Nordia
Geographical Publications

Volume 47:3

Large-scale patterns of biodiversity in northern streams: insights from species, traits and phylogeny

Mariana Perez Rocha

ACADEMIC DISSERTATION

to be presented with the permission of the Doctoral Training Committee of
Technology and Natural Sciences of the University of Oulu Graduate School
(UniOGS), for public discussion in the lecture hall L10,
on the 12th of October, 2018, at 12 noon.

Nordia
Geographical Publications

Volume 47:3

Large-scale patterns of biodiversity in northern streams: insights from species, traits and phylogeny

Mariana Perez Rocha

Nordia Geographical Publications

Publications of
The Geographical Society of Northern Finland
and
Geography Research Unit, University of Oulu

Address: Geography Research Unit
P.O. Box 3000
FIN-90014 University of Oulu
FINLAND
heikki.sirvio@oulu.fi

Editor: Teijo Klemettilä

Nordia Geographical Publications
ISBN 978-952-62-2002-4
ISSN 1238-2086

Juvenes Print

Oulu 2018

Large-scale patterns of biodiversity in northern streams: insights from species, traits and phylogeny

Contents

Appendices

Abstract

Large-scale patterns of biodiversity in northern streams: insights from species, traits and phylogeny

Rocha, Mariana Perez, Geography Research Unit, University of Oulu, 2018

Keywords: benthic macroinvertebrates, beta diversity facets, biodiversity, catchment, climate, community composition, diatoms, environmental variation, northern streams, spatial variation, species phylogeny, species traits

Recently, ecologists and biogeographers have recognized the need of analyzing the multiscale phenomena of biodiversity in the light of a multifaceted concept: the investigation of multiple facets and multiple drivers operating at different spatial scales. The variation in species-based information has been the most commonly used approach to quantify how biodiversity varies through space and time, omitting the different evolutionary histories of each species and the fact that communities are constituted of species with different ecological roles. Stream biodiversity patterns have been demonstrated to be related to local-, catchment-, and regional-scale variables, but it is still an open question how these different sets of variables affect different facets of biodiversity in streams ecosystems (i.e., traits and phylogeny). The aim of this thesis was to investigate large-scale biodiversity patterns across northern streams by assessing the influence of different sets of variables (ranging from local habitat to large-scale geographical) underlying these patterns and through the investigation of different facets of biodiversity (i.e., species, traits and phylogenies). The results showed clearly the importance of local environmental variables and spatial factors in explaining large-scale biodiversity patterns in streams ecosystems, whilst the catchment and climate factors were less important. In addition, the results evidenced that the inference of trait-based and phylogeny-based biodiversity patterns might depend on an array of different mechanisms and complex factors that cannot be forecasted before the analysis. Overall, these findings elucidated that understanding both local- and large-scale factors are necessary for a better assessment of the mechanisms influencing the biodiversity and ecosystem processes of streams. Moreover, this thesis added trait-based and phylogeny-based views into the study of biodiversity patterns, enabling a better understanding of the different mechanisms associated with different facets of biological communities in streams.

Supervisors

Dr. Jani Heino
Finnish Environment Institute, Biodiversity Centre
Oulu, Finland

Prof. Jan Hjort, Geography Research Unit
University of Oulu, Finland

Prof. Luis Mauricio Bini
Department of Ecology (ICB), Universidade Federal de Goiás
Goiânia, Brazil

Pre-examiners

Prof. Daniel Hering
Faculty of Biology and Aquatic Ecology, University of Duisburg-Essen
Essen, Germany

Prof. Leonard Sandin
Department of Aquatic Resources, Swedish University of Agricultural Sciences
Drottningholm, Sweden

Official Opponent

Prof. Nikolai Friberg
Norwegian Institute for Water Research
Oslo, Norway

and

University of Copenhagen
Copenhagen, Denmark

Original publications

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

I. Rocha, M.P., Bini, L.M., Siqueira, T., Hjort, J., Grönroos, M., Lindholm, M., Karjalainen S-M., Heino, J. (2018). Predicting occupancy and abundance by niche position, niche breadth and body size in stream organisms. *Oecologia*, 186, 205-216.

II. Rocha, M.P., Bini, L.M., Domisch, S., Tolonen K.T., Jyrkänkallio-Mikkola, J., Soininen J., Hjort, J., Heino, J. (Manuscript). Local environment and space drive multiple facets of stream macroinvertebrate beta diversity, while climate and catchment features are less important.

III. Rocha, M.P., Bini, L.M., Grönroos, M., Hjort, J., Lindholm, M., Karjalainen S-M., Tolonen, K.E., Heino, J. (Manuscript). Untangling the correlates of different facets and components of beta diversity in subarctic stream organisms.

Responsibilities of the authors

	Paper I	Paper II	Paper III
Original ideas	MPR, JH	MPR, JH, JS	MPR, JH
Study design and methods	MPR, JH, JHJ	MPR, JH, JHJ	MPR, JH, JHJ
Data sampling	MG	JJM, KTT	MG
Sample identification	MG, ML, SMK	KTT, MPR	MG, ML, SMK
Trait data	MPR	KTT, MPR	KET, MPR
Processing variables	MPR, JHJ	MPR, SD	MPR
Statistical analysis	MPR, JH, LMB, TS	MPR, JH, LMB	MPR, JH, LMB
Manuscript preparation	MPR, JH, LMB	MPR, JH, LMB, JS	MPR, JH, LMB

MPR = Mariana Perez Rocha, JH = Jani Heino, LMB = Luis Mauricio Bini, JHJ = Jan Hjort, TS = Tadeu Siqueira, MG = Mira Grönroos, ML = Marja Lindholm, SMK = Satu Maaria Karjalainen, SD = Sami Domisch, KTT = Kimmo T. Tolonen, JJM = Jenny Jyrkänkallio-Mikkola, JS = Janne Soininen, KET = Katri E. Tolonen.

Acknowledgements

This thesis is a fruit of hard work, great collaboration, and tons of patience of several people, which of each contributed enormously to the big thesis-puzzle and without many, this thesis could have been even tougher. First of all, I thank billions of times my main supervisor, Jani Heino. I thank you for trusting on me since the first e-mail we exchanged when I was still back in Brazil. Here, I would like to give my deepest and sincere gratitude for all your guidance, great discussions, good and bad comments, patience, and good temper. Merely words are not enough to capture and demonstrate how thankful I am, so once again: thank you. My second and third supervisors, respectively Jan Hjort and Luis Mauricio Bini, deserve very special and big thanks for all of their help and support throughout this tough PhD journey. I would also like to thank all the co-authors involved in this thesis and other projects: Mira Grönroos, Tadeu Siqueira, Kimmo Tolonen, Marja Lindholm, Satu-Maaria Karjalainen, Katri Tolonen, Annika Vilmi, Sami Domisch, Janne Alahuhta, Janne Soininen, and Jenny Jyrkänkallio-Mikkola. Next, I want to thank the pre-examiners of this thesis, Leonard Sandin and Daniel Hering, for their very nice and constructive comments, and I want to thank Nikolai Friberg for agreeing to be my opponent.

I am very grateful for all the colleagues in the Finnish Environment Institute and Geography Research Unit for the cozy atmosphere, cheerful lunch or coffee breaks (or tea parties), and also for helping in so many practical and non-practical aspects. Huge thanks to Jarmo Rusanen (Geography Research Unit) for all his patience with me, and for agreeing on supporting (together with the whole Unit) my lack of funding in the end of this journey. I also thank CAPES Foundation, Ministry of Education of Brazil, for funding the majority of my stay in Finland. Special thanks to all of my friends, from around the globe and from Brazil, which were always supportive and worried about my wellbeing in this so-often cold (and dark) part of the World. I also thank my fluffy-best-friend-cat “Mustikka” for all her daily love and cuddling all over these years.

Finally, I want to thank my family. Mother, you have always supported me in some many ways that I could never be more grateful for the strong woman I got to be assigned as my Mom. Thanks for your daily text messages and weekly calls just to check on me and chat about whatever I was in need. Special thanks to my Brother (and his family), for sheltering me every fall/winter that I had to escape from Finland because it was too dark and depressive. Huge thanks to Sister and Grandma for always being there when I needed you. Last but not least, I thank my Father for the gift of life and being supportive.

Oulu, August 2018.

1 Introduction

1.1 A general overview of biodiversity studies and their implications

The diversity of life on Earth, i.e., biodiversity, is a broad concept that covers the variability among living organisms ranging from genes to biomes (Gaston 2000). Historically, the scientific study of biodiversity dates from early 1960s, when the ecologists recognized that species diversity is an important aspect of ecological communities (Whittaker 1960). However, the term 'biodiversity' was first used in the literature by E. O. Wilson (1988) in the late 1980s, and it has been continually used over the past 30 years in ecological research. This emphasis on a single general term is important as biodiversity is in jeopardy. Changes in biodiversity are evident at global, regional and local scales, and findings regarding this research topic have thus received considerable attention in the past decades (Connell 1978; Naeem *et al.* 1994; Tilman *et al.* 1997; Sankaran & McNaughton 1999; Sala *et al.* 2000).

