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Katri Tolonen

TAXONOMIC AND FUNCTIONAL ORGANIZATION OF MACROINVERTEBRATE COMMUNITIES IN SUBARCTIC STREAMS

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KATRI TOLONEN

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Abstract

Ecological research based on both species and their traits help us to understand the main mechanisms and environmental factors structuring biological communities. In general, variation in community composition is thought to be a consequence of both stochastic and deterministic factors. In stream ecology, the traditional view has been that the local habitat conditions pose a strong environmental filter that selects only species with the right functional traits into the local communities. However, recent studies on streams have also suggested that the responses of species to environmental gradients may be independent of those of other species due to stochastic factors, such as species dispersal, which then result in more continuous communities along environmental gradients. The aim of this thesis was to explore the relative importance of the deterministic and stochastic factors in the structuring of taxonomic and functional trait-based macroinvertebrate communities in streams in a high-latitude catchment by comparing the variation in these community facets along environmental and spatial gradients. Also, the relationship between environment and the functionally-defined communities was explored closely. The results indicated how the taxonomic composition of the communities may be more closely related to the stochastic and dispersal-related factors, whereas the functional composition of the communities may be more closely related to the deterministic environmental filtering processes. However, the overall structure of the communities seems to be strongly controlled by the variation in environment, although the heterogeneous and harsh conditions of the streams may preclude the formation of predictable community types. Nonetheless, some noticeable responses of different traits to different environmental factors were found, suggesting that definable functional trait-environment relationships may be discovered if key traits of the species can be identified. Overall, these findings underline the benefits of describing both taxonomic and functional-based communities when exploring the mechanisms behind the structuring of macroinvertebrate communities. The results also have applications for conservation practices. Conservation efforts should focus on varying environmental conditions in order to cover all aspects of macroinvertebrate community variation.

Keywords: benthic macroinvertebrates, biodiversity, community composition, environmental filters, environmental variation, linear modelling, spatial variation, species traits, subarctic streams

Tolonen, Katri, Pohjoisten virtavesien pohjaeläinyhteisöjen taksonominen ja toiminnallinen rakenne.
Oulun yliopiston tutkijakoulu; Oulun yliopisto, Luonnontieteellinen tiedekunta; Suomen ympäristökeskus
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Tiivistelmä

Lajeihin ja lajien toiminnallisiin lajiominaisuuksiin pohjautuva ekologinen tutkimus tuo uutta tietoa biologisten yhteisöjen taustalla vaikuttavista tekijöistä. Yleisesti yhteisöjen rakentumiseen vaikuttavat niin deterministiset kuin stokastiset ympäristössä vaikuttavat tekijät. Virtavesiyhteisöjen on perinteisesti ajateltu rakentuneen niin sanottujen ympäristösuodattimien mukaisesti, jolloin ympäristön vaihtelu suodattaa tietynlaisiin ympäristöihin vain lajit, joilla on tarvittavat ominaisuudet paikalla selviytyäkseen. Useat viimeaikaiset tutkimukset ovat kuitenkin osoittaneet virtavesiyhteisöissä elävien lajien esiintymisen vaihtelevan ympäristössä myös itsenäisesti erilaisista stokastisista, kuten lajien dispersaaliin vaikuttavista, tekijöistä johtuen. Tässä väitöstutkimuksessa tutkin näiden determinististen ja stokastisten ympäristötekijöiden suhteellisia vaikutuksia taksonomisesti ja toiminnallisesti luokiteltujen pohjaeläinyhteisöjen rakentumiseen pohjoisissa virtavesissä. Myös yksittäisten lajiominaisuuksien ja toiminnallisten yhteisöjen suhde pohjoisten virtavesien ympäristöolosuhteisiin oli tarkastelun alla. Tutkimuksen tulokset antoivat viitteitä siitä, että ympäristössä toimivat stokastiset ja lajien dispersaaliin liittyvät tekijät vaikuttaisivat voimakkaammin taksonomisesti luokiteltujen yhteisöjen vaihteluun, kun taas toiminnallisesti luokitellut yhteisöt vaikuttaisivat rakentuneen enemmän determinististen ympäristöprosessien mukaisesti. Kokonaisuudessaan yhteisöt vaikuttaisivat kuitenkin rakentuneen voimakkaasti vaihtelevien ympäristöolosuhteiden ohjaamana, ja tämä vaihtelu voi estää selkeästi ennustettavien yhteisörakenteiden synnyn. Muutamia selkeitä lajiominaisuusvasteita kuitenkin löytyi, mikä antaa viitteitä ennustettavissa olevien toiminnallisten yhteisöjen olemassaolosta, mikäli yhteisöjen menestymisen kannalta merkittävimmät lajiominaisuudet vain osataan määrittää. Nämä tulokset osoittavat, miten sekä taksonomisesti että toiminnallisesti luokiteltujen yhteisöjen käyttäminen rinnakkain yhteisöekologisissa tutkimuksissa voi auttaa selventämään yhteisöjen synnyn taustalla vaikuttavia tekijöitä. Tuloksilla on merkitystä myös virtavesiyhteisöjen suojelun kannalta. Suojelutoimenpiteet tulisi kohdistaa kattamaan ympäristöolosuhteita laajasti, jotta ympäristöolosuhteiden mukaan vaihtelevat yhteisöt tulisivat parhaalla mahdollisella tavalla katetuiksi.

Asiasanat: lajiominaisuudet, lineaarinen mallinnus, luonnon monimuotoisuus, pohjaeläinyhteisöt, spatiaalinen vaihtelu, subarktiset purot, yhteisörakenne, ympäristönvaihtelu, ympäristösuodatin

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7.12.2017 Katri Tolonen

Abbreviations

AIC	Akaike Information Criterion
BUR	Burrower
CLIM	Climber
CLIN	Clinger
CPOM	Coarse particular organic matter
CVRE	Cross-validated relative error statistic
DET	Detritus feeder
FFG	Functional feeding group
FIL	Filterer
GAT	Gatherer
GLM	General linear model
GRA	Grazer
GW	Groundwater
HTG	Habit trait group
IndVal	Indicator species analysis
LCBD	Local contribution to beta diversity
LCBD-f	Ecological uniqueness values calculated based on functional data
LCBD-t	Ecological uniqueness values calculated based on taxonomic data
MRT	Multivariate regression tree
PCNM	principal coordinates of neighbour matrices
PCoA	Principal coordinates analysis
PIER	Piercer
PRE	Predator
RDA	redundancy analysis
SCR	Scraper
SHR	Shredder
SLAP2	Standard Light Antarctic Precipitation 2
SPR	Sprawler
SWIM	Swimmer
UTC	Unique trait combinations
VIF	Variance inflation factor
VSMOW	Vienna Standard Mean Ocean Water

List of original publications

This thesis is based on the following publications which are referred throughout the text by their Roman numerals:

I Tolonen KE, Tokola L, Grönroos M, Hjort J, Kärnä O-M, Erkinaro J & Heino J (2016) Hierarchical decomposition of trait patterns of macroinvertebrate communities in subarctic streams. Freshwater Science 35(3): 1032–1048.

II Tolonen KE, Leinonen K, Marttila H, Erkinaro J & Heino J (2017) Environmental predictability of taxonomic and functional community composition in high-latitude streams. Freshwater Biology 62(1): 1-16.

III Tolonen KE, Leinonen K, Erkinaro J & Heino J (2017) Ecological uniqueness of macroinvertebrate communities in high-latitude streams is a consequence of deterministic environmental filtering processes. Aquatic Ecology. doi:10.1007/s10452-017-9642-3

Contents

1 Introduction

Organization of biological communities in nature has traditionally been explored through methods based on variation in taxonomic properties of the communities. However, even though taxonomic approaches have yielded many insights into the processes structuring biological communities (e.g. Leibold *et al.*, 2004), these approaches have not been able to produce general rules capable of predicting variation in community compositions at differing sites (McGill, Enquist, Weiher, & Westoby, 2006; Verberk, van Noordwijk, & Hildrew, 2013). This is largely because of the various restrictions associated with the taxonomic approaches. One restriction is that the variation in taxonomic composition of the communities at different sites is affected by various biogeographical and stochastic factors, which limit the reliability of predictions made about the community compositions at different sites (Hoeinghaus, Winemiller, & Birnbaum, 2007). Many studies have also focused only on species interactions, ignoring the profound effect of the abiotic environment on the biological communities (McGill *et al.*, 2006). Finding a new way to overcome these obstacles would help our understanding of the organization of communities, which in turn would benefit greatly the aims of many assessment, restoration and conservation programs. One potential way to overcome these problems is based on species functional traits (McGill *et al.*, 2006; Poff, 1997; Verberk *et al.*, 2013). In this approach, species co-existence in biological communities is explained through the relationships between species traits and their environments (Poff, 1997).

1.1 Functionally-defined communities and the environmental filtering

Species traits are attributes of organisms that reflect species adaptations to their environments. These traits are measurable at the individual level and comparable among different species (McGill *et al.*, 2006). For instance, benthic macroinvertebrates may be categorized into different functional feeding groups, where an individual trait describes the way how the species acquire their food (Merritt & Cummins, 1996). In general, functional traits are traits that strongly influence an organism's performance in its environment (McGill *et al.*, 2006).

The usability of the functional traits in community studies is based on the mechanistic link formed between species traits and their environments (Poff, 1997; Verberk *et al.*, 2013). For instance, in streams, leaf litter originating from the surrounding riparian vegetation contributes greatly to the occurrence, abundance and survival of macroinvertebrates with the functional feeding trait of “shredding” that utilize leaf litter as their main food resource (Cummins, Wilzbach, Gates, Perry, & Taliaferro, 1989; Masese *et al.*, 2014). Changes in the riparian vegetation may thus have significant effects on the distribution of these species in the local communities (Cummins *et al.*, 1989). In this way, local habitat conditions act as an environmental filter selecting only species with the right functional traits to be present in the local communities (Cavalli, Baattrup-Pedersen, & Riis, 2014; Poff, 1997; Southwood, 1977). Such mechanistic links between species and their environment hence play their part in determining the overall species compositions and diversity at a site (Keddy, 1992) and can therefore be an important factor structuring the variation in biodiversity in the whole region (Pausas & Austin, 2001). Thus, studying the interplay of functionally-defined communities and the environment adds considerably to our knowledge of the overall diversity patterns in nature (Fløjgaard, Normand, Skov, & Svenning, 2011; Heino & Peckarsky, 2014; Marquet, Fernández, Navarrete, & Valdovinos, 2004).

1.2 The organization of taxonomically and functionally-defined communities

Using approaches based on both taxonomically and functionally-defined communities can provide complementary information about the processes behind the organization of biological communities, as the taxonomic and trait composition of the communities may be structured by partly different processes (Heino, Mykrä, Kotanen, & Muotka, 2007; Hoeinghaus *et al.*, 2007). The taxonomic composition of a community at a site is a subset of all the species found in the regional species pool. Although species are generally assumed to be able to disperse everywhere in a region when given enough time, the composition of the regional species pool may still vary strongly geographically (Heino, Schmera, & Erős, 2013; Hoeinghaus *et al.*, 2007). This variation may be the result of constraints posed by history, climate and other biogeographical and stochastic factors that affect the distribution patterns of the species (Heino *et al.*, 2007; Hoeinghaus *et al.*, 2007). For instance, variation in landscape features along spatial gradients may pose direct dispersal barriers for species with differing dispersal abilities, leading to differences in the occurrences of single species in communities along ecological gradients (Blanchet, Helmus, Brosse, & Grenouillet, 2014; Heino *et al.*, 2007; Hoeinghaus *et al.*, 2007; Kärnä *et al.*, 2015; Leibold *et al.*, 2004; Menge & Olson., 1990). In contrast, the functional trait composition of local communities is thought to reflect variation in local environmental conditions, as species have been filtered into different habitats via their traits (Southwood, 1977; Townsend, Dolédec, Scarsbrook, & Zealand, 1997). Therefore, similar habitat conditions at different sites could be anticipated to select for similar functional composition, despite the varying species pool in the region (Hoeinghaus *et al.*, 2007; Pausas & Austin, 2001). However, before establishing into the community, species have to pass through a series of environmental filters active at different hierarchical scales (Keddy, 1992; Poff, 1997). For instance, in streams, species are filtered into their communities through filtering processes working at the progressively larger microhabitat, channel unit and watershed scales (Townsend & Hildrew, 1994).

