition among sites were concurrent and equal in magnitude, a measure of community similarity between two successive sampling occasions (temporal turnover) was used based on Jaccard coefficient of similarity. Coherence was measured also for physical (precipitation, air temperature, water depth, macrophyte cover) and chemical (pH, conductivity, color, total N and P) variables.

Coherence was calculated for each biological variable at three spatial extents: 1) among riffles within a stream, 2) among streams within a region, and 3) among regions, using Spearman rank correlation coefficient between all possible site pairs,

with no time lag. Then the mean coherence for each variable was obtained as an average across all possible site pairs separately for each spatial extent. For physical and chemical variables, coherence was calculated at the among-stream and among-region extents only. To gain statistical inference, bootstrapped 95% confidence intervals for each variable at each spatial extent were calculated, by resampling time instead of sites (Lillegård *et al.* 2005) across 1000 iterations with replacement. To take temporal autocorrelation into account, segments of consecutive time points were resampled instead of individual points ('block resampling'). The observed coherence at each spatial extent was considered statistically significant if the bootstrapped 95% confidence intervals did not overlap zero. Similarly, differences in coherence values between spatial extents were considered statistically significant if the bootstrapped confidence intervals did not overlap among the extents.

At both study regions, the year 2002 was extremely dry, equally severe droughts being experienced once in a century. At its lowest, the annual precipitation dropped to only half of the long-term average. To assess whether shared disturbance gave rise to synchronous community dynamics (see Pham *et al.* 2008), one year at a time was excluded from the data matrix and coherence values were recalculated without that particular year for total abundance, taxonomic richness and evenness, following otherwise the same procedures as above (Rusak *et al.* 1999, 2008). If a particular year has a synchronizing effect on community dynamics, the level of coherence is expected to decrease when that year is excluded from the analysis.

3.4.3 Temporal turnover of benthic communities (papers III & IV)

To analyze temporal turnover, i.e. inter-annual changes in community composition, Bray-Curtis dissimilarity index, based on $\log(x+1)$ -transformed abundance data, was used. This measure of temporal turnover describes community change both in the identity of species and numbers of individuals ('differentiation diversity', sensu Jurasinski *et al.* 2009). It catches not only losses and gains, but also changes in abundances of each taxon, being thus more sensitive to changes in the environment than indices based on presence/absence data.

The level of temporal turnover was assessed separately for each site by calculating dissimilarity values for all consecutive year pairs (13 pairs); then the site-specific mean dissimilarity across these pairs was used as a measure of observed temporal turnover (β_{obs}). To explore whether the observed level of temporal turnover deviates from that expected by chance, and to differentiate variation in community composition arising from deterministic vs. stochastic

processes, a null model approach was used (Chase *et al.* 2011, Kraft *et al.* 2011, Stegen *et al.* 2013). A quantitative null model was constructed separately for each site (R package *vegan* 2.2-0, Oksanen *et al.* 2014). These models randomly shuffled species presences and abundances, keeping species richness, total abundance of each sample, and species frequencies similar to original data. The end product was the mean (across 1000 iterations) expected temporal turnover (β_{exp}) in a null community, calculated similarly as for observed dissimilarity as site-specific mean dissimilarity across consecutive year pairs. Departure of the observed dissimilarity from the null expectation, expressed either a) as $\beta_{\text{dep}} = \beta_{\text{obs}} - \beta_{\text{exp}}$ (paper IV), or b) as effect size, i.e. $\beta_{\text{dep}} = (\beta_{\text{obs}} - \beta_{\text{exp}}) / \text{SD}\beta_{\text{exp}}$ (III), estimates the level of temporal turnover independent of chance alone. Negative β_{dep} values indicate community composition among consecutive years to be less dissimilar than expected by chance (low level of temporal turnover, i.e. high stability), while positive values indicate more dissimilar communities than expected (high level of turnover, i.e. low stability).