The understanding of factors driving biodiversity patterns is still among the key research topics in ecological, biogeographical and conservation research. Traditionally, the studies on biodiversity have been based on variation in species identities, which have yielded much information about the processes that structure biological communities (Leibold *et al.* 2004; Holyoak *et al.* 2005, Logue *et al.* 2011). However, an approach based only on species identities ignores the effects of abiotic environment that are mediated by the species traits (McGill *et al.* 2006) and evolutionary history of species, both of which affect the organization of biological communities (Webb *et al.* 2002). Recently, community ecologists have recognized the need to study biological communities in the light of complementary approaches incorporating trait-based and phylogenetic information (Devictor *et al.* 2010; Gianuca *et al.* 2017; Heino & Tolonen 2017). Hence, integrating different approaches into biodiversity studies may provide valuable additional and complementary information about the determinants of community composition (Cavender-Bares *et al.* 2009; Devictor *et al.* 2010), which, in turn, would greatly benefit the goals of many biodiversity restoration, conservation and assessment programs (e.g., Devictor *et al.* 2010).

Biodiversity patterns and their potential causes for some terrestrial organism groups have been well studied (e.g., Hawkins *et al.* 2003; Gaston & Spicer 2004), but they remain relatively poorly studied for many freshwater groups (Vinson & Hawkins 1998; Heino 2011). However, recent global analyses have suggested that freshwater species are declining at a much faster pace than those in marine or terrestrial ecosystems (Young *et al.* 2016). Thus, a deeper understanding of patterns and processes shaping biodiversity in freshwater ecosystems is urgently needed to enable better predictions and protection of factors that are responsible for the variation of freshwater biodiversity in the face of current and future global change impacts (Dudgeon *et al.* 2006). These rates of decline are mostly due to the small areal extent of freshwater ecosystems. The freshwater ecosystems (i.e., streams, rivers, lakes, ponds, springs and wetlands) harbor more than 10% of all animal species described in the world, although these ecosystems cover only 0.8% of the Earth's surface and contain only around 0.01% of the water of the world (Dudgeon *et al.* 2006).

Running waters (i.e., streams and rivers) are considered to be one of the most threatened and impacted ecosystems in the world (Malmqvist & Rundle 2002; Strayer & Dudgeon 2010). However, the knowledge of the biodiversity of running waters is still inadequate (e.g., Stendera *et al.* 2012), especially of smaller organisms (e.g., macroinvertebrates, diatoms). Thus, understanding which factors determine the variation in running water communities would have important implications for stream restoration, conservation and assessment programs. This is particularly true for northern streams, which are highly sensitive to various environmental threats (Heino *et al.* 2009; Wrona *et al.* 2013) and projected to be impacted by global climate change (Chapin *et al.* 2005; Wrona *et al.* 2013).

1.2 Species-, trait- and phylogeny-based approaches in biodiversity research

Understanding patterns of biodiversity in space and time has been and is a challenging task for ecologists and biogeographers (Rosenzweig 1995). However, this challenge is accentuated by the multifaceted nature of the biodiversity phenomena. Thus, when biodiversity patterns are explored, the use of approaches based on species, trait and phylogenetic data may provide complementary information about the factors and processes behind the organization of biological communities, as these different facets may be partly governed by different processes (Weinstein *et al.* 2014; Heino & Tolonen 2017; Gianuca *et al.* 2017). Analyzing variation in species-based data is the most common approach to measure the variability among species, treating all of them equally and neglecting the fact that communities are composed of species with different ecological functions (Villéger *et al.* 2013) and different evolutionary histories (Webb *et al.* 2002). Next, these different approaches are briefly described and compared.

In general, the species-based approach suggests that, given enough time, species are able to disperse everywhere in a region, and the community composition at a site is a subset of the regional pool of species, with strong geographical variation (Heino *et al.* 2013; Hoeinghaus *et al.* 2007; Kärnä *et al.* 2015). Patterns of geographical distribution of species may be due to variation in species performance along the ecological gradients (e.g., local, climate and catchment factors), resulting in different local communities, both in terms of composition and abundance (Leibold *et al.* 2004; Heino *et al.* 2007; Hoeinghaus *et al.* 2007). The species-based approach, however, remains silent about the evolutionary history of species and their functional relationships with environmental variation (Webb *et al.* 2002; McGill *et al.* 2006).

The phylogeny-based approach is expected to provide valuable additional information about the drivers of biodiversity (Graham & Fine 2008, Weinstein *et al.* 2014). This approach may reveal the role of species interactions and biogeography history, providing information on the evolutionary constraints of community composition neglected by the sole analysis of species identities (e.g., Webb *et al.* 2002). This is because the closely-related species tend to resemble each other in their traits more than distantly-related species, leading related species to co-occur more often in the same community with their shared environmental tolerances and behavioral characteristics (Webb *et al.* 2002). In contrast, biotic interactions such as competition tend to limit the coexistence of similar species, leading to competition among related species and selection of less related and functionally less similar species to co-occur in local communities (e.g., Webb *et al.* 2002). However, these interpretations have also been challenged recently, and thus care should be taken while solving the intricacies of community assembly through phylogenetic approaches (e.g., Gerhold *et al.* 2015).

Species traits are often considered a key to understanding how environmental conditions filter species into communities (Poff 1997), linking the ecological features of species to diversity patterns and ecosystem functions (McGill *et al.* 2006; Verberk *et al.* 2013). Hence, similar environmental conditions at different sites could select an array of similar trait composition despite of the pool of species varying regionally (Statzner *et al.* 2004; Villéger *et al.* 2013; Heino & Tolonen 2017). Nevertheless, in stream ecosystems, there are a variety of environmental filters at different scales (e.g., Poff 1997), ranging from the local habitat to regional scales. Therefore, before a species is established into the local community, it has to pass through a series of environmental filters that are mediated by species traits (Keddy 1992; Poff 1997). It should be noted that conclusions obtained by trait-based approach are not always similar to those provided by phylogenetic approaches (e.g., Losos 2008). In fact, the phylogeny of species in a community may be a reliable proxy for phylogenetically conserved traits, while environmental processes may also have effects on some more evolutionarily labile traits (e.g., Pavoine & Bonsall 2010).

1.3 Large-scale patterns of biodiversity through the lens of species, trait-based and phylogenetic approaches

The variability of life in stream ecosystems is not only visible at the community level but also in the regional distribution and local abundance of single species. Patterns in species distributions (or occupancy) and abundances have fascinated ecologists for a long time (Hanski *et al.* 1993; Gaston *et al.* 2000). The occupancy-abundance relationship is a classic topic in macroecology, but some of its aspects are not well understood (Gaston *et al.* 2000; Gregory & Gaston 2000). For example, there is a continuing controversy on the relative roles of niche position or niche breadth in driving species occupancy and abundance (Passy 2012; Slatyer *et al.* 2013).

The local abundance and regional occupancy of species tend to be positively correlated. This means that species decreasing in local abundance often tend to show decreases in the number of sites that they occupy, whereas species increasing in local abundance tend to increase their occupancy. A positive occupancy-abundance relationship has been documented for a wide variety of taxa, including birds (e.g., Gaston & Blackburn 1996), insects (e.g., Gaston & Lawton 1988) and mammals (e.g., Blackburn *et al.* 1997). This relationship has also been known to remain consistent across multiple spatial scales (Gaston & Lawton 1990) and in different habitats (Gaston *et al.* 2000). Therefore, the studies on the occupancy–abundance relationship should focus on examining the contribution of individual species to this relationship (e.g., Gaston *et al.* 2000), where each species may be influenced by the interplay between ecological conditions (e.g., resource availability; Heino & Grönroos 2014) and biological traits (e.g., body size; Tales *et al.* 2004). The regional occupancy and local abundance of species are affected by resources because, on average, widespread and abundant species use a greater variety of resources than rare, narrowly distributed species (i.e., the niche breadth hypothesis; Brown 1984), or because widespread and abundant species use common resources (i.e., the niche position hypothesis; Venier & Fahrig 1996). In addition, body size has been shown to be related to the regional occupancy and local abundance of species (Heino & Grönroos 2014; Tales *et al.* 2004).

Another important aspect of large-scale patterns of biodiversity is the change in species identities across space (i.e., beta diversity), which provides a direct link between local-scale and regional-scale diversity owing to the spatial variation in community composition (Whittaker 1960; Anderson *et al.* 2011). Beta diversity can be decomposed into different components, each of which may suggest different ecological processes underlying community assembly (Legendre 2014). Baselga (2010) proposed that these components should be divided into the turnover component and the nestedness component. The turnover component implies the change in species composition due to environmental changes, competition and historical events (Leprieur *et al.* 2011), reflecting the influence of ecological gradients on controlling community structure. Podani and Schmera (2011) proposed the concepts of species replacement and richness difference, referring as species replacement the trend of species to replace each other along broad ecological gradients, which also implies simultaneous gain and loss of species. The richness (or abundance) difference component mirrors the fact that a community may include a larger number of species than another community in a different location across the study area (Podani & Schmera 2011), whilst the nestedness component proposed by Baselga (2010) is a type of richness difference characterized by the species at a site being a subset of the species at a richer site (Baselga 2012).Therefore, these two different approaches (i.e., Baselga (2010) and Podani & Schmera (2011)) that proposed to decompose beta diversity into its components are complementary and correspond to different ecological processes (Legendre 2014).