Because of differences in the mechanisms behind the organization of taxonomic and functional-based communities, it has been suggested that the compositions of the taxonomically-defined communities should be more affected by the stochastic and dispersal related factors associated with spatial gradients (Göthe, Angeler, & Sandin, 2013; Heino, Schmera, *et al.*, 2013; Schmera, Erős, & Heino, 2013), whereas composition of the functionally-defined communities should be more under the control of selection by the local environmental factors (Göthe *et al.*, 2013; Southwood, 1977; Townsend *et al.*, 1997). These differences in the organization of the different community facets may further be predicted to be seen in the continuity of the communities along environmental gradients. Because of environmental filtering, functionally-defined communities could be expected to form predictable community types around specific environmental conditions, as species with similar functional traits have been selected into the same habitats, leading to more discrete community variation in the environment (Clements, 1916). However, the responses of single species to environmental gradients may be independent of those of other species due to the stochastic and dispersal related factors, which then results in more continuous community variation along the environment (Gleason, 1926). Either way, understanding how communities vary in space have important implications for conservation practices (Heino, Muotka, Mykrä, *et al.*, 2003).

In my thesis, I focus on the organization of taxonomically and functionally-defined macroinvertebrate communities in varying environmental conditions in streams in a high-latitude catchment.

1.3 Organization of benthic macroinvertebrate communities along streams' environmental gradients

1.3.1 The River Continuum Concept

To be able to understand variation in functional trait communities and the associated overall community changes in streams, it is useful to be familiar with the classic River Continuum Concept (RCC; Vannote, Minshall, Cummins, Sedell, & Cushing, 1980), where changes in benthic macroinvertebrate assemblages are explained through changes in the functional feeding structure of the communities in relation to the gradual environmental variation of the river's longitudinal gradient. Hence, the RCC theory can be seen to provide a background for the study of functional trait and community variation and helps to understand, how the community trait patterns are related to the varying environmental conditions in riverine systems (Greathouse & Pringle, 2006; Statzner & Higler, 1985).

Streams increase in size from the headwaters toward the river's mouth (Allan & Castillo, 2007). They typically begin as small and steep streams, with streambeds composed of boulders and cobbles. The water is cool because of ample shading by the riparian vegetation. Primary production in the headwater streams is often low, and energy is obtained primarily as allochthonous matter from the riparian vegetation (Allan & Castillo, 2007; Vannote *et al.*, 1980). Therefore, macroinvertebrates with the functional feeding traits of collecting and shredding are the dominant invertebrate groups in these streams (orders 1 to 3). In the mid reaches (orders 4 to 6), shading of the streams decrease as streams increase in their size. When the channels are exposed to more sunlight, water becomes warmer, allowing the growth of periphyton and hence changing the streams towards more autochthonous energy production (Allan & Castillo, 2007). As a result, grazers feeding on periphyton become the dominant functional feeding group. In the lower reaches (order 7 and larger), the streams become deeper and wider. Streambed has gradually changed into smaller grain size made of gravel and sand, which largely inhibits the growth of periphyton (Allan & Castillo, 2007). At this point, most of the energy comes as fine particulate organic matter from upstream resources and, hence, collectors and filterers are the dominant functional feeding groups in larger rivers (Vannote *et al.*, 1980).

This idea of matching a given functional feeding trait with particular environmental conditions can and has also been successfully applied in studies of other types of functional traits and ecosystems (Fierer, Bradford, & Jackson, 2007;

Hausner, Yoccoz, & Ims, 2003; Rabení, Doisy, & Zweig, 2005; Townsend & Hildrew, 1994; Usseglio-Polatera, Bournaud, Richoux, & Tachet, 2000; Verheyen, Honnay, Motzkin, Hermy, & Foster, 2003).

1.3.2 Variation in species composition of benthic macroinvertebrate communities along stream's environmental gradients

Streams and rivers harbor high levels of biodiversity, and especially headwater streams contribute substantially to the biodiversity of the whole river network (Clarke, MacNally, Bond, & Lake, 2008; Meyer *et al.*, 2007). A substantial part of this biological diversity is attributable to benthic macroinvertebrates, which are an important component of the functioning of healthy stream ecosystems (Wallace & Webster, 1996). They are an important part of food webs, and changes in their abundances can have cascading effects throughout the food chain (Allan & Castillo, 2007). Macroinvertebrates also play an important role in the biomass production and the nutrient cycling of the streams (Wallace & Webster, 1996).

One explanation for the high biodiversity of streams is that they are environmentally highly heterogeneous, providing various environmental niches, in which multiple different species can then occur (Chesson, 2000; Heino, Melo, & Bini, 2015). A traditional view in stream ecology has therefore been that the surrounding landscape and the local habitat conditions in streams create nested and highly effective filters that work on various spatial scales leading to predictable community types (Poff, 1997). These community types can then differ sharply even among adjacent sites, as only certain species with the right trait combinations are filtered to occur in the different environmental conditions prevailing in each site (Hawkins *et al.*, 2000; Poff, 1997). However, a few studies conducted in streams have also demonstrated more continuous rather than discrete community variation along environmental gradients (Heino, Muotka, Mykrä, *et al.*, 2003; Sandin, 2003). One of the suggested reasons for this is that because of the different environmental niches of individual species, species respond independently to the varying environmental conditions in space (Heino, 2005b). Second, factors related to species dispersal may cause the communities to vary continuously (Blanchet *et al.*, 2014; Hoeinghaus *et al.*, 2007; Leibold *et al.*, 2004; Menge & Olson, 1990). A third explanation is that because streams are characterized by unpredictable and frequent disturbances, these may lead to random extinctions and recolonizations of individual species at sites, making the variation in community assemblages difficult to predict (Grönroos *et al.*, 2013; Heino, Muotka, Mykrä, *et al.*, 2003).

1.4 Why study trait variation in freshwater communities?

Lotic ecosystems are among the most threatened and altered ecosystems in the world (e.g. Strayer & Dudgeon, 2010). Hence, recognizing the factors organizing the communities of stream macroinvertebrate species has important implications for streams' assessment, restoration and conservation programs. Further, approaches using functional traits have been highlighted as one of the most promising tools emerging for biomonitoring freshwater ecosystems (Baattrup-Pedersen, Göthe, Riis, & O'Hare, 2016; Menezes, Baird, & Soares, 2010), as the sensitivity of the macroinvertebrate trait characteristics to environmental changes has been identified (Hering *et al.*, 2009).

However, even though the trait-based approach has the benefit of producing results independent of the confounding effects of species dispersal and other biogeographical factors, it has not been able to describe the trait-environment relationships adequately enough to develop into sound research method (Verberk *et al.*, 2013). The reasons for this are manifold. One problem is that our understanding of how individual traits are correlated with each other is not sufficient (Poff *et al.*, 2006). Second, even though the environment superficially poses a similar arena for different organisms, they may perceive environmental variability very differently, which hinders the ability to find strong trait patterns at the community level. Third, finding all the relevant environmental filters that can operate at several spatial scales is difficult, and accurate information about the main environmental features structuring the communities at multiple spatial scales is therefore required (Lamouroux *et al.*, 2004). Fourth, before functional approaches can be used to indicate anthropogenic changes in the environment, it is necessary to understand the sensitivity of the communities to natural environmental variation, before any precise conclusions about the effects of the anthropogenic stressors can be made (Schmera *et al.*, 2013). Therefore, more research is needed for better understanding of the natural variation of stream community patterns in nature (Menezes *et al.*, 2010).

1.4.1 Subarctic streams as model systems

Subarctic streams provide an ideal ecosystem for testing the natural relationships between taxonomically and functionally-defined communities and the environment. Unlike many other freshwater ecosystems in the world, which have been subjected to centuries of severe anthropogenic stress and modifications, subarctic streams have remained in fairly pristine condition (Roussel *et al.*, 2014; Wrona *et al.*, 2013). Environmental conditions in high-latitude catchments are also severe and natural variation is high (Wrona *et al.*, 2013). Therefore, species living there can be expected to be under strong selection by the local environmental conditions. Hence, high-latitude streams should provide an environment where strong trait-environment relationships can be found in the absence of human impacts.

Northern freshwater ecosystems are also highly sensitive to various environmental threats (Jyväsjärvi *et al.*, 2015; Vilmi *et al.*, 2017; Wrona *et al.*, 2013). The global climate change, for instance, has been projected to induce notable environmental changes especially in the north (Chapin *et al.*, 2005; Krankina, Dixon, Kirilenko, & Kobak, 1997; Wrona *et al.*, 2013), which could then have prominent effects on high-latitude streams (Heino, Virkkala, & Toivonen, 2009). Therefore, understanding the structuring of the taxonomically and functionally-defined community compositions of the macroinvertebrate communities in the present day could help in predicting the possible changes in the functioning of the high-latitude streams in the future. Further, understanding the main environmental factors behind the variation in these communities may help to recognize and protect environmental conditions important in maintaining lotic biodiversity in high-latitude regions.

2 Aims of the thesis

The main aim of this thesis is to explore the environmental factors structuring benthic macroinvertebrate communities in pristine streams of a high-latitude catchment.

The first study question of this thesis is: (i) what are the potential factors behind the structuring of the taxonomically and functionally-defined macroinvertebrate communities? If the communities are organized through the environmental filtering process, they should be more closely associated to variation in the smaller-scale environmental variables, whereas if the communities are more affected by the stochastic and dispersal-related factors, they should be more closely associated to the larger-scale variables. In paper I, this question was addressed by comparing the relative importance of variables measured at smaller and larger-scales on the variation in taxonomically and functionally-defined community compositions by means of variation partitioning. In paper III, this question was addressed by comparing the relative importance of spatial and local environmental variables on the structuring of the ecological uniqueness values calculated based on both taxonomic and functional trait data by means of linear regressions and associated variation partitioning.

The second study question of this thesis is: (ii) what are the main environmental variables structuring the variation in taxonomically and functionally-defined community compositions and how do the different components of the functionally-defined communities respond to the variation in these variables? If the communities are structured through the environmental filtering processes, clear trait-environment relationships could be expected to be found between species and these variables, as species with particular traits are filtered to particular sites (Poff, 1997; Vannote *et al.*, 1980). This in turn would result the species to form distinct communities in specific habitat conditions. In paper II, these questions were addressed by comparing the results of multivariate regression trees and indicator species analysis for taxonomically and functionally-defined communities. The continuity of the communities was tested through constrained ordination analysis. In papers II and III, the most important environmental variables structuring the communities were further studied in two different seasons to see if there is seasonal variation in the importance of the different factors structuring the macroinvertebrate communities.

Overall, the questions studied here by using both taxonomically and functionally-defined stream communities provide a deeper understanding of the ecological responses of these communities to different stochastic and deterministic factors, and thereby further contribute to the broader discussion among ecologists about the drivers that influence patterns of biodiversity in general.

3 Methods

3.1 Study area

The study area is situated in the River Tenojoki drainage basin in the northernmost Finland and Norway (centered on 70ºN, 27ºE), with total basin area of 16,386 km^2. The landscape is characterized by arctic–alpine vegetation with barren tundra at higher altitude and mountain birch (*Betula pubescens ssp. czerepanovii*) forests at lower altitude. Some Scots pine (*Pinus sylvestris*) forests are also present, but at a very low proportion, and coniferous trees were practically absent in the sampling sites. The landscape in the area has remained in pristine or near-pristine condition (Erkinaro & Erkinaro, 1998; Roussel *et al.*, 2014). Stream waters in the basin are circumneutral with nutrient levels indicating ultraoligotrophic conditions (Heino, Muotka, & Paavola, 2003).