In paper IV, site-specific values for both β_{obs} and β_{dep} were calculated as a mean of consecutive years also for other study periods, starting from the year 2000 and then increasing the temporal distance one year at a time until the year 2013 ('trajectory approach'). In addition, β_{obs} and β_{dep} were calculated only between the "first" and the "last" year of each study period ('snapshot approach'). To explore the comparability of results from studies using trajectory data, but of different duration, β_{obs} and β_{dep} were calculated also for four different time intervals: randomly ordered non-overlapping sequences of two, five and seven consecutive years, and the whole study period of 14 years (see Bengtsson *et al.* 1997). The randomly ordered non-overlapping sequences were used to keep different durations independent of each other.

The relationships between environmental variables and temporal turnover were examined using multimodel inference in multiple linear regressions (Burnham & Anderson 2002, Johnson & Omland 2004) with the R package MuMIn (Barton 2012). We were specifically interested in the influence of environmental stability (BMI), within-habitat heterogeneity (Simpson index for substrate diversity), the amount of in-stream vegetation, water temperature and connectivity, on community variability. The explanatory power of alternative models was compared using Akaike Information Criterion (AICc), the best model being the one with the smallest AICc score. In addition, model weights across all models that included a certain variable were summed ('importance value') to compare the relative importance of explanatory variables (Burnham & Anderson 2002, Johnson &

Omland 2004). To identify the processes through which different factors affect temporal turnover (deterministic vs. stochastic), both the observed level of turnover (β_{obs}) and departure from null (β_{dep}) were used as response variable. If an explanatory variable affects temporal turnover through stochastic processes, its role should become non-significant, whereas factors reflecting deterministic processes will remain (or become) significant, once stochastic effects are controlled for.

4 Results and discussion

4.1 Variation in community composition through time

Macroinvertebrate communities of our study streams exhibited major changes in species ranks across years, but also more minor changes in species abundances that did not necessarily result in species rank shifts. The site-specific among-year Bray-Curtis dissimilarity from the year 2000 to 2013, describing the level of temporal community turnover, was on average 0.288, site-specific values ranging from 0.210 to 0.375 (paper III, Fig. 1a). However, a great majority of the study sites experienced significantly lower level of temporal turnover than expected by chance ($\beta_{\text{dep}} < -2$; paper III, Fig. 1b), indicating that macroinvertebrate communities of near-pristine boreal forest streams are rather stable through time.

The observation of high constancy of stream macroinvertebrate communities through time was supported also by low level of inter-annual variation in taxonomic completeness (O/E). During the 11-yr study period, the median of O/E values at unmodified test sites varied from 0.910 (year 2006) to 1.157 (2008; paper I, Fig. 3). The mean standard deviation of O/E across years at unmodified test sites was relatively low (0.145) and declined even more (to 0.123) when data from the exceptionally dry summer of 2006 was excluded. As expected, modified test sites missed more taxa that were predicted to occur at a site than did the unmodified sites, leading to considerably lower mean O/E values at modified sites. At modified test sites, the median of O/E values varied from 0.638 (year 2008) to 0.881 (2006; paper I, Fig. 4) during the five-year study period.

In theory, high species richness should buffer community variability or turnover against environmental change due to species' differential responses ("insurance effect"; Yachi & Loreau 1999, Ives *et al.* 2000, Jacobsen *et al.* 2014). One could then expect that variation in community structure and, consequently, in O/E, would be higher at human impacted, modified sites due to their lower species richness, fewer species being then present to cope with disturbances (e.g. Feio *et al.* 2010). However, it is equally possible that community structure at impacted sites is persistent across years, because species remaining at these sites may be the most tolerant ones of those present in the regional species pool. In our case, inter-annual variation in taxonomic completeness was rather low also at modified sites (mean $O/E_{\text{SD}} = 0.142$), giving support to the latter hypothesis. In addition, taxa missing from the unmodified sites in the drought year of 2006 were mostly species

indicating reference conditions (EPT taxa), whereas at modified test sites, the climatically exceptional year did not have a similar effect on community composition. Thus species occurring at modified sites might indeed be more tolerant not only of anthropogenic stress but also of natural disturbances such as discharge variability.

Despite the rather low level of absolute variation in O/E across years both at unmodified and modified test sites, ecological status assessment varied from bad to high status class, set based on the O/E range of the model calibration sites. Especially assessment of modified sites varied considerably among years (paper I, table 2), suggesting that samples from a single year may not represent adequately the ecological condition of a site. At unmodified test sites, variation in status assessment was mostly related to the drought year of 2006.