Beta diversity can also be examined through different facets (i.e., species-, trait- and phylogeny-based) (e.g., Cardoso *et al.* 2014), which in turn may increase our understanding of community assembly by providing a clearer picture of the spatial patterning of ecological communities (Graham & Fine 2008; Meynard *et al.* 2011). This is because there should be a close association between species traits and environmental conditions (e.g., Verberk *et al.* 2013) together with closely-related species being adapted to similar environmental conditions (e.g., Webb *et al.* 2002). In contrast, species-identities are typically affected by environmental conditions, dispersal-related phenomena and stochasticity (Heino *et al.* 2015; Leibold & Chase 2018). Thus, integrating these different facets of beta diversity into the same study may provide complementary information on how ecological communities are assembled and how biodiversity is patterned (Heino & Tolonen 2017; Gianuca *et al.* 2018).

1.4 The roles of environmental factors structuring biodiversity patterns in stream ecosystems

Previous studies have addressed the importance of environmental variables measured at different scales (e.g., from local habitat to large-scale geographical variables) on biodiversity patterns in stream ecosystems and have revealed that community structure is correlated with factors operating at multiple spatial scales (Townsend *et al.* 2003; Sandin & Johnson 2004; Jyrkänkallio *et al.* 2017). It has been recognized that stream biodiversity patterns are a product of combined forces acting on multiple spatial and temporal scales (Poff 1997; Townsend *et al.* 2003; Sandin & Johnson 2004). In particular, the biodiversity in stream ecosystems may be influenced by local environmental characteristics and large-scale features or jointly by both, because the occurrence of species in a certain location depends on filtering processes operating at different scales, ranging from regional to microhabitat (Poff 1997; Tonn 1990).

Various catchment properties (e.g., land cover, slope and area) have been shown to be correlated with stream biodiversity patterns (e.g., Townsend *et al.* 2003), and they have been demonstrated to be as important as, or even more important than, local stream characteristics (Hynes 1975; Corkum 1989). A strong influence of catchment-scale variables on local environmental features of streams is also expected (Hynes 1970; Corkum 1992). Thus, the catchment-scale variables should be more likely to integrate into the environmental changes in the basin area, which in turn would affect the local environmental factors and biological communities over longer time scales (e.g., Soininen *et al.* 2015).

Climate may play a strong role in determining variation in stream biodiversity (Pajunen *et al.* 2015; Mustonen *et al.* 2018), and sometimes it may overcome the importance of local environmental and catchment features on stream biodiversity (e.g., Kampichler *et al.* 2012). Therefore, disentangling the relative roles of large-scale and local-scale variables for biodiversity patterns is especially relevant because local habitat features (e.g., physical and chemical variables) are also partly determined by large-scale processes (Hynes 1975; Corkum 1989; Frissell *et al.* 1986) (Figure 1). However, relatively little is known about how ecological variables measured at multiple spatial scales affect variation in the functional or phylogenetic facets of the biodiversity in stream ecosystems (but see Sandin & Johnson 2004; Heino *et al.* 2007).

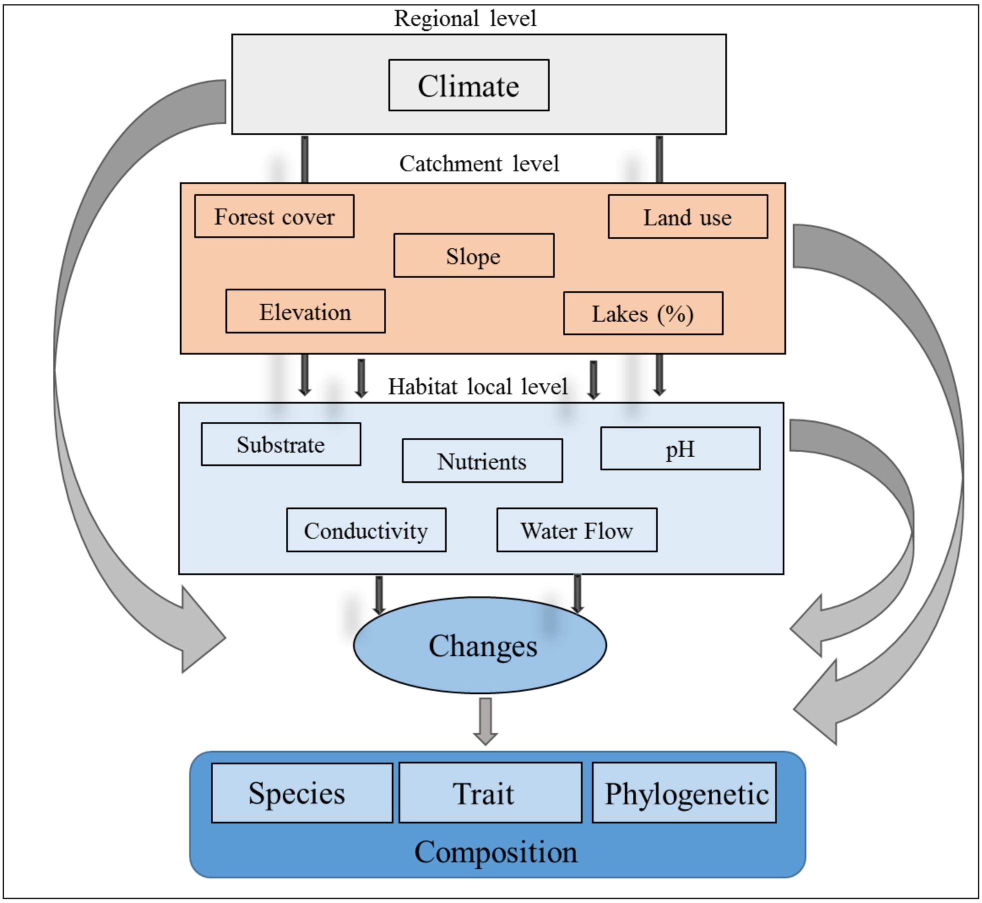

Figure 1. Multi-level variables scheme illustrating how ecological variables measured at different spatial scales affect variation in different facets of biodiversity (i.e., species, traits and phylogeny) in stream ecosystems.

2 Aims of the thesis

The objective of this thesis was to investigate large-scale biodiversity patterns across northern streams by assessing the influence of environmental factors underpinning these patterns, ranging from local habitat to large-scale geographical variables, and through the exploration of different facets of biodiversity (i.e., species, traits and phylogenies). Although the following study questions were approached using different methods, they were chosen in an effort to provide complementary perspectives on the phenomena investigated. More specifically, I investigated (i) what are the relative roles of local, catchment and climate factors influencing biodiversity patterns across northern streams, and (ii) do trait-based and phylogeny-based approaches provide more comprehensive insights into biodiversity patterns than the traditional species-based approach?

Stream biodiversity patterns have been demonstrated to be related to variables ranging from local to regional scales, emphasizing the multiscale nature of the determinants of biodiversity. In general, species-based biodiversity patterns should be strongly affected by local and regional processes, owing to the somewhat stochastic nature of species distributions (e.g., dispersal, drift), whereas trait- and phylogeny-based beta diversity should mostly be affected by local-scale features because of their strong interactions with organism-environment relationships (Poff 1997; Verberk *et al.* 2013, Soininen *et al.* 2016; Leibold & Chase 2018). In addition, when exploring how different niche variables based on local environmental and catchment variables link with variation in regional occupancy and local abundance of stream organisms, I predicted that catchment-based niche variables would outperform local environmental niche variables (e.g., Siqueira *et al.* 2009) because catchment variables have been demonstrated to integrate multiple catchment processes and have effects on local communities through influencing stream characteristics (e.g., Soininen *et al.* 2015).

In Paper I, I approached this question (i) by exploring the use of different niche variables based on local environmental and catchment variables accounting for variation in the regional occupancy or local abundance across species. I compared models containing measures of habitat-related explanations (i.e., niche breadth and niche position) and body size of different stream organism groups (i.e., diatoms and insects) to analyze the roles of 'local environmental niches' *versus* 'catchment niches' contributing to the across-species variation in the occupancy-abundance relationship in subarctic streams. In Paper II, the question (i) was addressed using three different sets of ecological variables measured at different scales: at the local level (including physical-chemical environmental variables), at the catchment level (comprising land cover and land use characteristics) and at the regional level (incorporating climate variables). In addition, spatial structure in species-, traits- and phylogeny-based beta diversity was taken into account in the analyses using spatial variables. I explored the influence of these different sets of variables on macroinvertebrate species-, traits- and phylogeny-based beta diversity.