3.2 Biological and environmental variables

The study questions were tested by using two different data sets collected partly from the same streams. The data used in paper I was collected between 6th June and 18th June in 2012 from 55 rivers and streams draining into the River Tenojoki in Finland. A 50 m^2 riffle section was surveyed at each stream site. Riffle sites were chosen to be sampled, as they usually contain the most diverse and sensitive invertebrate assemblages compared to other habitat types found in streams (e.g. Barbour, Gerritsen, Snyder, & Stribling, 1999). Benthic macroinvertebrates were collected by taking six 30-s kick samples (mesh size = 0.3 mm) covering the most microhabitats found in the riffle area. These samples were then pooled together to provide a collective 3-min sample for each site, and the samples were preserved in alcohol. Macroinvertebrates were later identified in the laboratory. Local and riparian environmental variables were measured at each stream site (Table 1). Local variables in paper I refer to variables that were measured directly in the streams. Water depth (cm) and current velocity (m sec^{-1}) were measured from 30 randomly selected locations in cross-channel transects within the riffle section. Current velocity was measured at 0.6 × depth with a Miniair20 (Schiltknecht, Immendingen, Switzerland). Stream width (cm) was measured at 5 cross-channel transects. Particle sizes of the streambed were visually assessed at 10 randomly selected 1 × 1 m quadrats by means of a modified Wentworth scale (Wentworth, 1922): boulder

(257–1024 mm), cobble (65–256 mm), pebble (17–64 mm), gravel (2–16 mm) and sand (<2 mm). Visual estimates of percentages of moss cover (%) were made at the same squares. YSI multiprobe field meter (model 556MPS; Yellow Springs Instruments, Ohio) was used to measure the water conductivity (µS/cm^{-1}) and pH. Water samples were further taken for analyses of nitrogen, iron, manganese (µg/L^{-1}), and colour (mg Pt/l). Water samples were analyzed following the Finnish national standards (National Board of Waters and the Environment, 1981) in the laboratory.

In paper I, riparian scale covered an area of 2 m stretch from the stream banks' edge toward inland. Height of the bank (cm) was measured from the water level to the beginning of terrestrial vegetation, whereas steepness of the stream bank was measured as the stream bank rise (cm) over 2 m perpendicular to the stream. These variables were measured from five points on both sides of the stream within the area of the sampling riffle. Shading by overhanging vegetation was evaluated as the percentage of shading by mountain birch and willow (*Salix* spp.; Table 1).

Catchment variables used in paper I were calculated using ArcGIS 10.1 software (Environmental Systems Research Institute, Redlands, California). The catchment scale encompassed the drainage area of each individual study stream (Table 1). The total drainage area, stream length and distance to the upstream lake for the streams were digitized and calculated with maps obtained from the National Land Survey of Finland (2010a, b). When no upstream lake existed, a value of 2× the longest measured distance to an upstream lake was used. Proportions of peatlands, lakes, block fields and rock and shrub cover in the catchment area for each stream were also calculated. The proportion of migmatic metapelite in the catchment was calculated with maps from Geological Survey of Finland (2010). The greenness variable was calculated from satellite images (Landsat 7 ETM+; Hjort and Luoto 2006). Greenness is a measure of the abundance of green vegetation in the catchment area of each stream site (Crist, Laurin, & Cicone, 1986).

The biological and environmental data used in papers II and III were collected in two different seasons in 2013. The late spring data were collected between 6th June and 16th June from 50 rivers and streams draining into the River Tenojoki in both Finland and Norway. The early autumn data were collected between 6th September and 13th September from the same streams. The data were collected using fairly similar methods as in paper I. A 30 m^2 riffle section was surveyed at each site and macroinvertebrates were collected by taking kick samples (see above). Stream width (cm), depth (cm), current velocity (m/sec^{-1}), pH and conductivity (µS/cm^{-1}) were measured as in paper I. Particle sizes of the streambed were assessed at 10 randomly selected 50 × 50 cm quadrates by using the modified Wentworth scale (1922; see above). These were then used to count a weighted average particle size for the streams in paper III. Visual estimates of the percentage of moss cover (%) and coarse particulate organic matter (CPOM; %) were made at the same squares. Water samples were taken for analyses of nitrogen ($\mu g/L^{-1}$) and colour (mg Pt/l). Shading by overhanging vegetation was estimated as percentage (%) of shading by deciduous trees (*Salix* spp.; Table 1).

Isotope data

In 2013, an additional 50 ml water sample from each stream site was taken for the analysis of stable isotopes of water ($\delta^{18}O$, $\delta^{2}H$) and silica (SiO_2). Isotope samples were taken in order to examine the proportion of different water sources (e.g. precipitation, surface water and groundwater) in the streams (Table 1). In relation to this, 23 supplementary reference water samples were also taken from small brooks, ponds and springs near the River Tenojoki during the spring campaign and eight samples during the autumn campaign. Local precipitation samples for analyzing $\delta^{18}O$ and $\delta^{2}H$ were collected from the Kevo Research Station's weather station following the instructions of the International Atomic Energy Agency (2014). Further, snowpack isotope samples were taken from the Kevo Research Station in March 2013 by sampling the snowpack depth from several locations. Additionally, natural springs were sampled to obtain "groundwater signal" and lakes were sampled for "evaporation signal". All the samples were stored in cold (4°C ± 1°C) and dark prior the analysis. In addition, available isotope data from previous studies were used to complete the data set.

The analyses for the stable isotopes ($\delta^{18}O$, $\delta^{2}H$) and dissolved silica (SiO_2) begun by rinsing a sampling bottle with the sampled water before filling it completely. The isotope ratios, $^{2}H/^{1}H$ and $^{18}O/^{16}O$, of the samples were determined using cavity ring-down spectroscopy with Picarro L2120-i analyzer (Picarro Inc., California). The measured ratios are stated using δ notation relative to in-house standards that are calibrated with Vienna Standard Mean Ocean Water (VSMOW) and Standard Light Antarctic Precipitation 2 (SLAP2) samples. Precision of $\delta^{18}O$ and $\delta^{2}H$ values are ±0.1 ‰ and ±1.0 ‰ respectively. SiO_2 samples were analyzed using Finnish national standards (National Board of Waters and the Environment, 1981).

Isotope samples were used to calculate deuterium excess, inverse transit time proxies (Tetzlaff *et al.*, 2009), and groundwater (GW) proportion in the water. For the GW analysis, end-member mixing (hydrograph separation) was used to determine GW proportion in the study catchment. Also SiO_2 was used as surrogate for GW, which is typical in groundwater and surface water mixing studies as precipitation usually has a very low concentration of SiO_2.

Spatial variables

In papers I and III, spatial variables, obtained by using distance-based Moran's eigenvector maps (formerly called principal coordinates of neighbour matrices, PCNM; Borcard & Legendre, 2002), were used to represent spatial processes, such as environmental autocorrelation, historical effects and species dispersal between sites, which may affect the macroinvertebrate communities (Dray *et al.*, 2012; Table 1). The first step in obtaining the variables was to construct a matrix of Euclidean distances among the sites by using the y- and x-coordinates of the sampling sites as input variables (Borcard & Legendre, 2002). This matrix was then truncated with a truncation threshold, under which the distances between two sites were kept as measured and above which the distances were considered large. The longest distance between two sampling sites in the minimum spanning tree of the matrix was used as the threshold (Oksanen *et al.*, 2013). The distances above the threshold were given a value of 4 × threshold. In the second step, principal coordinates of the modified distance matrix was computed with the principal coordinates analysis (PCoA; Borcard & Legendre, 2002). The positive eigenvalues represent the Euclidean components of the neighbour relationships of the matrix, so only the spatial variables with positive eigenvalues showing positive spatial autocorrelation from the PCoA were used in the subsequent analyses. Spatial variables with small eigenvalues represent patterns occurring at smaller-scales and spatial variables with large eigenvalues represent patterns occurring at larger-scales (Griffith & Peres-Neto, 2006).

Table 1. The explanatory variables used in the analyses in papers I, II and III.

Measured variables	Paper I	Paper II	Paper III
In-stream variables	Stream width and depth, current velocity, streambed particle size, moss cover, pH, conductivity, nitrogen, iron, manganese, colour	Stream width and depth, current velocity, streambed particle size, moss cover, CPOM, conductivity, pH, nitrogen, colour, isotope variables	Stream width and depth, current velocity, weighted average streambed particle size, moss cover, CPOM, conductivity, pH, nitrogen, colour
Riparian variables	Height and steepness of the stream bank, percentage of shading by birch and willows	Percentage of shading by deciduous trees	Percentage of shading by deciduous trees
Catchment variables	Stream length, drainage area, distance to upstream lake, proportions of peatland, lakes, block fields, rock and shrub cover, migmatic metapelite		
Spatial variables	PCNM		PCNM

3.3 Taxonomic and functional trait data

In paper I, macroinvertebrates were identified to species (~77%) or genus level. In papers II and III, the lowest identification level for most of the macroinvertebrates was genus (~90%) whereas the rest were identified to family level. Studies have shown that genus and family level of identification can be used effectively to examine community-environment and trait-environment relationships in stream environments (Gayraud *et al.*, 2003; Heino, 2008).

Macroinvertebrates were assigned into their functional trait groups, i.e. grouping features, each including several individual traits (Schmera, Podani, Heino, Erős, & Poff, 2015). In all the papers (I, II, III), macroinvertebrates were assigned into functional feeding groups (FFG), habit trait groups (HTG) and size groups. In paper III, macroinvertebrates were also categorized according to their means of respiration. Here, the term "trait group" is hence used to refer to the whole set of individual traits in one grouping feature (FFG, HTG, size or respiratory grouping) and the term "trait" is used to refer to an individual trait (Schmera *et al.*, 2015).

Functional feeding traits describe the way how macroinvertebrates acquire their food. FFGs include the traits filterers, gatherers, piercers, shredders, scrapers or grazers and predators (Cummins & Klug, 1979; Merritt & Cummins, 1996). Macroinvertebrates were assigned into their functional feeding groups mainly according to Moog (2002), where each species is given 1 to 10 points for each of the possible feeding trait. Here, species was assigned to the FFG for which its score was ≥5. If a species was missing from Moog (2002), Merritt *et al.* (2008) classification or judgement based on the FFGs of closely related species was used.

Functional habit traits (HTG) describe the mobility and microhabitat use of the macroinvertebrates (Merritt *et al.*, 2008). HTGs followed the classifications by Merritt *et al.* (2008) and included the traits burrowers, climbers, clingers, sprawlers and swimmers.

Each taxon was further assigned into different size groups: 0–0.25 cm, 0.25–0.5 cm, 0.5–1 cm, 1–2 cm, 2–4 cm and 4–8 cm. The body size categorization refers to maximum larval body length. In papers I and II, categorizations were based on data provided by personal communication with S. Dolédec (University of Lyon, France), J. Ilmonen (Metsähallitus, Natural Heritage Services, Vantaa, Finland), and L. Paasivirta (Salo, Finland). In paper III, the body size categorization followed Tachet *et al.* (2010).

Last, macroinvertebrates were assigned into groups according to their ways of respiration. Here, macroinvertebrates respire either with their teguments, gills, plastrons or spiracles. This categorization also followed the categorization of Tachet *et al.* (2010).

The trait information obtained from these trait groups were further combined to form the unique trait combinations (UTC) of the macroinvertebrate taxa (Schmera, Podani, & Erős, 2009). UTCs were formed by combining the abundances of individual taxa with identical traits into the same UTCs. UTCs can thus be seen as describing parts of species ecological niches (Schmera *et al.*, 2009). In papers I and II, the UTCs included traits from the FFG, HTG and size groupings. In paper III, the respiration trait was also added to the UTCs. As an example, the mayfly genus *Baetis* is a grazer by its feeding trait, swimmer by its habit trait, it belongs to the size group 1–2 cm and it breathes with gills. Combining these four traits we get *Baetis´* UTC: grazer/swimmer/1–2 cm/gill.

Overall, matrices containing the abundances of different taxa and UTCs, the abundances of the whole functional groupings of FFG, HTG and size, and matrices containing the abundances of individual traits at each stream site were used as response variables in paper I. In paper II, in turn, the response data included the taxonomic and UTC data matrices and the functional grouping matrices (FFH, HTG and size). In paper III, taxonomic and UTC matrices were used as basis to calculate the final response variables (see below).

3.4 Statistical methods

Data transformations

Before the taxonomic and trait abundance data were suitable for the statistical methods, such as redundancy analysis (RDA), clustering and ordination, the data sets were *Hellinger*-transformed (Legendre & Gallagher, 2001). *Hellinger*-transformation is a square root of the observed values that have first been divided by row (i.e. site) sums (Legendre & Gallagher, 2001). However, Hellinger transformation is not appropriate for response matrices with only a single column (i.e. single trait data). Therefore, in cases where the data matrix contained the abundances of only a single trait, the data was log (x + 1) transformed.