4.2 Regional control of temporal community variability

Climatic factors operating on large spatial scales may have a strong impact on the long-term variability of stream macroinvertebrate communities (e.g. Chessman 2009, Durance & Ormerod 2009, Webb & King 2009). In addition, climatic phenomena, such as North Atlantic Oscillation and El Niño Southern Oscillation, have been reported to synchronize lake physics and chemistry (George *et al.* 2000), biotic food-web interactions (Straile 2002), and dynamics of individual taxa (Rusak *et al.* 2008) or whole communities (Bradley & Ormerod 2001).

In our study, temporal coherence of stream macroinvertebrate communities generally increased as spatial extent decreased, as expected (paper II, Fig. 2&3). Nevertheless, coherence values between spatial extents did not differ significantly, and for several variables, coherence was significantly positive even at the largest spatial extent (see also Peltonen *et al.* 2002 (forest insects), Koenig & Knops 1998 (squirrels)). Such a high level of coherence across broad spatial extents suggests that large-scale extrinsic factors are driving population or community dynamics (Kratz *et al.* 1987, Rusak *et al.* 1999). In our case, also air temperature and precipitation showed high, and almost equal, coherence at all studied extents. Biological variables exhibited high coherence across the same spatial extents, implying that Moran effect was operating, thus emphasizing the primacy of climatic factors in regulating the dynamics of stream invertebrate communities.

Regional heterogeneity in local variables, i.e. differences in site-specific properties, may obscure the effects of large-scale regional processes (Benson *et al.* 2000, Arnott *et al.* 2003, Jacobsen *et al.* 2014). Then, higher coherence could be

expected among sites with more similar local environment (Rusak *et al.* 1999, Lansac-Tôha *et al.* 2008). In our study, northeastern Finnish streams were more similar based on their environmental attributes than southern Finnish streams (paper II, Fig. 5a), yet there were no great differences in coherence values between the regions, thus further emphasizing the primacy of climatic factors on driving community dynamics of stream invertebrates. A similar pattern of large scale climatic factors obscuring any impact of local environmental factors on community composition has been reported by Bradley & Ormerod (2001) and Louhi *et al.* (2011).

Yet another reflection of the regional control of community dynamics is the strong imprint that shared disturbances, such as severe weather conditions (e.g. Gilbert *et al.* 2008, Pham *et al.* 2008, Hansen *et al.* 2013) or reduction in pH (Keitt 2008), may have on geographically distinct biological systems. Similarly to Rusak *et al.* (2008), who reported that exclusion of a year with unusual environmental conditions strongly modified the observed patterns of synchrony of zooplankton communities, we also found a synchronizing effect of a drought year on macroinvertebrate abundance and taxa richness (paper II, Fig. 4).

4.2.1 The effect of climatically exceptional years

At long-term monitoring sites in the Oulanka area, NE Finland, the drought year of 2006 had a clear impact on taxonomic completeness of macroinvertebrate communities (paper I, Fig. 3). Inter-annual variation in O/E, and consequently in status assessments, was generally low at unmodified test sites, yet many of these sites obtained exceptionally low O/E values in 2006, causing status assessments to drop from status class good (or better) to weaker than moderate at some of the sites. Similar observations of the greatest changes in benthic invertebrate community composition in years or seasons of lowest precipitation have been reported from Mediterranean (Bêche & Resh 2007, Feio *et al.* 2010) and monsoonal streams (Leung & Dudgeon 2011), i.e. in environments that differ strongly from boreal forest streams. However, at modified sites, O/E values in the year 2006 did not differ statistically from the others, suggesting that communities in unmodified and modified streams responded differentially to climatic variation.

The effect of the drought year of 2006 in pristine sites was obvious also when comparing the study outcomes of two different approaches to temporal variability in community composition, snapshot vs. trajectory approach. In climatically exceptional years, the difference between the outcomes of the two approaches was

much clearer than in climatically regular years (paper IV, Fig. 2). The use of the snapshot approach, based on Bray-Curtis dissimilarity between two distinct points in time, yielded much higher estimation for temporal turnover of community composition compared to the trajectory approach (based on site-specific mean dissimilarity averaged across all consecutive years within the study period).