The analysis of biodiversity patterns only from the species-based approach may fall short when inferring about mechanisms underlying biodiversity patterns because it treats all species as equally different from each other. However, two communities of equal number of species may be composed of individual species with either similar or very different phylogenetic histories (Webb et al 2002; Graham & Fine 2008), or two individual species may exhibit completely different or similar traits (McGill et al 2006; Villéger *et al.* 2013). In Paper II, I addressed the question (ii) by exploring macroinvertebrate species-, trait- and phylogeny-based beta diversity using different sets of ecological variables as explanatory factors. In order to understand the ecological mechanisms underlying the variation in composition across the study area, I decomposed species-, traits- and phylogeny-based beta diversity into their components (i.e., total, replacement and abundance-difference; Podani & Schmera 2011). This question (ii) was also addressed in Paper III, where I correlated the turnover in diatom and macroinvertebrate species- and trait-based beta diversity with environmental and spatial distances. In addition, to better understand the mechanisms behind the variation in species and trait composition, I partitioned species-based and trait-based beta diversity into different components (i.e., overall, turnover and nestedness; Baselga 2010).

In general, the study questions I investigated involved different approaches and different scales of variables. My thesis should thus provide a deeper understanding of biodiversity patterns and their underlying mechanisms, further contributing to the current discussion about the drivers of biodiversity variation across spatial scales based on information about species, traits and phylogeny. This is an urgent topic in ecology, biogeography and conservation biology because changes in the functional trait and phylogenetic composition of biotic communities may be more (or less) pronounced than those only visible in species identities.

3 Methods

3.1 Study areas

This thesis comprised of two different data sets of biological data sampled in different periods from Finnish streams. In Papers I and III, biological (diatom and macroinvertebrate) and environmental data were collected at 54 wilderness streams in the Tenojoki River drainage basin (centered on 70°N 27°E, total basin area 16386 km^2), located in the northernmost part of Finland and Norway (Figure 2). These streams were sampled in 2012. The Tenojoki basin can be characterized as a very sparsely populated area where forestry and agriculture are uncommon activities. In this study area, stream waters show a pristine or near-pristine state and nutrient levels indicative of highly oligotrophic conditions (Heino 2013). A different study area was surveyed in Paper II. This data set was based on samples from 105 streams sites covering the western part of Finland and encompassing a territorial extension of 520 km in north-south and 330 km in east-west direction (Figure 3). These streams were sampled in 2014. The streams surveyed in this area belonged to 21 major river basins draining mainly into the Gulf of Bothnia and ranging from almost pristine forest to agricultural landscapes (Jyrkänkallio *et al.* 2017).

3.2 Field sampling and data processing

3.2.1 The Tenojoki River Basin data

Each of the 54 stream sites surveyed in the Tenojoki River basin for macroinvertebrates were sampled using a 3-minute kick-net sampling effort, consisting of six 30-second and 1-meter subsamples that covered gradients in depth, current velocity, particle size and moss cover within a riffle section of ca. 50 m^2 (Mykrä *et al.* 2004). In the field, these six subsamples were pooled into a composite sample and preserved in 70% alcohol. In the laboratory, the macroinvertebrates were identified to species level, but the early larval stages were identified to genus level because some individuals did not show adequate morphological characteristics to allow the identification to species level. For simplicity, hereafter I call taxa as species because more than 90% of the macroinvertebrates were identified to species level. In Paper I, I focused only on insects because body size was used as a surrogate of potential dispersal capability, and this would not be meaningful across all macroinvertebrate species (e.g., Oligochaeta *versus* Insecta).

The same 54 stream sites surveyed for macroinvertebrates were also surveyed for diatoms. Ten stones ranging in size from 10 to 30 cm were randomly collected at depths of 10 to 30 cm, and diatoms were scraped off from these stones, and from each stone, an area of 5 cm × 5 cm was scraped, totaling a 250 cm^2 sampled area for each stream

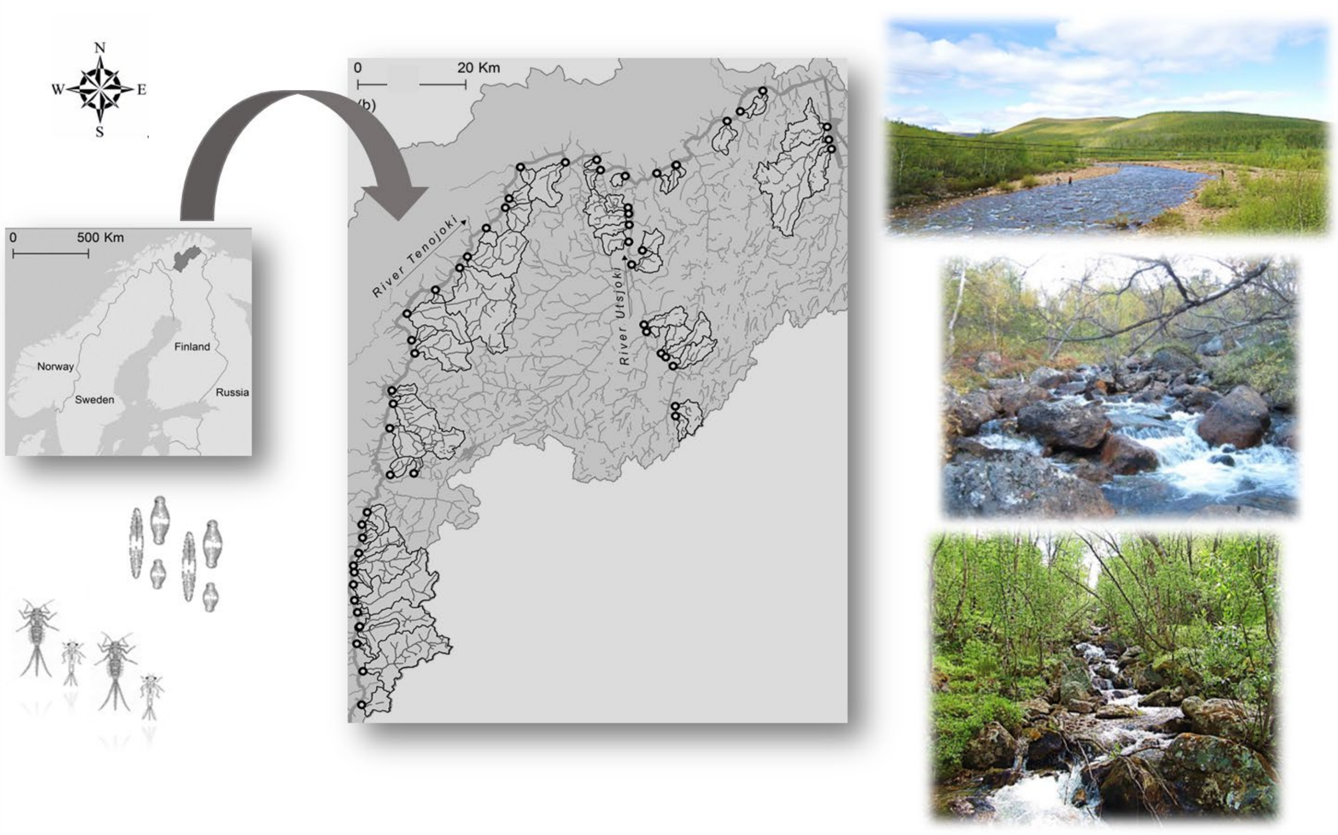

Figure 2. A map of the study area in the Tenojoki River basin in Finland showing the locations of the 54 streams sampling sites. Photos illustrate different types of streams in this area.