Variable selection methods

In paper I, Pearson's (r) correlation tests were run within each environmental variable set measured from the different spatial scales (local, riparian and catchment) in order to eliminate strongly correlated variables. A correlation level of $r \geq 0.8$ was used as a threshold for removing variables.

To further reduce the number of explanatory variables used in the subsequent analysis in paper I, a forward selection of variables with two stopping rules (Blanchet, Legendre, & Borcard, 2008) was run for each environmental variable set, as well as for the spatial variables. First, a global test of significance using all the explanatory variables in the explanatory variable set was run. If the global test was significant, the procedure continued with the forward selection. If the forward selection then identified a variable that brought the variance explained by the selected variables over the explained variance of the global test, the variable was rejected and the procedure stopped (Blanchet *et al.*, 2008). This variable selection method was also used in paper II to select the explanatory variables used in the subsequent constrained ordination analyses.

In paper III, the number of variables used in the main analyses was first reduced by eliminating the environmental variables with the highest multicollinearity with each other. This was done by first running a full model of GLM with the response variables (see below) and all the possible environmental variables measured from the streams. After this, variance inflation factors (VIF) were calculated for each of the explanatory variables in the model. Then, the explanatory variable with the highest VIF was eliminated and the GLM was repeated with the remaining variables. This procedure was repeated until all the VIFs were below the pre-determined threshold of ≥1.9 (Zuur, Ieno, & Elphick, 2010). After removing the most correlated environmental variables, a forward variable selection of Akaike Information Criterion (AIC) was run for the remaining variables in order to select the final environmental variables used in the analyses. The VIF procedure, however, was not feasible for the selection of spatial variables used in paper III, as those are by default orthogonal to each other (Borcard & Legendre, 2002). Therefore, in order to reduce the number of spatial variables, GLMs with the full set of spatial variables were run, after which forward AIC variable selections were performed.

Measuring ecological uniqueness

In paper III, ecological uniqueness values, also called local contributions to beta diversity (LCBD), were used as response variables to describe the taxonomically and functionally-defined communities. The ecological uniqueness value of a site describes the contribution of the community at that site to the overall beta diversity of the region under study. The higher the ecological uniqueness is, the more different or unique species composition the site has compared to the other sites (Legendre & De Cáceres, 2013). Large values may therefore indicate sites that have a special ecological status, such as exceptionally good or bad environmental conditions for the communities (Legendre & De Cáceres, 2013). Hence, variation in the LCBD values can be used to explore the factors that structure the overall biodiversity of the region (Lopes *et al.*, 2014; Tonkin, Heino, Sundermann, Haase, & Jähnig, 2016).

The calculation of the ecological uniqueness values for taxonomic data (LCBD-t) began by calculating the squared differences between the *Hellinger*-transformed, taxonomic abundance values at a site and the mean abundance of the corresponding taxon. After this, all the values of this matrix containing the squared differences were summed up to obtain the total sum of squares (SS) of the data matrix. The LCBD-t value of a site was then obtained by dividing the sum of squares corresponding to the site by the total sum of squares (Legendre & De Cáceres, 2013). The same procedure was then repeated for the UTC abundance matrix in order to obtain the LCBD-f values, used here to describe the ecological uniqueness of the functionally-defined communities.

Variation partitioning

Variation partitioning is a method for partitioning variation in the response variable into different components explained by the different explanatory variable sets by means of constrained ordination or regression techniques (Borcard, Gillet, & Legendre, 2011). It calculates the (i) unique and (ii) shared fractions of variance that is explained by the different explanatory variable sets, as well as (iii) the amount of unexplained variation (Borcard *et al.*, 2011; Fig. 1). In paper I, variation partitioning was used to partition variation in the taxonomically and functionally-defined communities by the variable sets representing different spatial scales (local, riparian, catchment and spatial scale). Variation partitioning in RDA (Rao, 1964) was used for the multivariate response data (i.e., taxonomic data, FHS, FFG, HTG and size matrices), and linear regressions were used for the univariate response data (i.e., individual traits; Borcard *et al.*, 2011). The decomposition of the variation into different fractions was based on adjusted R^2 values which take into account the different number of explanatory variables in the explanatory variable sets (Peres-Neto, Legendre, Dray, & Borcard, 2006).

Variation partitioning was also used in paper III to investigate the relative importance of the local and spatial variables in driving the variation in the LCBD-t and LCBD-f values.

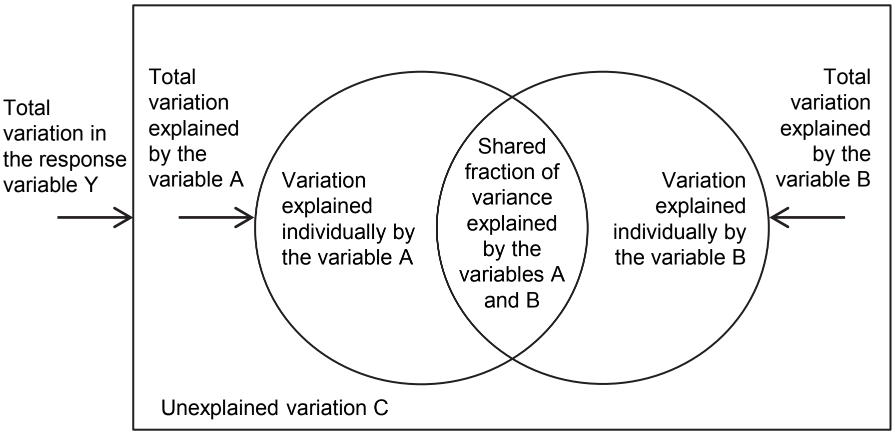

Fig. 1. An illustration of Venn diagram formed in the variation partitioning procedure run by using two explanatory variable sets (A and B). The rectangle represents 100% of the variation in the response variable Y. Modified scheme from Legendre & Legendre (2012).

Multivariate regression tree and indicator species analysis

In paper II, multivariate regression trees (MRT) were used to explore the threshold variables organizing the taxonomically and functionally-defined communities along stream environmental gradients. MRT is a method based on constrained clustering, where discrete clusters of sites are formed by splitting the response data on the basis of values of the explanatory variables (De'ath, 2002). The splits are generated by clustering sites with minimal dissimilarity with each other. The procedure defines specific threshold values (nodes) of the explanatory variables that divide the data. As a result, a tree is formed where the terminal "leaves" are composed of a subset of sites with the smallest possible within-group sums of squares (Fig. 2). After this, cross-validation of the results is run to prune the tree to obtain the best predictive tree. This is done by dividing the data randomly into test groups of the objects. As one test group at a time is left aside, a new tree is constructed by using the remaining objects. Then, the one test group is allocated to the reconstructed tree and distances are computed from each object of the test group to the centroids of the groups located in the leaves of the reconstructed tree. When the tree is valid, the test group locates near centroid of the tree. Then, overall cross-validated relative error statistic (CVRE) is run for each of the partitioning. CVRE is the ratio of variation unexplained by the tree to the total variation in the response data. When cross-validation is repeated a number of times, the mean and standard error of all CVRE estimates can be computed. CVRE varies from a zero for a perfect fit to one for a poor fit (Legendre & Legendre, 2012). Here, the tree with minimum CVRE was picked. The MRT were run for taxonomic and UTC data and for the trait groupings of FFG, HTG and size by using local environmental variables.

In addition to the MRT, an indicator species analysis (IndVal; Dufrêne & Legendre, 1997) was run in order to detect significant indicator taxa and "indicator traits" for the nodes and leaves of the final trees in paper II. IndVal combines the mean abundance and occurrence of taxa in each cluster of sites. A high indicator value is obtained when a taxon is both abundant and also occurs in most sites of a given cluster. The indicator values range from zero to one, one referring to a perfect indicator status. The significance of the indicator taxa and traits were further tested with a permutation procedure with 1000 permutations (Dufrêne & Legendre, 1997).

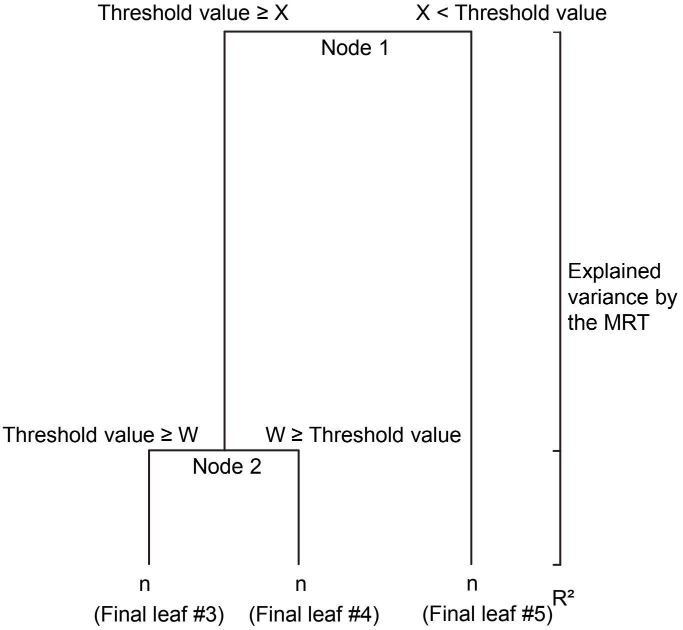

Fig. 2. An illustration of an MRT tree that is formed in the multivariate regression analysis. The nodes describe the splits of the sites based on the values of the threshold

variables (X and W). The final “leaves” are composed of a subset of sites with the smallest within-group sums of squares of the communities. Modified scheme from Legendre & Legendre (2012).

Constrained ordination and linear modelling

To further explore the continuity of the taxonomically and functionally-defined communities in paper II, a constrained ordination using redundancy analysis (RDA; Legendre & Legendre, 2012) was run for the taxonomic and functional data sets with variables selected in the variable selection procedure. After this, the groupings of the final leaves of the MRT trees were plotted on the resulting ordination plots.

In paper III, generalized linear modelling (GLM) with Gaussian error terms (Legendre & Legendre, 2012) was, in turn, used to model the variation in the taxonomically and functionally-defined LCBD values against the selected environmental and spatial variables.

Pearson’s chi-squared tests

In papers I and II, Pearson’s chi-squared ($\chi 2$) tests were used to test whether classifications of the macroinvertebrates based on the FFG, HTG and size groupings matched with each other. The results therefore indicate if the traits in the different grouping features show affinity to each other.

Table 2 gives an overall summary of the methods and statistical analyses used in the analyses in papers I, II and III.

Table 2. Methods and statistical analyses used in the analyses in papers I, II and III.

	Response variable	Explanatory variables	Used data transformations	Variable selection methods	Statistical analysis
Paper I	Taxonomic and UTC data, FFG, HTG and size groupings, individual traits	Environmental variables measured from local, riparian and catchment scale, spatial variables	Hellinger, log(x+1)	Pearson's (r), forward selection of Blanchet *et al.* (2008)	Variation partitioning, Pearson's chi-squared test
Paper II	Taxonomic and UTC data, FFG, HTG and size groupings	Local environmental variables (including shading)	Hellinger	Pearson's (r), forward selection of Blanchet *et al.* (2008)	MRT, IndVal, ordination and clustering, Pearson's chi-squared test,
Paper III	LCDB values calculated based on both taxonomic and UTC data	Local environmental variables (including shading), spatial variables	Hellinger	VIF, AIC	GLM, variation partitioning

4 Results and discussion

4.1 The organization of the taxonomically and functionally-defined macroinvertebrate communities in high-latitude streams

The first study question of the thesis was: what are the main mechanisms or factors structuring macroinvertebrate communities in high-latitude streams? If these communities are driven by deterministic factors, strong relationship between the environmental factors of the streams and the functionally-defined communities can be expected, as species with differing traits are filtered to occur in environmentally different sites (Lebrija-Trejos, Pérez-García, Meave, Bongers, & Poorter, 2010; Poff, 1997). However, if the communities are strongly influenced by spatially-related dispersal and stochastic factors, the trait-environment relationship should be weaker, as this relationship is interfered by species possibly occurring even in suboptimal sites irrespective of their traits (Brown & Kodric-Brown, 1977; Leibold *et al.*, 2004). Therefore, the taxonomic composition of the communities may be more strongly related to the spatial variables.