However, macroinvertebrate communities in boreal streams showed high resilience, communities recovering to the pre-disturbance state within a year. For example, O/E values at unmodified sites did not differ strongly from most other years in 2007, a year after the drought (paper I, Fig. 3).

4.3 Local control of temporal community variability

While we observed coherence to be rather high for most biological variables at the regional scale, it was lower than expected at the within-stream scale (paper II). High coherence was expected, since successive riffles must exhibit the same climatic factors, as well as unlimited dispersal (downstream drift and adult flight; Hershey *et al.* 1993, Winterbourn & Crowe 2008), both of which should promote synchrony. The lower-than-expected level of coherence then implies that synchrony, and control of community dynamics more generally, may be driven by different processes at different extents, climatic factors operating at large spatial scales inducing region-wide synchrony, whereas synchrony at smaller extents is dictated additionally by local factors (Koseki & Fleming 2007, Bunnell *et al.* 2010).

Boreal stream macroinvertebrate community dynamics seem to be strongly controlled by in-stream vegetation. In the study on temporal turnover of stream invertebrate communities (III), connectivity among sites first appeared to be the most important determinant of the observed turnover. However, after stochastic effects were accounted for (by the use departure from null as the response variable) connectivity lost its importance, implying that it contributes to community turnover mainly via stochastic dispersal processes (paper III, table 1). After taking stochastic effects into account, temporal turnover was best explained by in-stream macrophyte cover; inter-annual community variability decreasing with increasing cover of macrophytes, thus supporting earlier findings about the key role of macrophytes in enhancing the stability of benthic communities (Mykrä *et al.* 2011). Also in the coherence study (paper II), among-riffle coherence was related to macrophyte cover, with the probability of synchronous community dynamics increasing with increasing amount of in-stream vegetation.

The mechanism by which in-stream vegetation begets enhanced stability of benthic invertebrate communities is likely related to environmental variability. Macrophyte cover may provide refugia for benthic invertebrates during adverse conditions, e.g. against flow-related disturbances. This interpretation is further supported by the finding for temporal turnover in paper IV. Dissimilarity between years 2000 (hydrologically normal year) and 2006 (drought year) was best explained by macrophyte cover (importance value = 0.998), community similarity of these two years clearly increasing with the increasing amount of in-stream vegetation. In addition, although only few invertebrates consume macrophytes, they afford abundant and predictable food resources for invertebrates by acting as substrate for epiphytic algae, and also by increasing retention of organic matter (Suren & Winterbourn 1992, Muotka & Laasonen 2003).

Other factors shown elsewhere to be important drivers of spatial (and partly also temporal) turnover, especially disturbance and within-stream heterogeneity, were of negligible importance in explaining community turnover in this study. Within-stream heterogeneity (i.e. substratum diversity) was expected to decrease community turnover for largely the same reasons than in-stream vegetation, but against the findings of Brown (2003) and Brown & Lawson (2010), such a relationship was not detected. The reason for not observing a relationship between bed disturbance and community turnover may be the relatively restricted disturbance gradient of the study: even the highest spring floods moved only about one-third of the stones, compared to 100% in other studies using the same method to measure disturbance (Townsend *et al.* 1997, Lepori & Malmqvist 2007). However, the observed disturbance gradient seems realistic for near-pristine boreal forest streams, where disturbances that cause a complete turnover of the streambed are likely to be very rare.

4.4 Potential sources for different outcomes

One of the key challenges to community ecologists trying to understand patterns of species turnover, either in space or time, is to identify whether observed relationships arise from deterministic or stochastic processes. Similarly to Stegen *et al.* (2013), also results of this thesis show that both the identity and relative importance of variables identified to best explain the observed patterns vary depending on whether turnover is measured as raw (observed) dissimilarity or as departure from null (paper III, table 1). The deviating outcomes depending on the choice of the response variable indicate that stochastic processes may dampen, or

even obscure, the role of deterministic processes in controlling community turnover. This may affect drastically our ability to understand and predict changes in biological communities through time. For example, without controlling for the effects of stochastic factors, we would have completely ignored the importance of local habitat filters, particularly in-stream vegetation.