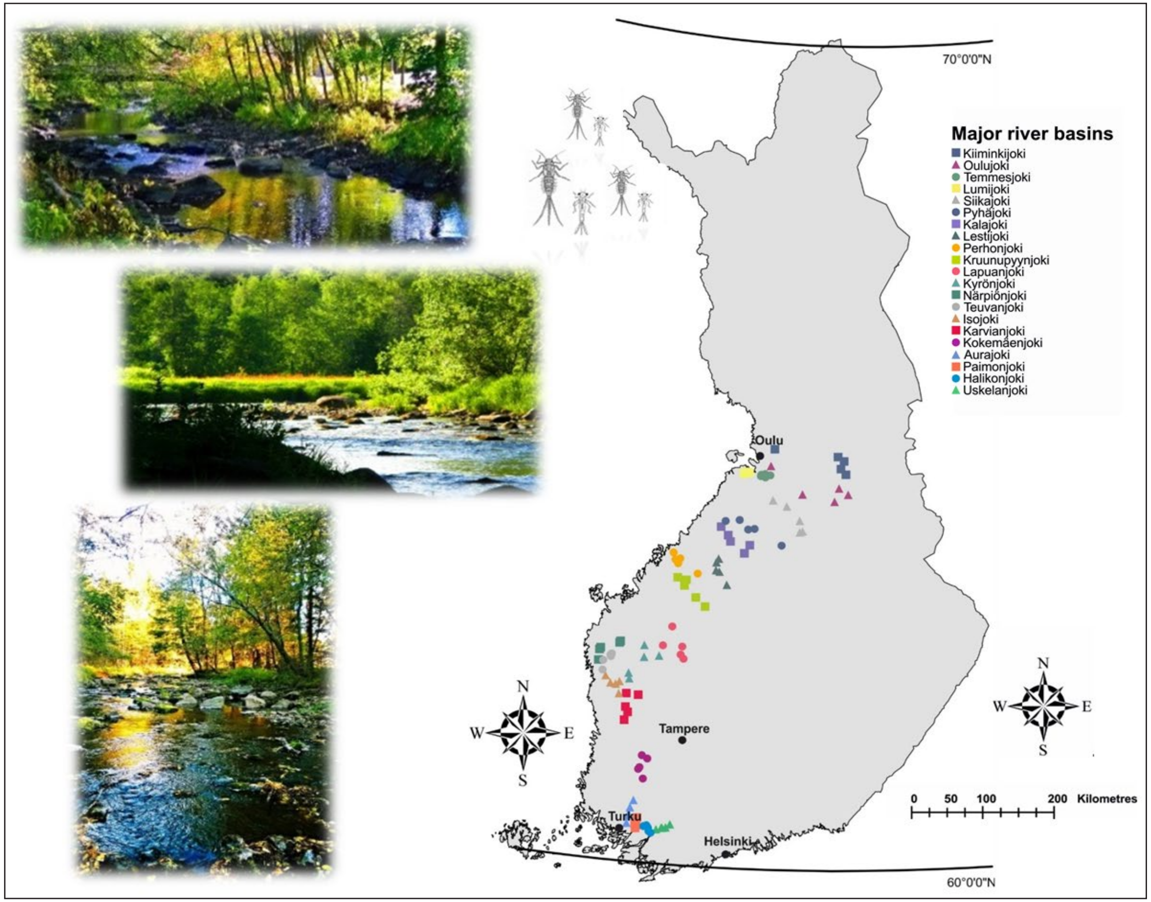

Figure 3. A map of the study area in Western Finland showing the locations of the 105 stream sampling sites belonging to 21 major rivers basins in Finland. Pictures illustrate different types of streams in this area.

site. Further, these samples were prepared. in the laboratory, based on standardized methods (SFS-EN 14407 2005; Kelly *et al.* 1998). Most of the diatoms were identified to the species level, with few individuals to genus level (less than 2%). Again, for simplicity, I hereafter call these taxa species.

3.2.2 The Western Finland data

The 105 stream sites in Western Finland were surveyed for macroinvertebrates using a 2-minute kick-net sampling effort this time (Mykrä *et al.* 2004). The same method of sampling and identification as used for the Tenojoki River basin data was used here for the Western Finland data, but this time four 30-second and 1-meter subsamples were taken within a riffle site of ca. 50 m^2, pooled into a composite sample and immediately preserved in 70% alcohol in the field. In the laboratory, the macroinvertebrates in these samples were identified to the species level (ca. 88 %), but early larval stages were identified to genus level (ca. 12 %) only because of lack of morphological features that characterize species. Again, for the sake of simplicity, I hereafter call all these taxa species.

3.3 Trait-based and phylogenetic information of species

In Paper I, information on body size (BS) classes were gathered for insects and diatoms and were subsequently used as a proxy for dispersal. For insects, each species was assigned to one of five size classes used to represent insect body size, which were based on the maximal larval length, following the five body length ranks: (1) 0–0.25 cm; (2) 0.25–0.50 cm; (3) 0.5-1 cm; (4) 1–2 cm and (5) 2–4 cm. This information was obtained based on Tachet *et al.* (2010) and personal communication (S. Doledéc, Université Lyon, France; J. Ilmonen, Metsähallitus, Natural Heritage Services, Finland; and L. Paasivirta, Salo, Finland). For diatoms, information on cell size (biovolume) was gathered representing diatom BS, and this information was obtained from Rimet & Bouchez (2012), following the five cell size ranks: (1) 0–99 μm^3; (2) 100–299 μm^3, (3) 300–599 μm3, (4) 600–1499 μm^3; (5) ≥ 1500 μm^3.

In Paper III, I used the set of traits described below in order to make sure that functional trait groups were as similar as possible for diatoms and macroinvertebrates, and that the results obtained were as comparable as possible. Thus, macroinvertebrates were assigned to three trait groups following functional traits used in previous studies on high-latitude streams (Tolonen *et al.* 2016; 2017). Functional feeding groups (FFG) were based on Moog (2002), Merritt & Cummins (1996) and Tachet *et al.* (2010), comprising the feeding mode of macroinvertebrates (i.e., filterers, gatherers, shredders, scrapers and predators). Habit trait groups (HTG) were based on information about macroinvertebrate mobility and their use of microhabitats (i.e., burrowers, climbers, clingers, sprawlers, semi-sessile and swimmers) (Merritt & Cummins 1996; Merritt *et al.* 2008; Tachet *et al.* 2010). The BS referred to maximum larval body length, and this time, each species was assigned to one of the following six size categories: >0–0.25 cm (1), 0.25–0.5 cm (2), 0.5–1 cm (3), 1–2 cm (4), 2–4 cm (5) and 4–8 cm (6).

Diatoms were assigned to different morphological guilds, cell-size classes and life-forms (e.g., Rimet & Bouchez 2012) in Paper III. Morphological guilds (portraying how diatoms utilize environmental resources) included species of short stature and tightly attached to the substratum (low-profile), large species or those which tend to form colonies (high-profile), species capable of moving (motile) and species that have features that help to resist sedimentation (planktic). The first three morphological guilds mentioned above (i.e., low-profile, high-profile and motile) were based on diatom growth morphology according to Passy's (2007) approach, and the planktic guild was suggested by Rimet & Bouchez (2012) to complement Passy's (2007) classification. Life form classifications were based on non-colonial (solitary cells either attached or non-attached to substratum) and colonial (floating or attached diatoms) information gathered from Round *et al.* (1990) and Rimet & Bouchez (2012). The same source of information used in Paper I for diatom biovolume was also used in Paper III to represent cell size classes (i.e., (1) 0–99 μm^3; (2) 100–299 μm^3, (3) 300–599 μm^3, (4) 600–1499 μm^3; (5) $\geq$ 1500 μm^3).

The same trait groups assigned for macroinvertebrates in Paper III (i.e., FFG, HTG and BS) were also used for macroinvertebrates species in Paper II. An exception was that this time BS was accounted for each individual species based on the length-weight relationships and calculated as the potential maximum size (as dry mass) of the aquatic stages (list of literature described later in the appendices section).

In Paper II, taxonomic distances based on the path lengths in the Linnean taxonomic trees were used as a proxy for macroinvertebrates phylogeny in the absence of true phylogeny data (Clarke and Warwick 1998; Winter *et al.* 2013), and the taxonomic information utilized was cross-checked using information available online in an open database (www.faunaeuropea.org).

3.4 Environmental predictor variables

Two different sets of variables were used in Paper I (i.e., local stream environmental and catchment variables) (Table 1). For the local stream environmental variables, current velocity (m s^{-1}) and depth (cm) were measured at 30 random spots in each stream surveyed. Based on five cross-channel measurements of the sampling sites, the mean width (m) of each stream site was obtained. Plots of 1 m^2 (10 plots) in each riffle site were randomly selected to visually estimate moss cover (%) and streambed particle size. Also, shading (%) by riparian vegetation was visually estimated by a person standing in the center of each stream channel. A modified Wentworth's scale (1922) was applied to classify bottom particle size as follows: sand (0.25–2 mm), gravel (2–19 mm), pebble (16–64 mm), cobble

(64–256 mm) and boulder (256–1024 mm). In the field, pH and conductivity (µS/cm^{-1}) were measured, and water samples were collected and taken to the laboratory to be analyzed for total nitrogen (µg/L^{-1}), color (Pt-Co mg/L), iron (µg/L^{-1}) and manganese (µg/L^{-1}) following the Finnish National Standard (National Board of Waters and the Environment 1981).

The catchment-scale variables for the entire drainage area (the Tenojoki basin) were computed using ArcGIS 10.1 software (ESRI, Redlands, USA). A total of seven catchment variables were measured (Table 1). The drainage basin area (km^2), the distance to the nearest upstream lake (km) and proportions of mire and lakes (%) were obtained from the National Land Survey of Finland data sets (2010a, b). In situations where there was no lake upstream, a value representing two-times the longest distance to an upstream lake was used. Vegetation abundance (i.e., mean of tasseled cap greenness; Crist & Cicone 1984) was computed from a Landsat 7 ETM+ satellite image (see Hjort & Luoto 2006). Based on a 25-m resolution digital elevation model (DEMs; National Land Survey of Finland 2000c), a mean of slope angle (°) and topography-derived moisture conditions (Topographic wetness index) of the catchment area of each study site were calculated (Beven & Kirkby 1979).