In paper I, the above-mentioned idea was addressed by comparing the results of variation partitioning run separately for the taxonomic and UTC-based communities with variable sets representing different spatial scales. The results showed how the total variation explained by the catchment and spatial variables was higher for taxonomic composition (28%) than for functional composition (25%), while at the same time the smaller-scale in-stream and riparian variables explained more variation for UTC (28%) than for taxonomic composition (26%). Also, the total amount of variation explained by the in-stream variables was higher for UTC (27%) than for the taxonomic composition (23%), whereas the spatial variables explained more variation for taxonomic composition (13%) than for UTC composition (6%).

In paper III, the question was addressed by comparing results obtained from the GLM and variation partitioning analysis run for the LCBD-t and LCBD-f values. The GLM analysis showed how the environmental variables were better at explaining variation in both the LCBD-t and LCBD-f values in the spring (adj. $R^2 = 0.342$, $p < 0.001$, adj. $R^2 = 0.362$, $p < 0.001$, respectively) than what the spatial variables were (adj. $R^2 = 0.07$, $p = 0.092$, adj. $R^2 = 0.04$, $p = 0.091$, respectively). The variation partitioning showed how 8% and 4% of the variances explained by the environmental variables were shared (Fig. 3). The results from the GLM analysis in the autumn, however, were slightly different. The environmental and spatial variables explained nearly the same amounts of variation in the LCBD-t values (adj. $R^2 = 0.150$, $p = 0.003$, adj. $R^2 = 0.167$, $p = 0.010$, respectively), of which the variation partitioning showed that 3% was shared between the different variable sets. For LCBD-f, the variations explained by the environmental and spatial variables were also the same (adj. $R^2 = 0.219$, $p = 0.002$, adj. $R^2 = 0.217$, $p = 0.003$), and variation partitioning showed that 5% of the variation was shared between the variable sets (Fig. 3).

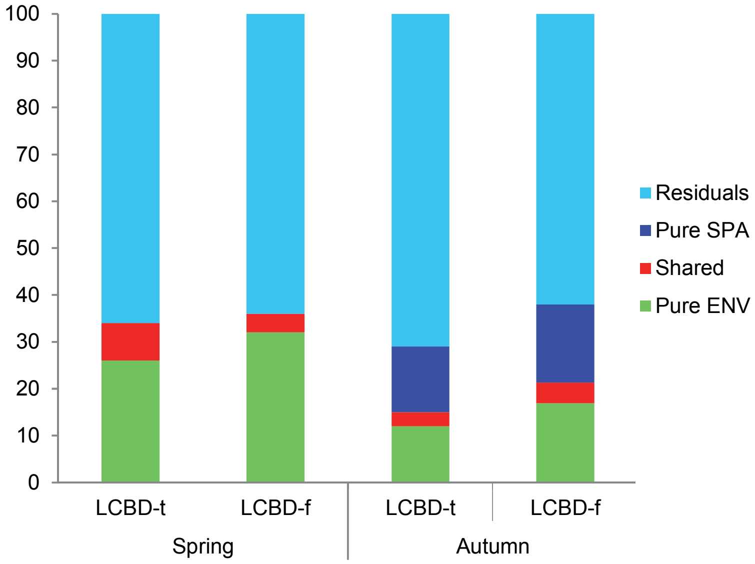

Fig. 3. Results of the GLM and the variation partitioning analyses from paper III. Expressed are the proportions of variations explained purely by environmental variables (ENV) and purely by spatial variables (SPA) in the analyses run with the taxonomic-based (LCBD-t) and functional trait-based (LCBD-t) ecological uniqueness values. Also, shared and unexplained fractions are shown.

The results of the variation partitioning in paper I give some support for the idea that the taxonomically and functionally-defined community compositions in high-latitude streams could be structured partly by different processes. The taxonomic composition may be seen to be more structured through the spatially related processes, as the larger-scale variables were better at explaining variation in their composition. At the same time, the functional composition may be seen to be structured through the deterministic processes, as the smaller-scale variables were better at explaining variation in the functional composition of the communities. It could be that within the taxonomic composition, the different dispersal abilities of the species combined with the dispersal limitations posed by the surrounding landscape result in a situation where all sites are not reached by all the species (Heino, Melo, Siqueira, *et al.*, 2015; Leibold *et al.*, 2004), which leads to the closer association of species composition with the larger-scale catchment and spatial variables (Heino, Melo, Siqueira, *et al.*, 2015; Leibold *et al.*, 2004). Indeed, the landscape of the Tenojoki river basin is characterized by varying altitudes and landscapes (Kärnä *et al.*, 2015), which potentially act as an effective filter for the macroinvertebrate communities (Townsend, Dolèdec, Norris, Peacock, & Arbuckle, 2003). For the functionally-defined communities, however, the local environmental conditions have selected only specific trait combinations fit to the particular environmental conditions prevailing in the streams, therefore leading to closer association of the functional composition of the communities with the smaller-scale variables (Heino *et al.*, 2007; Lamouroux, Dolédec, & Gayraud, 2004; Schmera *et al.*, 2013). However, it should be noted that the differences in the amounts of explained variations among the different scales were rather small, and hence can be seen as suggestive, not strongly conclusive. Nonetheless, the results are still congruent with previous studies, where taxonomic composition has been associated more strongly with geographical and spatial factors (Göthe *et al.*, 2017; Hoeinghaus *et al.*, 2007) and trait composition with local environmental variation (Göthe *et al.*, 2017; Heino *et al.*, 2007). Compared to other studies, this study was conducted within one drainage basin and therefore smaller differences in the explained variations can be expected. It should also be noted that clear separation of the effects of environmental and spatial variables is impossible, as different environmental variables and process are always somehow connected. This should hence be taken into account when comparing the relative importance of processes working on different scales. Nonetheless, the notion that the different processes may have different effects on the taxonomically and functionally-defined communities even within a single drainage basin should be taken into consideration in conservation and biomonitoring studies. This is because the analyses based on taxonomic communities may suggest species distributional or stochastic patterns, whereas analyses based on functional communities may reveal more clearly the relationships of the communities to the local environment (Hoeinghaus *et al.*, 2007).

However, despite the fact that the results from paper I are indicative of the idea that different mechanisms may be behind the structuring of the taxonomically and functionally-defined communities, the results from the GLM and the variation partitioning in paper III, give further support for the idea that highlight the effect of environmental filtering on the structuring of the stream macroinvertebrate communities. This is because the environmental variables were better at explaining variation in both LCBD-t and LCBD-f values especially in the spring. However, this conclusion seemed to be less clear in the autumn, as the importance of the environmental factors for both the LCBD-t and LCBD-f values decreased from spring to autumn, while the importance of the spatial factors increased notably.

The ecological uniqueness of the macroinvertebrate communities in the spring could be more closely associated with the local environmental conditions if the extreme habitat conditions during the past winter and spring have removed taxa with unsuitable traits from the communities. For instance, Huryn *et al.* (2005) have found evidence of how substratum freezing and instability may determine variation in taxonomic and functional-based communities in streams experiencing extreme disturbance during winter. Hence, the extreme environmental conditions of the high-latitude streams during the winter could 'reset' the communities to vary according to the local habitat conditions tightening the trait-environment and therefore also the community-environment relationships.

Another possible explanation for the different associations of the LCBD-t and LCBD-f values on the different factors between the seasons may relate to the different life cycles of the species (Linke, Bailey, & Schwindt, 1999). Many of the macroinvertebrate taxa in high-latitudes show varying life cycles and emergence patterns (Ulfstrand, 1968), possibly leading to situations where some species are present in the streams in the autumn and not in the spring (or vice versa; Ulfstrand, 1968). It could be, for instance, that the eggs of some taxa were in diapause or their juveniles were in hyporheos during the sampling period in the spring (Ulfstrand, 1968). Then, as the new cohorts of these taxa emerge from the streams during the summer, the spatially related stochastic drift and dispersal may allow some of these individuals to enter even suboptimal habitats in the autumn through processes such as the mass effect (Leibold *et al.*, 2004; Vellend, 2010). This would then blur the community compositions among the sites in the autumn leading to the increasing importance of the spatial variables for the communities. Subsequently, the taxa settled in suboptimal habitats could be later removed by the next winter and spring conditions. Overall, these seasonal differences in the factors structuring the macroinvertebrate communities demonstrate how stream's temporal community turnover can be simultaneously driven by ecological, physical, as well as geographical factors between seasons within the same year (Korhonen, Soininen, & Hillebrand, 2010).

4.2 Main environmental variables structuring variation in the taxonomically and functionally-defined community compositions in high-latitude streams

The second aim of this thesis was to explore the main environmental variables that structure the variation in the taxonomically and functionally-defined community compositions, and how the different components of the functionally-defined communities respond to the variation in the environment. If the communities are structured through the environmental filtering processes, clear trait-environment relationships could be expected to be found (Lamouroux *et al.*, 2004; Poff, 1997; Vannote *et al.*, 1980).

In paper I, these questions were approached by comparing the results from the variable selection and the variation partitioning. The results showed how the taxonomically and functionally-defined communities vary along different environmental factors, and that the importance of these factors is different for different traits. For instance, the variable selection procedure selected slightly different sets of environmental variables from the different spatial scales to explain variation in the different community facets. Overall, it should be noted that the following percentages are total fractions of explained variances by the different explanatory variable sets obtained from the variation partitioning and hence include the shared variances with other scale variables as well.

For taxonomic data, in-stream (moss cover, stream width, manganese, boulder, conductivity) and riparian (shading by birch and willow, bank height and steepness) variables explained 23% and 14% of the variation, and catchment (distance to upstream lake, catchment area, proportion of shrub, lakes in the catchment, migmatic metapelite, greenness) and spatial (V1, V3, V2, V9) variables explained 23% and 13% of the variation, respectively (Fig.4A). For UTC, in turn, in-stream (moss cover, depth, stream width, boulder) and riparian (shading by birch and willow, bank height) variables explained 27% and 14%, and catchment (migmatic metapelite, distance to upstream lake, proportion of shrub, catchment area, lakes in the catchment) and spatial (V3, V1) variables explained 24% and 6% of the variation, respectively (Fig. 4A).

For FFG, the total amount of explained variation was 44%. In-stream (moss cover, stream width) and riparian (shading by willow and birch, bank height) variables explained 34% and 18% of the variation, whereas catchment (migmatic metapelite, catchment area, distance to upstream lake, proportion of shrub) and spatial (V1, V2) variables explained 34% and 11% of the variation, respectively (Fig. 4B). Variation partitioning for the individual feeding traits was done for gatherers, predators, and shredders, as for filterers and scrapers, only in-stream variables were selected in the forward selection. For gatherers, the total explained variation was 73%, of which in-stream (moss cover, boulder, conductivity) and riparian (shading by birch and willow, bank height) variables explained 45% and 27%, and catchment (proportion of shrub, catchment area) and spatial (V1, V2) variables explained 49% and 24%, respectively (Fig. 4B). For predators, the total amount of explained variance was 50%, of which in-stream (moss cover, cobble), riparian (shading by birch) and catchment (migmatic metapelite, proportion of shrub, peatland) variables explained 38%, 8% and 28%, respectively (Fig. 4B). For shredders, the total amount of explained variance was 44%, of which in-stream (stream width, moss cover), riparian (shading by willow and birch) and catchment (catchment area) variables explained 39%, 32% and 21%, respectively (Fig. 4B). For filterers and scrapers, the only selected in-stream variables (cobble for filterers, boulder for scrapers) explained both 8% of the variation in these traits (Fig. 4B).