The outcomes of the trajectory vs. snapshot approach were compared to test whether results on temporal turnover remained the same independent of the choice of the approach (paper IV, Fig. 2). The two approaches led to clearly different outcomes for the level of observed temporal turnover only in the hydrologically exceptional year 2006, although temporal turnover was generally somewhat higher when the snapshot approach was used. For departure from null, the difference between the two was more obvious, with the results using snapshot data indicating that the level of temporal turnover did not greatly differ from that expected by chance, whereas with the trajectory approach, benthic communities seemed rather stable. In addition, the two approaches largely disagreed about the best explanatory factors for temporal turnover (paper IV, table 1). The study outcomes were more variable when the snapshot approach was used, and only the trajectory approach consistently identified the key role of macrophyte cover in enhancing the stability of stream macroinvertebrate communities. These results further indicate that, for the snapshot approach, the identity of the particular years to be compared may play a crucial role in affecting the study outcomes, whereas with the trajectory approach, the effect of extraordinary years tends to be averaged out. Similarly, Vaughn & Young (2010) reported several significant ‘treatment by initiation-year’ interactions from a variety of field experiments, implying that the year of initiation may greatly affect the outcomes of experiments (the “year effect”).

Differing lengths of trajectory data showed, against expectations, rather minor differences in the level of temporal turnover, except for the shortest durations (paper IV, Fig. 3). The same was observed for the explanatory variables as well: the shortest data set of two years differed from the rest, while the longer data sets more consistently revealed the decreasing role of connectivity and increasing role of macrophyte cover in explaining community stability (Paper IV, Fig. 4). At a first glance, our findings seem to be against those of Bengtsson *et al.* (1997) who reported community variability to clearly increase with time. They showed that in less stable habitats experiencing vegetation succession, the rate of decrease in community predictability over time is faster than in mature habitats. However, as all our study sites were in pristine or near-pristine streams experiencing no

directional change or anthropogenic stress, low variability between different study durations might be expected.

5 Conclusions: implications for study designs and bioassessment

Temporal stability of communities is a basic assumption in modern bioassessment (Bunn & Davies 2000, Robinson *et al.* 2000). For example, predictive models are only applicable if communities are persistent through time; otherwise biased assessment outcomes can occur when the fauna/flora observed is compared to expected based on data from different years (Metzeling *et al.* 2003, Milner *et al.* 2006). If taxa are not persistent at reference or test sites, then type I or type II errors, i.e. inferring a change when one is not present or failing to detect a change when one is present, may result simply from natural community variation and not from true biological impairment. Such biased assessment outcomes can have a detrimental effect on decisions about actions to improve stream integrity: with type II error, appropriate actions may not be launched although a site is impaired, whereas with type I error, expensive actions may be undertaken when they in reality are not needed.

Based on the results of this thesis, it seems that macroinvertebrate communities in near-pristine boreal streams are rather stable and predictable over time, as long as extrinsic factors do not change considerably. This may be considered good news for bioassessment. It seems that reference conditions established based on one year data can be extrapolated across years with relative safety to predict community structure at test sites (see also Robinson *et al.* 2000, Hawkins 2006). However, the representativeness of otherwise seemingly stable reference conditions may be challenged by exceptional years that can cause notable changes in communities, unrelated to anthropogenic impact. This could be problematic particularly if data from all reference sites were concentrated to the same, ‘anormal’ year which would likely weaken the sensitivity of the model to true impairment. It is then possible that comparisons between impacted and reference sites that do not use temporally synchronous data may indicate differences that are in fact a result of natural variation rather than human activity (MacDonald & Côte 2013). One way to control for the “year effect”, i.e. the influence of a particular year, might be by incorporating climatic variability into the models as predictors, or by calibrating the threshold for impairment separately for each year by resampling a set of reference sites. Representativeness of reference conditions likely increases also if reference data were collected from different sites in different years, thus increasing natural variation among model calibration sites.