The same set of local stream environmental variables as was used in Paper I was also utilized in Paper III (Table 1). In addition, riparian variables were added and gathered from measurements of five points on both sides of the stream where the stream width measurements were taken. The height of stream bank (cm) was also used and measured from the water level surface to the edge of terrestrial vegetation, and steepness (cm) was quantified by how much the stream bank rose along the 2 m perpendicular to the stream site.

A multiscale set of environmental variables were used in Paper II (Table 1): physical-chemical environmental variables, land cover and land use characteristics, climate variables and spatial variables. At the local level, current velocity (m s^{-1}) and water depth (cm) measurements were taken from 30 random spots in a riffle, and stream width measures were derived from 10 locations covering the stream site by using a tape-measure. Based on 50 × 50 cm quadrats randomly placed in locations of each stream site, bottom particle size and moss cover were visually estimated from 10 locations. A modified Wentworth scale was again applied to classify particle size (see above). In the field, pH and conductivity (µS/cm^{-1}) were measured. In the laboratory, water samples taken from the field were analyzed for phosphorus (µg/L), total nitrogen (µg L^{-1}), and water color (Co-Pt mg/L).

At the catchment level, variables were calculated based on GTOPO 30 digital elevation model (www.worldcliml.org) delineating the upstream catchment of each sampling site. This was based on using the program GRASS-GIS to extract stream-specific variables (Domisch *et al.* 2015; Neteler *et al.* 2012), and the following variables were obtained: elevation (m), slope (° * 100), open water (all in %) and flow accumulation (number of upstream cells). Land cover variables (i.e., forest cover, cultivated and managed vegetation, regularly flooded vegetation, urban/built-up, ice cover and sparse vegetation) were also

Table 1. An overview of the all environmental variables and biological groups used in the analyses of the Papers I, II and III. Abbreviations: Hydro = hydroclimatic variables denoting regional climate; db-MEM = distance-based Moran's eigenvector maps.

	Paper I	**Paper II**	**Paper III**
Environmental variables			
Local	Chemical (pH, conductivity, total nitrogen, color, iron and manganese) and physical variables (current velocity, depth, stream width, moss cover, shading and bottom particle size)	Chemical (pH, conductivity, total nitrogen, color, iron and manganese) and physical variables (current velocity, discharge, depth, stream width, moss cover, shading, and bottom particle size and substratum diversity)	Chemical (pH, conductivity, total nitrogen, color, iron and manganese) and physical variables (current velocity, depth, stream width, moss cover, shading, bottom particle size, height of stream bank and steepness)
Catchment	Drainage area, distance to the nearest upstream lake (or two times the longest measured distance to an upstream lake when no lake was detected), proportion of mire, proportion of lakes, tasseled cap greenness, slope angle and topography wetness index	Forest cover, cultivated and managed vegetation, regularly flooded vegetation, urban/built-up, ice cover, sparse vegetation, open water (in %), human footprint, elevation, slope angle and flow accumulation	
Climate		Snow cover, variables describing variation in temperature (from Hydro1 to Hydro11) and precipitation (from Hydro12 to Hydro19)	
Spatial		db-MEM based on overland distances	Overland distances as measure of spatial distances
Biological group	Diatoms and Insects	Macroinvertebrates	Diatoms and Macroinvertebrates

extracted (Tuanmu & Jetz 2014). The variable 'Human Footprint' was calculated based on Sanderson *et al.* (2002) and obtained through the data accessed from Global Human Footprint (http://sedac.ciesin.columbia.edu). At the regional level, climate variables were obtained and extracted by the same procedure as described above for the catchment variables. In total, 19 hydroclimatic (*sensu* Domisch *et al.* 2015) variables describing temperature and precipitation were derived from the Worldclim database (Hijmans *et al.* 2005), in addition to the temperature and precipitation values that were aggregated across the catchment area (Domisch *et al.* 2015). The trends of snow-cover (2000-2015) were also obtained from the Global Snowpack dataset (Dietz *et al.* 2015).

3.5 Spatial variables

Distance-based Moran's eigenvector maps (formerly called principal coordinates of neighbor matrices, PCNM; Borcard & Legendre, 2002) were used to model spatial structures (i.e., spatial variables) of community variation across the geographical extent covered by the sampling area in Western Finland (Paper II). This method produces several spatial variables representing spatial organization of sites at different scales, ranging from large-scale patterns (such as south-north gradient) to small-scale patterns (such as aggregated groups of sites). The first spatial variables obtained through these calculations indicate large-scale spatial patterns among sites, whereas the last variables indicate very small-scale spatial patterns among sites. The calculations of these variables were based on a matrix of Euclidean distances among the sampled sites using the north and east coordinates of the sampling sites as input (Borcard & Legendre 2002). The details of the calculation of spatial variables can be found in Borcard & Legendre (2002) and Borcard *et al.* (2004). Moran's eigenvector showing positive spatial autocorrelation were retained as spatial variables in the statistical analyses of Paper II because they represent the Euclidean components of the neighbor relationships of the matrix. In this study, there were 25 spatial variables showing positive spatial autocorrelation.

3.6 Statistical analyses

All the statistical analyses were conducted in the R environment (R Core Team, 2017). Basic preliminarily statistical examinations such as tests of normality, scatter plots, boxplots, tests for multicollinearity and correlation tests were done prior to the main statistical analyses. In Paper I, to improve model fit, NP (niche position) and NB (niche breadth) were log-transformed prior to analyses. In Paper II, the multiscale data set of environmental variables used was very large, and thus explanatory variables showing variance inflation factor (VIF) > 10 were excluded from each of the four predictor variable sets.

3.6.1 Regional occupancy and local abundance

In Paper I, I firstly used local environmental and catchment variables to calculate different measurements of niches for each species of each organismal group (i.e., diatoms and insects) that occurred in more than two sites in the Tenojoki River basin. I used the outlying mean index (OMI) analysis (Doledéc *et al.* 2000) to obtain the different measures of niches (NP_e = NP based on local environmental variables; NP_c = NP based on catchment variables; NB_e = NB based on local environmental variables, and NB_c = NB based on catchment variables). Accordingly, NP was calculated by the distance from the mean environmental conditions used by a species and the mean environmental conditions of the entire study area. Based on this calculation, NP measures of each species got values ranging from high to low. Accordingly, species with low values of NP tend to occur in habitats with high availability in the study area, whereas species with high values of NP tend to occur in less common habitats. The NB measure is also provided by the OMI analysis called 'species tolerance'. Species having high values of NB tend to occur across a broad range of habitat conditions, whereas species that have low values of NB tend to occur in a limited range of conditions (Tales *et al.* 2004; Heino & Grönroos 2014).

Secondly, I explored the relationship between regional occupancy and local abundance against the set of predictors (i.e., NP_e, NP_c, NB_e, NB_c, and BS) using beta regression models (Ferrari & Cribari-Neto 2004) and negative binomial generalized linear models (Zeileis *et al.* 2008), respectively. I used two models to analyze regional occupancy (models 1 and 2) and two models to analyze local abundance (models 3 and 4) for diatoms and insects [(model 1) Occupancy ~ NP_e + NB_e + BS; (model 2) Occupancy ~ NP_c + NB_c + BS; (model 3) Abundance ~ NP_e + NB_e + BS; (model 4) Abundance ~ NP_c + NB_c + BS]. For all models described above, diatom and insect BS were used as ranked variables. I compared the performance of these models (i.e., 'local environmental models' *versus* 'catchment models') using the Akaike information criterion (Burnham & Anderson 2002). Running these pairs of models side by side, I was able to compare the power of 'local environmental models' versus 'catchment models' influencing across-species variation in occupancy and abundance.

3.6.2 Beta diversity

3.6.2.1 Beta diversity analysis in Paper II

In Paper II, I used distance-based redundancy analysis (db-RDA, Anderson & Legendre 1999), variation partitioning (Legendre *et al.* 2005) and four different sets of variables (i.e., local environmental, catchment, climate variables and spatial variables) to analyze the variation in macroinvertebrate species-, trait- and phylogeny-based beta diversity and its components (i.e., total, replacement and abundance-difference). Next, I will describe these analyses in three distinct phases.

In the first phase, I generated three dissimilarity matrices (i.e., total, replacement and abundance-difference) based on the macroinvertebrate species abundance data. The second step in the first phase was the selection of final local environmental (LE), catchment variables (CA), climatic variables (CC) and spatial variables (SP) based on the db-MEMs. In this case, the variable selection was based on stepwise selection of environmental variables based on their *P*-value and AIC. After the final sets of variables were selected, I ran distance-based redundancy analysis (db-RDA, Anderson & Legendre 1999), followed by variation partitioning (Legendre *et al.* 2005), based on each of the three response matrices obtained previously to assess the relative and shared effects of LE, CA, CC and SP variables on the macroinvertebrate community structure.

In the second phase, the same approach utilized for species-based calculations was used but this time on three dissimilarity matrices utilizing macroinvertebrate trait data (i.e., total$_f$, replecement$_f$ and abundance-difference$_f$). These matrices were derived through the calculation of between-species distances based on the trait data and a hierarchical clustering procedure (UPGMA method) in order to produce a functional tree for these macroinvertebrates species. This functional tree was used in association with the species abundance data to provide the site-by-site dissimilarity matrices. Thereafter, the variable selection proceeded with distance-based redundancy analysis (db-RDA) and partitioning the variation in the three dissimilarity matrices (i.e., total$_f$, replecement$_f$ and abundance-difference$_f$) were performed using LE, CA, CC and SP variable sets.