For HTG, the total amount of explained variance was 49%, of which in-stream (moss cover, stream width, boulder), riparian (shading by birch) and catchment (migmatic metapelite, distance to upstream lake, proportion of shrub, catchment area) variables explained 42%, 11% and 33%, respectively (Fig. 4C). Variation partitioning for the individual habit traits was done for burrowers, climbers, sprawlers and swimmers, as for clingers, only in-stream variables got selected. For climbers, the total amount of variation was 55%, of which in-stream (moss cover, boulder) and riparian (shading by willow and birch, bank height) variables explained 42 % and 32%, and catchment (distance to upstream lake) and spatial (VI) variables explained 31% and 11%, respectively (Fig. 4C). For burrowers, the total amount of variation was 68%, of which in-stream (moss cover, nitrogen, cobble, stream width), riparian (shading by birch, bank height) and catchment (migmatic metapelite) variables explained 58%, 35% and 30%, respectively (Fig. 4C). For sprawlers, the total explained variance was 31%, of which in-stream (moss cover), riparian (shading by birch) and catchment (migmatic metapelite, catchment area) variables explained 31%, 12% and 16%, respectively (Fig. 4C). For swimmers, the total explained variance was 11%, of which in-stream (moss cover) and catchment (proportion of shrub) variables explained 6% and 7%, respectively

(Fig. 4C). For clingers, the only selected in-stream variable (cobble) explained 7% of the variation in this trait (Fig. 4C).

For size grouping, the total explained variance was 46%, of which in-stream (moss cover), riparian (shading by birch) and catchment (lakes in the catchment, proportion of shrub, greenness, catchment area explained) variables explained 26%, 8% and 27%, respectively (Fig. 4D). For the individual size 0–0.25 cm, the amount of explained variance was 41%, of which the in-stream (moss cover, manganese), riparian (bank height) and catchment (lakes in the catchment) variables explained 33%, 7% and 9%, respectively (Fig. 4D). For the size 0.5–1cm, the total amount of explained variation was 35%, of which in-stream (moss cover), riparian (shading by willow) and catchment (greenness) variables explained 23%, 9% and 12%, respectively (Fig. 4D). For the size 2–4 cm, the total explained variance was 24%, of which the in-stream (boulder) and riparian variables explained 14% and 11% of the variation, respectively (Fig. 4D). For the size class 4–8 cm, the total explained variance was 52 %, of which in-stream, riparian and catchment variables explained 26%, 30% and 43% of the variation, respectively (Fig. 4D). For the size 0.25–0.5 cm, the only selected catchment (shading by birch, bank height) variables explained 17% of the variation, and for the size 1–2 cm, the only selected in-stream variables (cobble, conductivity) explained 17% of the variation, respectively (Fig. 4D).

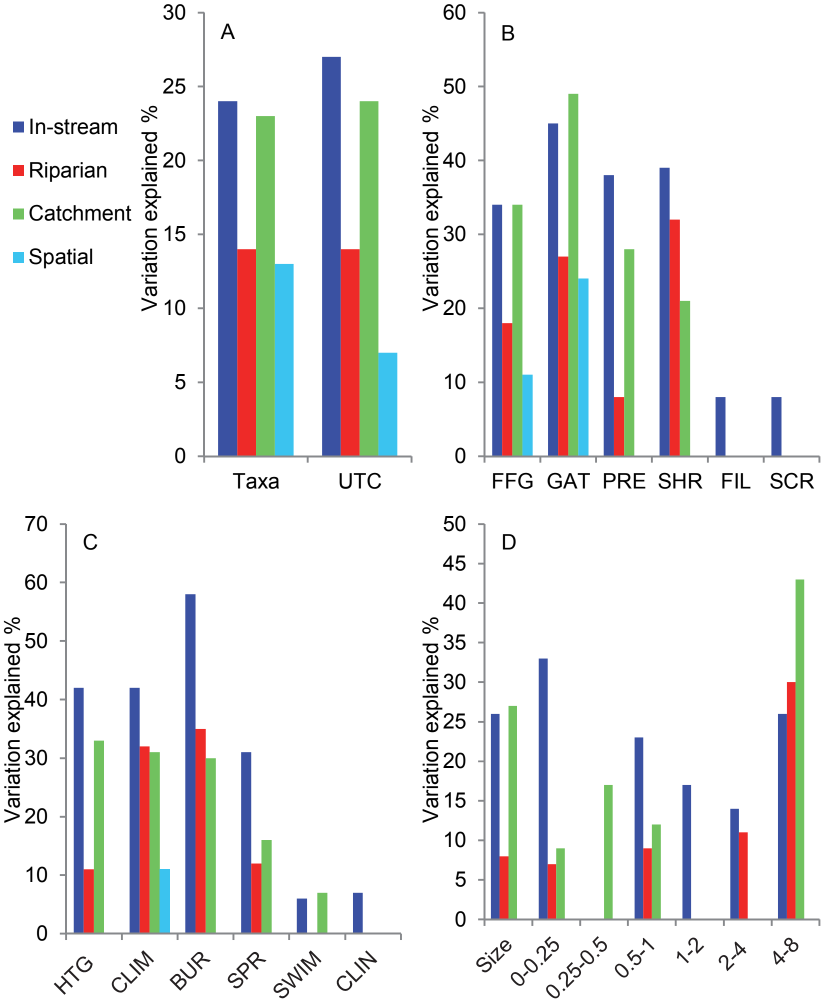

Fig. 4. The total explained variances by the in-stream, riparian, catchment and spatial variables for taxonomic and UTC data (A), for the whole functional feeding grouping (FFG; B) and the individual feeding traits gatherers (GAT; B), predators (PRE; B), shredders (SHR; B), filterers (FIL;B), scrapers (SCR; B), for the whole habit trait grouping (HTG; C) and for the individual habit traits climbers (CLIM; C), burrowers (BUR; C), sprawlers (SPR; C), swimmers (SWIM; C) clinger (CLIN; C), and for the whole size grouping (D) and for the size classes 0–0.25 cm (D), 0.25–0.5 cm (D), 0.5–1 cm (D), 1–2 cm (D), 2–4 cm (D) and 4–8 cm (D). The percentages are total fractions of explained variances by the different explanatory variable sets obtained from the variation partitioning from paper I and include the shared variances with other scale variables.

The results of variation partitioning showed how the different taxonomically and functionally-defined community facets responded differently to variables measured from the different spatial scales. For instance, for HTG and many of the individual habit traits, the importance of the variables from the different scales decreased from the local scale toward the more broad-scale variables. This result is logical, as the habit traits reflect the habitat and microhabitat use by the macroinvertebrates (Merritt *et al.*, 2008), and hence the local environmental conditions may be seen acting as the most important environmental filter for this trait grouping (Merritt *et al.*, 2008; Rabení *et al.*, 2005). However, more relative variation in the order of importance of the different scales was evident for FFG and its individual feeding traits. These findings could possibly be seen to reflect the food and microhabitat availability of the streams. For instance, the relatively higher effect of riparian variables on shredder abundance compared with its importance for other feeding traits could be expected, as shredders have been shown to feed on allochthonous riparian leaf and associated microbial biofilm (Cummins *et al.*, 1989).

In paper II, the most important environmental variables structuring the communities at the local scale were explored by running multivariate regression trees (MRT) for the taxonomic data and for the functional groupings of FFG, HTG and size. The analyses were accompanied with IndVal analyses in order to discover possible indicator taxa and traits for the community divisions formed in the MRT. Overall, the results in the spring indicated a prominent effect of the variable stream width in the structuring of the communities, as it was the first dividing variable for all the data sets.

For taxonomic, UTC and size data, stream width was also the only dividing variable, and therefore only two final leaves were formed in their MRTs. In total, the explained variances by the MRT for these data sets were 21%, 22% and 41%, respectively. The IndVal analysis further identified indicator taxa, UTCs and traits for the final leaves. The MRTs for taxonomic and UTC data divided the communities living in streams either with width ≥184 cm (leaf #2) or width <184 cm (leaf #3). The most characterizing taxa and UTC for these divisions were *Protonemura* and "shredder/sprawler/1–2 cm" for leaf #2 and *Nemoura* and shredder/sprawler/0.5–1 cm" for leaf #3, respectively. For size data, the MRT divided the communities living in streams either with width ≥171 (leaf #2) or width <171 (leaf #3), characterized by sizes "1–2 cm" and "0.5–1 cm", respectively.

Other threshold variables dividing the communities in FFG and HTG groupings were CPOM and gravel. Hence, the MRT for FFG had four nodes dividing the communities into five final leaves and the MRT for HTG had three nodes dividing the communities into four final leaves. The total explained variances for these data sets were 64% and 54%, respectively.

The first node of the MRT for FFG divided the communities living in streams either with width ≥184 (left leaf) or width <184 (right leaf). Indicator traits for this division were "grazing" for left leaf and "shredding" for right leaf. Communities in the left leaf were then divided by the second node into communities living in streams with width ≥445 cm (left leaf) or width < 445 cm (right leaf). Indicator traits for this division were "grazing" for left leaf and "shredding" and "predators" for right leaf. Communities divided into the left leaf of the second node constituted a final leaf #3, with indicator trait of "grazing". The third node of the MRT then divided communities in the right leaf of the second node into final leaves of #5 and #6 based on the amount of gravel in the streambed. This division was characterized by trait "grazing" for communities in streams with gravel < 3% (leaf #5) and by trait "shredding" for communities in streams with gravel ≥ 3% (leaf #6). Finally, the communities in the right leaf of the first node were divided by the fourth node into final leaves of #8 and #9 based on the amount of CPOM in the streams. Communities in streams with CPOM < 6% (leaf #8) were characterized by trait "shredding" and communities in streams with CPOM ≥ 6% (leaf #9) were characterized by trait "gathering".

The first node of the MRT for HTG also divided the communities living in streams either with width ≥184 (left leaf) or width <184 (right leaf). Communities in the right leaf also constituted a final leaf #7, with indicator traits of "sprawlers" and "burrowers". Indicator trait for the communities located in the left leaf of the first node was, in turn, "swimmers". Communities in the left leaf of the first node were further divided by the second node into communities living in streams either with width ≥445 (left leaf) or width < 445 (right leaf). Indicator traits for this division were "swimmers" for left leaf and "sprawlers" and "burrowers" for right leaf. Communities divided to the left leaf of the second node constituted a final leaf #3. The third node of the MRT then divided communities in the right leaf of the second node into the final leaves of #5 and #6 based on the amount of gravel in the streambed. Communities in leaf #5 live in streams with gravel < 3%, and communities in leaf #6 live in streams with gravel ≥ 3%. Indicator traits for this division were "swimmers" and "sprawlers", respectively.

The results of the MRT and IndVal analyses in the spring suggest how the macroinvertebrate communities of high-latitude streams show patterns that are partly in line with the predictions derived from the RCC and the habitat templet theory (Southwood, 1977; Vannote *et al.*, 1980), as variation in stream size, which is the basic element of the RCC theory, was the main factor structuring the communities. Its effect could also be seen in the results from the IndVal analyses. For instance, according to RCC, increasing stream size results in increasing periphyton stock in the larger streams due to better lighting conditions, which is then predicted to support species with the functional feeding trait of grazing (Vannote *et al.*, 1980). This prediction was supported by the MRT for FFG, as grazing was consistently important indicator trait for communities in larger streams. Concurrently, shredders showed preference for narrower streams, which, according to the RCC theory, should contain more leaf litter than the larger streams (Vannote *et al.*, 1980). Overall, these results are in line with previous studies that have demonstrated how stream size may relate to the variation in different facets of the taxonomically and functionally defined stream communities (e.g. Heino, 2005a; Heino *et al.*, 2005; Statzner, Dolédec, & Hugueny, 2004).

In the autumn, the results of the MRT for the taxonomically and functionally-defined communities indicated, in turn, the prominent effect of the variable current velocity in the structuring of the communities, as it was the first dividing variable for all the data sets. It was also the only dividing variable for UTC and size data, and only two final leaves were formed in their MRTs. The MRTs for UTC and size divided the communities living in streams either with velocities ≥ 0.33 m/sec-1 (leaf #2) or velocities < 0.33 m/sec-1 (leaf #3). The most characterizing UTCs and sizes were "gatherer/swimmer/1–2cm" and "1–2 cm" for leaf #2 and "predator/burrower/1–2 cm" and "0.5–1 cm." for leaf #3, respectively. In total, the explained variances by the MRT for these data sets were 24% and 41%, respectively.

Other variables dividing the taxonomic data and the FFG and HTG groupings were shading and CPOM. Hence, the MRTs for taxonomic data and for FFG had two nodes dividing the communities into three final leaves, and the MRT for HTG had three nodes dividing the communities into four final leaves. The total explained variances for these data sets were 29%, 36% and 59%, respectively.