Is it then safe to similarly assume that test site samples collected in a single year represent the true condition? This thesis shows that estimates for taxonomic completeness of human impacted sites vary depending on the study year. In the most extreme case, assessment result changed from poor to good status. Only two of the modified test sites were assessed as biologically impaired in all the study years, indicating that the use of only one year data from test sites may indeed promote erroneous management decisions. The use of single-year data is particularly problematic at sites where the disturbance is relatively subtle; in that case, inter-annual variation in O/E may lead to variation close to the boundary of the status classes moderate and good, causing management decisions to depend on the year of sampling. By contrast, grossly degraded sites will probably be identified as impaired in most years (MacDonald & Côte 2013). In principle, temporal variability in O/E might be acceptable from the perspective of the European Union Water Framework Directive (WFD), as long as it means variation between the ecological quality classes high and good, i.e. classes not demanding management actions. However, as WFD demands that if good ecological status is not achieved, then necessary actions must be launched to reach this minimum acceptable condition (OJEC 2000), robust distinction between sites in moderate-or-worse and those in good-or-better condition becomes essential (Hering *et al.* 2010).

The issues of the representativeness of single-year data are also central to the design of temporal studies in community ecology beyond bioassessment. Wiens (1981) criticized single-sample surveys of being unable to reveal real community patterns. Having limited resources for sampling and sample processing, one unavoidably confronts a trade-off between spatial and temporal replicates. By skipping yearly monitoring, one may be able to allocate more resources on spatial replicates instead of time, the selected approach then being more representative through space (e.g. snapshots for studying temporal variation), and vice versa. The level of coherence may determine whether site-specific results can be extrapolated across space, with high among-site coherence allowing for more spatial extrapolation (Magnuson *et al.* 1990). Results of this thesis show that community coherence across sites within a region, and even across regions, is quite high, implying that a few carefully selected sites might be sufficiently representative for long-term stream monitoring. The identity of a particular year may affect study outcomes more easily when the snapshot approach is being used. It therefore seems that part of the resources allocated to spatial replication might be more needed for replication through time to yield results less contingent on the inclusion of a certain year. How long a data set is then needed to detect reliably long-term patterns of

benthic community variability? The comparison of studies using trajectory data but of differing lengths implied that very short data sequences are sensitive to year effect. Time sequences of about 4–5 years may be enough for the among-year similarity of macroinvertebrate communities to stabilize in near-pristine forest streams, but for impacted sites, comparable information is to my knowledge unavailable. Thus, spatially replicated long-term data sets from anthropogenically stressed sites would be extremely important to test how sensitive the patterns of community variability are to certain study years or to different study durations at impacted sites.

To conclude, four main lessons can be drawn from this thesis. 1) Although temporal variation may seem rather low, it should not be underestimated or dismissed relative to spatial variation. 2) Climate is a strong regulator of benthic population and community dynamics, and climatically exceptional years may have a significant imprint on the patterns observed. 3) Variation at human impacted sites may be more erratic than, and not necessarily explained by the same factors as, at near-pristine sites. 4) At local scales, benthic community stability is largely explained by in-stream vegetation, but its role (as the role of deterministic processes more generally) may be obscured by stochastic factors.

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Original articles

- I Huttunen K-L, Mykrä H & Muotka T (2012) Temporal variability in taxonomic completeness of stream macroinvertebrate assemblages. *Freshwater Science* 31(2): 423–441.
- II Huttunen K-L, Mykrä H, Huusko A, Mäki-Petäys A, Vehanen T & Muotka T (2014) Testing for temporal coherence across spatial extents: the roles of climate and local factors in regulating stream macroinvertebrate community dynamics. *Ecography* 37(6): 599–608.
- III Huttunen K-L, Mykrä H, Oksanen J, Astorga A, Paavola R & Muotka T (manuscript) Habitat connectivity and in-stream vegetation control temporal turnover of benthic invertebrate communities.
- IV Huttunen K-L, Mykrä H, Paavola R & Muotka T (manuscript) Comparing snapshot vs. trajectory approaches to the assessment of temporal turnover of benthic macroinvertebrate communities.

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