In the third phase, three dissimilarity matrices utilizing macroinvertebrate taxonomic information as a proxy for phylogeny were generated (i.e., total$_p$, replecement$_p$ and abundance-difference$_p$). Before the generation of these matrices, the taxonomic distances between species were calculated and a hierarchical clustering procedure (UPGMA method) was applied to produce the phylogenetic tree for these macroinvertebrate species. This taxonomic tree was used in association with the species abundance data to provide the site-by-site dissimilarity matrices. After this step, the same procedure as used for species- and trait-based beta diversity was applied as follows: variable selection, db-RDA and partitioning variation on the three phylogeny matrices using LE, CA, CC, and SP as predictor variables.

3.6.2.2 Beta diversity analysis in Paper III

In Paper III, I used distance-based methods to analyze how species- and trait-based beta diversity and its components (i.e., turnover and nestedness) correlate with environmental and spatial distances, using presence-absence data separately for diatoms and macroinvertebrates.

The first phase consisted of the generation of three dissimilarity matrices (i.e., overall, turnover and nestedness) based on either the diatom or macroinvertebrate species data. Mantel tests and partial Mantel tests (Mantel 1967; Legendre & Legendre 2012) were run for each of the six dissimilarity matrices to test the relationships between biological dissimilarities and environmental or spatial distances. The best set of environmental variables that presented the strongest correlation between the biological dissimilarity matrix and environmental distances were selected using the bio-env analysis (Clarke & Ainsworth 1993).

In the second phase, three trait dissimilarity matrices (i.e., overall$_t$, turnover$_t$ and nestedness$_t$) were generated by using trait data for either diatoms or macroinvertebrates, following the approach devised by Villeger *et al.* (2013). Before calculating these matrices, Gower distance (Gower 1971) was used to calculate between-species distances based on the trait data. The next step in the second phase was carried out by using these trait distances in a PCoA producing trait vectors (Villeger *et al.* 2008) to be used in the upcoming steps. The step after producing the PCoA trait vectors included associating the trait vectors with site-by-species matrix and calculating site-by-site dissimilarity matrices. Thereafter, I proceeded with the analysis of the Mantel tests and partial Mantel tests.

4 Results and discussion

Biodiversity is a multiscaled and multifaceted concept that requires multiple approaches to be fully understood (Weinstein *et al.* 2014, Heino & Tolonen 2017, Gianuca *et al.* 2018). In order to properly comprehend biodiversity patterns, it is therefore crucial to perceive what the drivers of biodiversity are, at what spatial scale they are acting and what kind of a biodiversity approach should be considered. In this vein, I investigated the relative contribution of factors shaping biodiversity patterns across northern streams, analyzing the influences of different sets of environmental variables and exploring species-, trait- and phylogeny-based beta diversity patterns. I also focused on both species-level (Paper I) and community-level phenomena (Papers II and III).

4.1 The influence of local-, catchment- and regional-scale factors on stream biodiversity

4.1.1 Regional occupancy and local abundance

In Paper I, I found a strong and positive relationship between regional occupancy and local abundance for diatoms and insects (Figure 3). The OMI analysis showed that the most important local environmental variables related to the distribution of diatoms across the studied area were moss, shading, pebble, conductivity and boulder. Among the catchment variables, mean slope, lake percentage, greenness and mire were the most important variables related to the distribution of diatoms. The regional occupancy of diatoms was significantly and negatively related to NP and BS, also positively related to NB (Figure 4). These patterns were found independently of the variables used to define the models (i.e., local environmental or catchment niche variables, with pseudo $R^2 = 0.74$ and pseudo $R^2 = 0.57$, respectively; Figure 4).

The niche variables based on environmental variables were clearly superior to the ones based on catchment variables (delta AIC = 67.25; Figure 4). Compared to NB or BS, NP was the best variable to explain regional occupancy of diatoms. I also found that NP and BS were significantly and negatively related to diatom local abundance (Figure 4), and that the niche model based on local environmental variables was also superior to the one based on catchment variables (delta AIC = 8.98). NB_e was not a significant predictor of diatom mean local abundance (Figure 4).

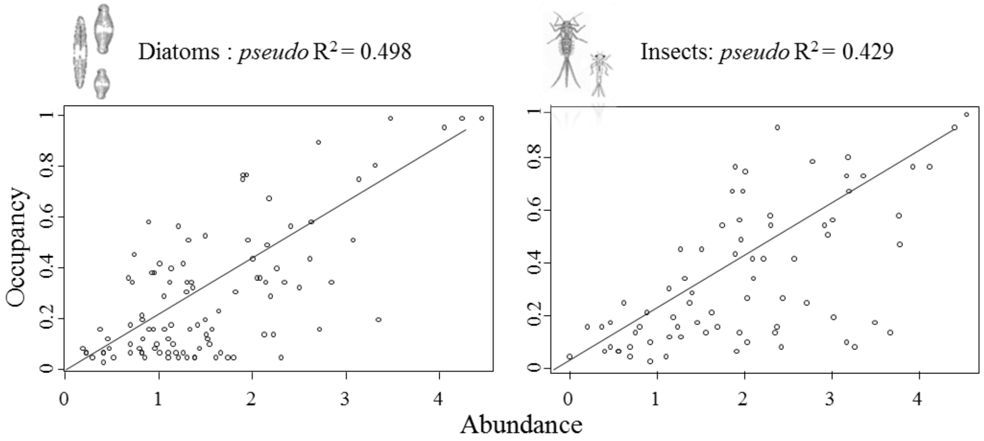

Figure 3. The relationships between regional occupancy and local abundance of diatoms and macroinvertebrates. These relationships were tested using beta regression (Ferrari & Cribari-Neto 2004).

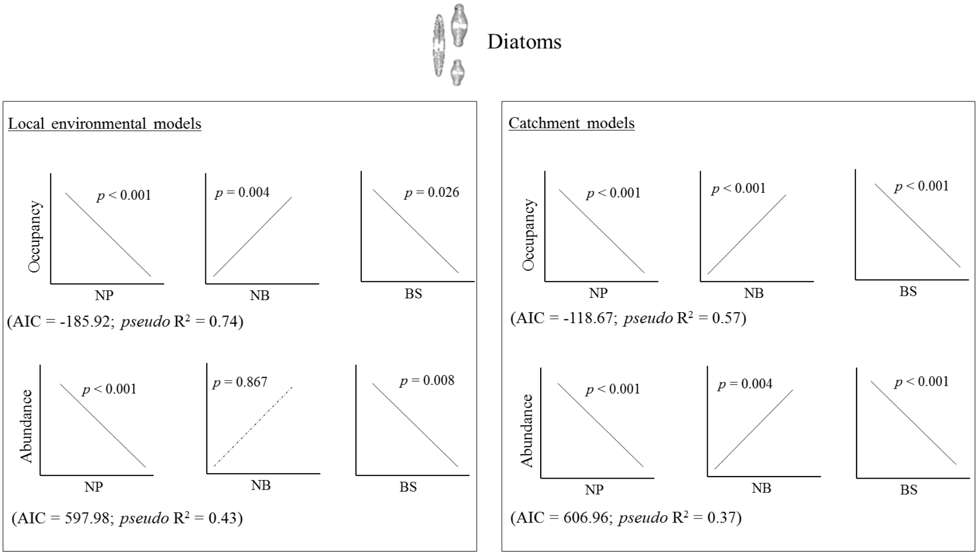

Figure 4. The result of models accounting for variation in the occupancy and abundance of diatoms. Legend: NP = niche position; NB = niche breadth; BS = body size. Dashed line denotes non-significant relationships. Significance: $P > 0.05$.

The OMI analysis showed that the most important local environmental variables for insect distributions were shading, moss, stream width, pebble, cobble and boulder. The most important catchment characteristics affecting insect distribution were mean slope, lake percentage, catchment area and the distance to an upstream lake. Insect regional occupancy was significantly and negatively related to NP and positively related to NB. NP was the main variable explaining insect regional occupancy (Figure 5), and the niche variables based on catchment characteristics had less support than the niche variables based on the local environmental variables (delta AIC = 26.35; Figure 5). The models explaining local insect abundance had lower explanatory power than those explaining regional occupancy (model based on local environmental variables: pseudo $R^2 = 0.31$; model based on catchment variables: pseudo $R^2 = 0.18$; Figure 5). A negative relationship between NP and local insect abundance was found considering the local environmental model. In addition, I found that NB was positively related to local abundance. However, only NP was significantly and negatively related to local insect abundance based on the catchment model (Figure 5).