The first node of the MRT for taxonomic data divided the communities living in streams either with velocities ≥0.33 m/sec^{-1} (left leaf) or velocities < 0.33 m/sec^{-1} (right leaf). The most important taxa for this division were *Baetis* for left leaf and *Dicranota* for right leaf. Communities in the right leaf also constituted a final leaf #5, for which the most important indicator taxa were *Nemoura* and *Dicranota*. Communities in the left leaf of the first node were then divided by the second node into final leaves of #3 and #4 based on the amount shading in the streams. Communities living in streams either with shading < 3% (leaf #3) or shading ≥ 3%

(leaf #4) were characterized the most by the taxa *Heptagenia* and *Ameletus*, and *Protonemura* and *Plectrocnemia,* respectively.

The first node of the MRT for FFG also divided the communities living in streams with either velocities ≥0.33 m/sec-1 (left leaf) or velocities < 0.33 m/sec-1 (right leaf). Indicator traits for this division were "grazers" for left leaf and "shredders" for right leaf. Communities in the right leaf also constituted a final leaf #5, with indicator trait of "shredding". Communities in the left leaf of the first node were then divided by the second node into final leaves of #3 and #4 based on the amount CPOM in the streams. The communities living either in streams with CPOM < 3% (leaf #3) or CPOM ≥ 3% (leaf #4) were characterized by the traits "grazing" and "shredding", respectively.

The first node of the MRT for HTG further divided the communities living in streams with either velocities ≥0.33 m/sec^{-1} (left leaf) or velocities < 0.33 m/sec^{-1} (right leaf). Indicator traits for this division were "swimmers" for left leaf and "burrowers" and "sprawlers" for right leaf. The left leaf of the first node was then divided by the second node into the final groups of #3 and #4 based on the amount of CPOM in the streams. The second node was characterized by the trait "swimmers" for communities living in streams with CPOM < 1% (left leaf) and by the traits "sprawlers" and "burrowers" for communities living in streams with CPOM ≥ 1% (right leaf). The recognized indicator trait for the final leaf #3 was "swimmers". Finally, the right leaf of the first node was divided by the third node into final leaves of #6 and #7 by the variable current velocity. The communities found in streams with velocities <0.25 m/sec-1 (leaf #6) or velocities ≥0.25m/sec-1 (leaf #7) were characterized by traits "sprawlers" and "burrowers", respectively.

Current velocity tends to increase with increasing stream size (Leopold, 1953) and therefore some of the RCC predictions related to stream size may also relate to current velocity. For instance, changes in the stream flow may have its effect on the availability of food for the invertebrates, as increasing velocities may reduce the amounts of CPOM retained in the streambed, and therefore affect the distribution of shredders (Richardson, 1991; Speaker, Moore, & Gregory, 1984). This type of effect could possibly be seen in the analysis for FFG, as the characteristic trait for streams with weaker velocities was shredding. Stream velocity may also profoundly affect the communities through its interaction with other environmental factors (Hoffman *et al.*, 2006). For instance, variation in velocity along the stream continuum have its effect on the structure of the streambed (Lorang & Hauer, 2003), which, in turn, may act as an environmental filter for the habit trait structure of the communities (e.g. Lamouroux *et al.*, 2004; Rabení *et al.*, 2005). Overall, the importance of this variable in the structuring of these communities is not surprising, as the pervasive and diverse effects of velocity on stream communities have been demonstrated frequently before (Hart & Finelli, 1999).

The second part of the second study question predicted that if the communities were, in fact, mainly structured through the environmental filtering process, this should be seen in the ways how the communities are organized in space. The idea was that if there are strong associations between the functional traits and the environmental variables, discrete functional community clusters should be formed along these environmental gradients (Rosenfeld, 2002). However, the situation with the taxonomically-defined communities may be different, as individuals in taxonomic communities are affected also by the stochastic factors (Vellend, 2010), which can lead the communities to vary less discretely in space. In paper II, these ideas were explored by first comparing the MRT trees of the taxonomically and functionally-defined communities and then by plotting the community groups formed in the MRTs into ordination plots run with the selected environmental variables.

The comparisons of the MRTs showed how the FFGs and HTGs were more deeply divided by the environmental variables than the taxonomically-defined communities, especially in the spring. Also, the amounts of explained variances in the MRTs were clearly higher for the functional groupings than for the taxonomic data, suggesting that the measured environmental variables fitted the functional groupings better. These results therefore suggest that the organization of the functionally-defined communities along specific environmental gradients is stronger compared to the organization of the taxonomically-defined communities. However, comparisons of the ordination plots during both seasons gave different results regarding the predictions made about the discreteness of the communities. Although the two community clusters formed in the MRTs for the size grouping separated in the ordination space during both seasons, the community clusters formed in the MRTs of FFG and HTG showed notable overlap (Figs. 5 and 6). Therefore, the results could indicate to overall more continuous rather than discrete variation of the communities in these high-latitude streams, a result supported by other studies conducted in the northern streams (Heino, Ilmonen, & Paasivirta, 2014; Sandin, 2003).

There might be several reasons explaining the more continuous variation of the communities in the study streams. First, the continuity of the communities can be explained by the stochastic factors that were demonstrated to affect the communities in papers I and III. However, the more independent responses of the different taxa in the communities may also be related to the habitat selection that acts on the taxa with multiple interacting traits at the local scale (Lamouroux *et al.*, 2004; Verberk *et al.*, 2013), which then results the communities to vary more independently in response to the variation in the environment. This interpretation is supported by the fact that almost all taxa were characterized by their own, individual trait combination, and hence the macroinvertebrate species may be seen to be filtered into the communities according to their unique environmental niches (Southwood, 1977). This, combined with the overall low number of taxa present in the northern streams, may prevent the formation of predictable community types (Heino, Muotka, Mykrä, *et al.*, 2003). At the same time, seasonal changes in the environmental variables together with the heterogeneous and unpredictable habitat conditions prevailing in the streams may further preclude the formation of clear community types (Heino, Muotka, Mykrä, *et al.*, 2003; Sandin, 2003), which can be seen in the overlapping community clusters of FFG and HTG in the ordination plots (Figs. 5 and 6).

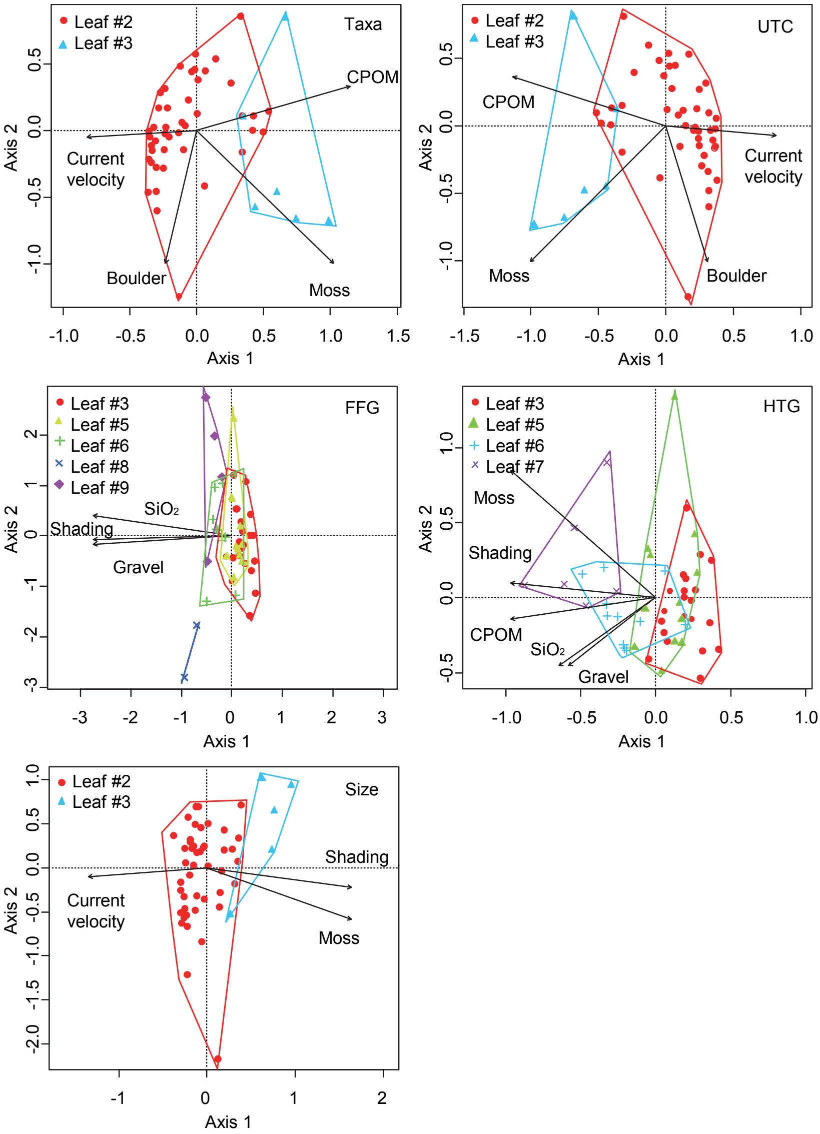

Fig. 5. RDA ordination plots for the taxonomically-defined communities (Taxa), for the UTC-defined communities (UTC), and for the functional feeding grouping (FFG), habit trait grouping (HTG) and the size grouping (Size) in the spring. The study sites are delimited based on the final leaves of the multivariate regression trees, and the ordinations were run based on the selected environmental variables for each response data sets.

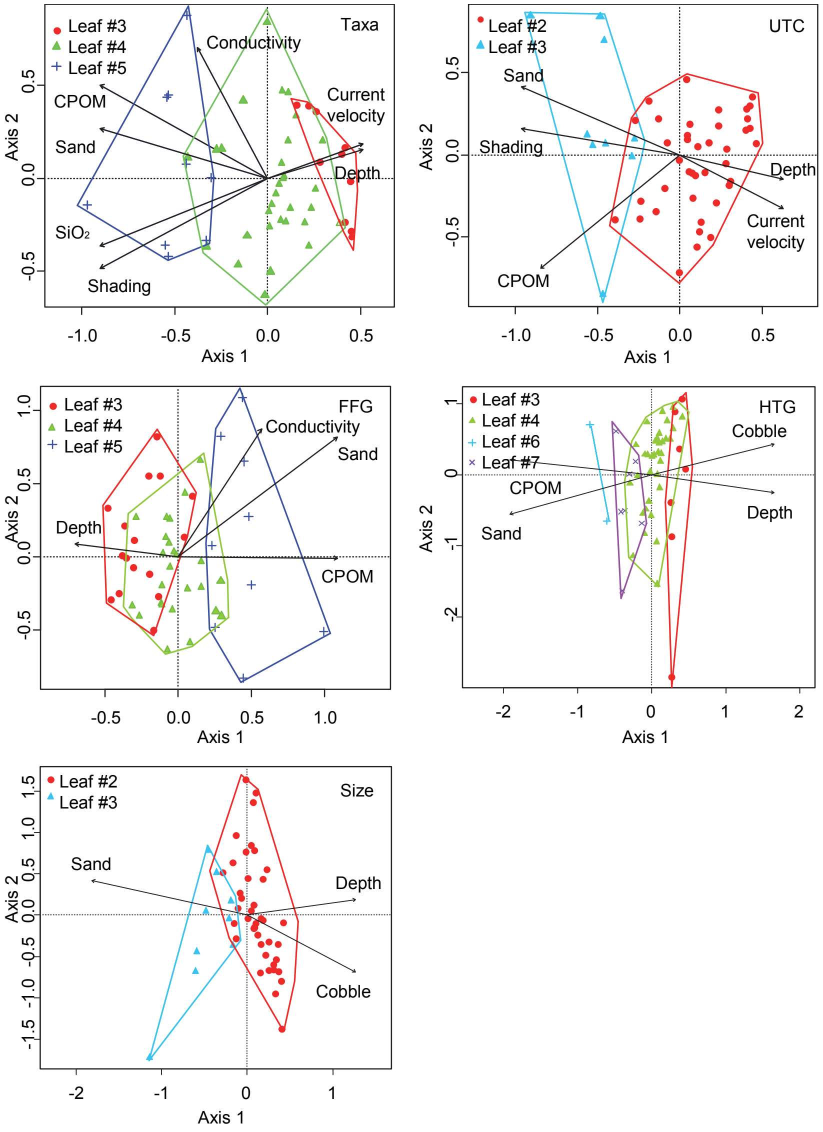

Fig. 6. RDA ordination plots for the taxonomically-defined communities (Taxa), for the UTC-defined communities (UTC), and for the functional feeding grouping (FFG), habit trait grouping (HTG) and the size grouping (Size) in the autumn. The study sites are delimited based on the final leaves of the multivariate regression trees, and the ordinations were run based on the selected environmental variables for each response data sets.

Environmental variables structuring the biodiversity of high-latitude macroinvertebrate communities

As the previous results have demonstrated, environmental filtering processes seem to play an important role in the structuring of the high-latitude macroinvertebrate communities. Therefore, recognizing the environmental variables that act as the most important filters for these communities at the local scale can help to recognize environments behind the structuring of the whole macroinvertebrate biodiversity in the region. This information also helps to protect important environments for the communities in the future (Heino *et al.*, 2009). In paper III, these important environmental variables structuring the biodiversity of the communities were studied by modelling the ecological uniqueness values calculated based on both taxonomic (LCBD-t) and functional (LCBD-f) data against the environmental variables measured from the streams (Legendre & De Cáceres, 2013). Modelling the LCBD values against the environmental variables helps to determine the main variables contributing to the whole biodiversity of the region (Lopes *et al.*, 2014; Tonkin *et al.*, 2016).

In the spring, the environmental variables selected to the GLM analyses for both the LCBD-t and LCBD-f values were moss cover, current velocity, pH, colour and particle size. The GLM resulted in significant negative relationships between the LCBD values and the variables pH and current velocity, whereas significant positive relationships between the LCBD values and the variables colour and moss cover were found. In the autumn, the environmental variables selected to the GLM analysis for LCBD-t included only the variable current velocity, with which a significant negative relationship was found. For LCBD-f, variables selected to the GLM were current velocity, nitrogen and shading, with which significant negative relationship was found between the LCBD-f and the variable current velocity.

Overall, all these environmental variables in both seasons explaining variation in the LCBD values concurred with the variables found to structure the communities already in papers I and II and with other studies describing the main environmental factors driving the variation in stream communities in general (Heino, 2005a; Heino *et al.*, 2007; Vinson & Hawkins, 1998). For instance, the pronounced effect of current velocity on the macroinvertebrate communities was discussed earlier (Cobb, Galloway, & Flannagan, 1992; Hart & Finelli, 1999; Richardson, 1991; Speaker *et al.*, 1984). The positive effect of moss cover on macroinvertebrate diversity is also commonly recognized, as moss provides shelter and food by retaining organic particles from the current (Wulf & Pearson, 2017), thereby possibly affecting the habit and feeding structures of the stream communities (e.g. Heino, 2005a). However, the notable effect of the variables pH and colour on the variation in the LCBD values was rather surprising. Although the importance of these variables for stream communities is not new (Vinson & Hawkins, 1998), their notable effect on the variation in the LCBD values in these northern streams is interesting, as the variation of these variables was not very large. However, water chemistry variables may generally affect the communities through many ways (Vinson & Hawkins, 1998). For instance, variation in pH may cause changes in other water chemistry variables, such as aluminum concentrations, which then may have effects on the respiration efficiencies of the macroinvertebrates (e.g. Herrmann & Andersson, 1987). Water chemistry variables, such as colour, may also have indirect effect on the communities by changing the stream conditions for algal communities and growth (Otto & Svensson, 1983; Paavola, 2003). Overall, it is possible that the communities containing only the few species capable of living in these harsh high-latitude streams are especially sensitive even to small scale changes in their habitat conditions, if they are already near to their limits in respect to other habitat factors also.

All these detected patterns of the different components of the functional communities and the LCBD values responding to these different environmental variables, which were seen in all three papers (I, II, III), were detected in streams with no detectable human influence (Roussel *et al.*, 2014). Therefore, these results give support for previous studies underscoring the importance of describing variation in the trait structure of the biological communities in natural systems before associating variation in the functional communities to various anthropogenic stressors (Schmera *et al.*, 2013).

The usability of the functional trait-based approaches in high-latitude streams

The results of all the papers (I, II, III) have demonstrated how using functional approaches in addition to taxonomic approaches can provide a deeper view into the mechanisms that structure the macroinvertebrate communities in streams (Lavorel & Garnier, 2002; McGill *et al.*, 2006; Verberk *et al.*, 2013). Overall, in all the papers the explained variances for the functionally-defined communities were generally higher than for the taxonomically-defined communities, indicating that the measured explanatory variables fitted the functionally-defined communities better. Although the differences in the explained variations were not always very large, they were still found from two different data sets. Therefore, changes in the functional trait composition may better demonstrate and predict variation in the environmental gradients than changes in the taxonomic composition in high-latitude streams (Göthe *et al.*, 2017; McGill *et al.*, 2006; Verberk *et al.*, 2013). However, there was still occasionally substantial amount of unexplained variation in the functional data sets. There might be a few reasons for this.

One possible reason leading to higher amounts of unexplained variation in functional trait-based studies might be that when studying the functional community-environment relationships by using either unique trait combinations or the whole functional grouping features, the variation in the data sets might be hindered by the possibly contradictory responses of the individual traits in the data sets to different environmental variables (Poff *et al.*, 2006). This kind of effect was possibly seen in the results of the variation partitioning in paper I, where in over half of the cases, the explained variation for the different trait groups and individual traits was higher than the explained variation for the UTC data. Also, in paper II, the explanatory powers of the MRTs for the different trait groupings were higher than for the UTC data. Further, results from the Pearson's chi-square tests in papers I and II showed how some of the trait classifications exhibited significant affinity to each other. These kinds of trait linkages within the species can then further obscure the results (Verberk *et al.*, 2013). In paper I, the $\chi2$ test showed how the HTG classification was related to the FFG ($\chi2 = 64.742$, $p < 0.001$) and to the size classification ($\chi2 = 53.395$, $p = 0.001$). The size classification was also related to the FFG ($\chi2 = 35.6749$, $p = 0.016$). In paper II, in turn, the HTG classification was related both to the FFG ($\chi2 = 28.44$, $P = 0.024$) and to the size classification ($\chi2 = 28.18$, $P = 0.018$) in the spring. The FFG classification, on the contrary, was not related to the size classification ($\chi2 = 18.14$, $P = 0.326$). In the autumn, however, none of the trait categories was significantly associated to the others (FFG × HTG: $\chi2 = 26.07$, $P = 0.157$; FFG × size: $\chi2 = 22.05$, $P = 0.325$; HTG × size: $\chi2 = 22.00$, $P = 0.139$). The observed increases in the amounts of explained variation from the unique trait combinations to the trait groupings and to individual traits could hence result simply from the decreased variability in the data sets. As the UTCs include traits from different trait groups, it also combines all the individual variation of the different traits into one matrix. The relationship between UTCs and the habitat characteristics may thus be ambiguous because the habitat filtering does not act exclusively on an individual trait, but on the whole species with differing trait combinations (Lamouroux *et al.*, 2004; Verberk *et al.*, 2013).

The results of the trait-based analyses may also suffer from the approaches used to categorize the taxa into their functional trait categories. The trait categorization used here is rather strict and does not take into account if the different taxa have changing affinities to different trait categories in different stages of their life cycles, or if the taxa exhibit generalist behavior (see freshwaterecology.info). It could also be that the species in the northern streams have overall different affinities to some specific trait category compared to the same genera in more southerly regions. Then, the species in the northern streams would be falsely categorized according to the affinities of the more generalized species in other regions (Masese *et al.*, 2014). Another problem, related especially to continuous traits, such as size, the a priori determined trait states for different taxonomic groups may not represent the true trait states of the individuals belonging to that taxon in the studied communities, as the trait states of the continuous variables among populations and individuals may differ among sites irrespective of the a priori predicted trait states (Orlofske & Baird, 2014). However, specific information about the trait affinities of the macroinvertebrates in high-latitude streams is not yet sufficiently available (freshwaterecology.info; Schmidt-Kloiber & Hering, 2015). Nonetheless, as the different facets of the functionally-defined communities did show significant responses to the variation in the environmental variables, this could be seen as an indication that the trait categorizations here were successful.

The usability of the functional trait-based approaches, especially the usage of the unique trait combinations, in high-latitude streams may also be hindered by the overall low number of taxa living in the region. This might make it more difficult to find differences between the taxonomically-defined communities and the UTC-defined communities, as most or all UTCs contain only one or a few individual taxa. If the species numbers were higher, the differences in the explained variation between taxonomic and UTC-based communities could also be larger and easier to interpret.

At last, the usability of the functional traits in high-latitudes may also suffer from the extreme and highly heterogeneous environmental conditions prevailing in the northern streams (Wrona *et al.*, 2013). For instance, the results of paper II suggested how the harsh and heterogeneous environmental conditions may play a role in preventing the formation of clear taxonomically and functionally-defined community types (Heino, Muotka, Mykrä, *et al.*, 2003). It could be that, if the study had been conducted in more clearly contrasting stream sites, stronger trait-environment responses could have been found.

However, the obtained results nonetheless suggest that rather than trying to find clear discrete communities, conservation efforts, for instance, should aim to cover varying environmental conditions in order to include all aspects of the communities in high-latitude streams. However, as some noticeable responses of individual traits to different environmental factors were detected, recognizable functionally defined communities may be found if key traits of the taxa can be identified. Hence, more research on the organization of the functional trait structure of the macroinvertebrate communities is needed for the development of trait-based biomonitoring and conservations methods for the high-latitude streams.

Implications for the future of high-latitude streams

Northern ecosystems and their biodiversity are highly sensitive to different anthropogenic stressors (IPCC, 2013; Vilmi *et al.*, 2017). Nonetheless, recent studies on the food webs and biological communities of the River Tenojoki and its tributaries have so far referred to environmental conditions typical of pristine aquatic ecosystems found generally in subarctic regions (e.g. Erkinaro & Erkinaro 1998). Also, long-term time series concerning variations in N and C in the food webs have shown virtually no anthropogenic impact in the catchment (Roussel *et al.*, 2014). However, the environmental conditions in the area may change drastically in the future. High-latitude areas have been projected to be greatly affected by the environmental changes caused by the ongoing climate change (Heino *et al.*, 2009; IPCC, 2013). These changes in the thermal regime, precipitation, hydrology, water chemistry and more (Chapin *et al.*, 2005; Hobbie *et al.*, 1999; Krankina *et al.*, 1997; Wrona *et al.*, 2013) can then have significant effects on the high-latitude stream communities (e.g Friberg, Bergfur, Rasmussen, & Sandin, 2013). For instance, the possible changes in riparian vegetation from barren tundra into more dense riparian forests (Krankina *et al.*, 1997) could change streams previously driven by autochthonous algal production towards streams depending on allochthonous leaf material as an energy source, which in turn could induce changes in the functional feeding structures of the macroinvertebrate communities (Wrona *et al.*, 2013). Based on the results of this study, the possible changes in precipitation and in overall hydrological conditions of the streams may also have drastic effects on the communities through their effects on stream sizes and velocities. As this study has suggested, the macroinvertebrate communities in these northern streams may also be highly sensitive even to small changes in their habitats. These findings combined with the low number of taxa living in these streams and to the low redundancy of the communities in respect to individual UTCs and taxa (Schmera *et al.*, 2013) could mean that environmental changes that would lead the communities to lose or gain a new taxon could also mean losing or gaining individual functional components from the streams (Schmera, Baur, & Erős, 2012). These changes in turn could have notable effects on the functioning of the whole stream ecosystems in high-latitudes (Chapin *et al.*, 2000; Petchey, 2003).

5 Conclusion

Because of the generally stronger responses of the functionally-defined communities to changes in the environmental factors compared to the taxonomically-defined communities, the trait-based approaches used in this study could provide a useful tool for detecting biological community changes in response to environmental changes in these highly sensitive high-latitude systems. The information obtained from this study may therefore be used as a background for developing new bioassessment approaches for high-latitude stream systems in the future, although more research is needed to find out the most informative traits responding to the environmental variation. Overall, this study has shown how functional trait-based research can help in recognizing the most important factors structuring the overall biodiversity of communities in a region, a piece of information critically needed to efficiently protect species communities in the changing world. The information gained from this study can hence be used to protect environments important for the healthy functioning of northern drainage basins in the future.

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