The positive relationship between regional occupancy and local abundance found for stream diatoms and insects concur with what previously has been found for a variety of organisms (Gaston *et al.* 2000; Gaston & Blackburn 2000). Exploring this relationship among the models used in the analysis, I found, based on the AIC criteria, that 'local environmental models' were more important than 'catchment models' in explaining regional occupancy and local abundance of diatoms and insects. Within these models, the measures of NP were always the main predictors of regional occupancy or local abundance of the studied organisms, especially when NP based on local environmental variables was utilized to explain these relationships (Figure 4 and 5, conclusion based on AIC values). Thus, species with marginal niche positions (i.e., those with high values for this variable) tended to have lower abundances and to be less widespread than those with non-marginal niche positions (i.e., those with low values), independently of the group of organisms.

These results demonstrated that the degree of species marginality in terms of local environmental variables is the chief determinant of regional occupancy and local abundance of species in northern streams. This finding is also in line with recent studies conducted in other freshwater environments (Tales *et al.* 2004; Heino & Gönroos 2014; Tonkin *et al.* 2016; Heino & Tolonen 2018). In my study, these results may be associated to the features of high-latitude streams, which are characterized by low temperatures, short growing seasons and harsh winter conditions (Wrona *et al.* 2013; Tolonen *et al.* 2017). These high-latitude features may dictate that NP along harsh environmental gradients is important in determining species regional occupancy and local abundance. In addition, the effects of NB and BS on regional occupancy and local abundance were less important, although they were sometimes significant. The weaker support for NB and BS has also been reported in previous studies (Cowley *et al.* 2001; Tales *et al.* 2004). The lesser importance of NB might, in part, be related to difficulties in generating adequate measurements for species niches (Gaston 1994). However, in this study, the

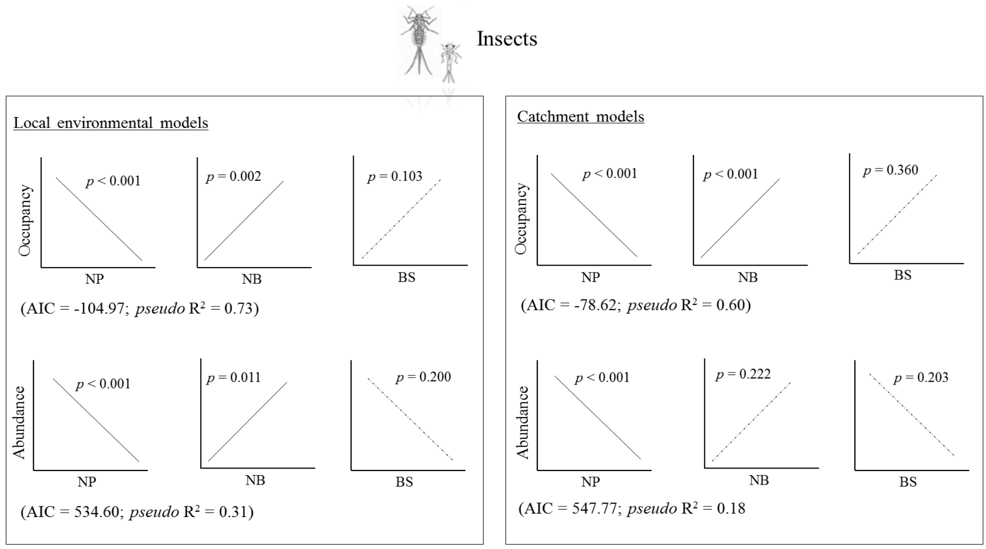

Figure 5. The result of models accounting for variation in the occupancy and abundance of diatoms. Legend: NP = niche position; NB = niche breadth; BS = body size. Dashed line denotes non-significant relationships. Significance: $P > 0.05$.

most influential local environmental and catchment variables affecting the distributions of diatom and insect species across northern streams were utilized (Heino & Soininen 2006; Heino & de Mendoza 2016), suggesting that NB measures should not be inferior to the NP measures in terms of their practical utility.

Consistent with what is expected to be found for small organisms, BS was negatively related to diatom regional occupancy and local abundance (Passy 2012). However, contrary to what I found and to previous research (Hoffsten 2004), BS was not significantly related to regional occupancy and local abundance of insects. Thus, it may be that the relative range of diatom BS was larger than the one observed for insect BS, helping to better explain the occupancy-abundance relationships only for diatoms. On the other hand, it may also be that the ecological niche features are simply more important than BS when predicting the regional occupancy and local abundance of insects in high-latitude streams.

In summary, models based on local environmental niche variables performed better than those based on catchment niche variables in explaining local abundance and regional occupancy of both diatoms and insects. This is slightly different from the findings of studies at the community level dealing with more strongly stressed-streams, in which catchment variables overrule local environmental conditions (Richards *et al.* 1997; Death & Joy 2004). Thus, the relationships between regional occupancy, local abundance and niche-related characteristics seem to be affected by the types of variables used to niche measures. I expected a priori that models based on catchment niche variables, when compared to local environmental niche models, should be better in explaining species regional occupancy and local abundance (e.g., Siqueira *et al.* 2009). This is due to the well-known effect of environmental variation at larger scales, such as that at the catchment scale, influencing that at the local scale where species are ultimately selected to occur in certain sites (Poff 1997; Vinson & Hawkins 1998). For instance, Siqueira *et al.* (2009) found that niche measures based on landscape variables were more important in explaining insect regional occupancy and local abundance across tropical streams than those based on local environmental variables. It is possible that the results in my study differed from those found by Siqueira *et al.* (2009) because the environmental features in tropical regions (e.g., temperature and seasonality) differ from those in high latitudes. In other words, it can be expected that different drivers are important for the occupancy and abundance of species in different regions.

4.1.2 Explaining variation in different facets of beta diversity

In Paper II, different subsets of variables measured at different scales (i.e., local, catchment, regional and spatial) were included in the models explaining variation in each beta diversity dimension investigated (i.e., species, trait and phylogeny) (Tables 2, 3 and 4). The variables selected at the local level demonstrated variation in water chemistry (e.g., pH, color and nutrient concentrations) and stream substratum diversity, whereas forest cover, cultivated-managed areas and stream slope were the subset of variables selected at the catchment level. Among the climatic variables, in general, the ones accounting for variation in temperature and snow cover were selected in the final models. The spatial variables selected in the models were mostly the first 10 variables produced by the db-MEM, which accounted for broad-scale to intermediate-scale spatial variation in the facets of beta diversity (Dray *et al.* 2012). In general, the relative influence of explanatory variables on each facet of diversity and component revealed relatively similar patterns (Tables 5, 6, and 7). The explained variance accounted by the local environmental and spatial factors was the largest fractions of variation explained in all facets of beta diversity, whereas catchment and climate fractions were less influential in explaining variation in the facets of beta diversity at the spatial scale studied (Tables 5, 6, and 7).

The similar findings explaining variation in different facets of beta diversity could be due to the spatial scale considered in this study, which may emphasize the roles of the environmental and spatial variables influencing beta diversity patterns (Heino & Tolonen 2017). The local environmental variables that accounted for variation in all facets of beta diversity have previously been found to be important in structuring macroinvertebrates community in studies based on species-identities only (Heino *et al.* 2003; Mykrä *et al.* 2007; Sanderson *et al.* 2005). Although the data analyzed comprised a relatively broad spatial extent (> 500 km in north-south extension), local environmental habitat features were more influential in structuring macroinvertebrate facets of beta diversity than

Table 2. The species-based analysis in Paper II: variable selection in db-RDA (distance-based Redundancy Analysis). Abbreviations: Hydro = hydroclimatic variables denoting regional climate; db-MEM = distance-based Moran's eigenvector Maps, V = spatial variables; LC = land cover.

Total	**Local**	**Catchment**	**Climate**	**Spatial (db-MEM)**
	pH	Forest	Hydro.1	V2
	Moss cover	Slope	Hydro.6	V1
	Total nitrogen	Elevation	Hydro.8	V8
	Velocity	Lakes	Hydro.10	V3
	Substratum diversity	Stream order	Snow cover	V6
	Color	LC.7*	Hydro.9	V9
	Pebble		Hydro.12	V5
	Depth		Hydro.14	V17
				V7
				V11
				V18
				V23
				V4
Replacement	**Local**	**Catchment**	**Climate**	**Spatial (db-MEM)**
	pH	Slope	Hydro.8	V2
	Substratum diversity	LC.7*	Snow cover	V8
	Total phosphorus	Elevation	Hydro.3	V3
	Conductivity		Hydro.9	V1
				V9
				V6
				V13
				V12
				V17
Abundance-diff	**Local**	**Catchment**	**Climate**	**Spatial (db-MEM)**
	Moss cover	Forest	Hydro.11	V11
	Substratum evenness		Hydro.17	V20
	Pebble		Snow cover	V7
	Color			V4
				V5
				V23
				V1
				V4

* LC7= Average upstream cover of cultivated and managed vegetation

Table 3. The trait-based analysis in Paper II: variable selection in db-RDA (distance-based Redundancy Analysis). Abbreviations: Hydro = hydroclimatic variables; db-MEM = distance-based Moran's eigenvector Maps, V = spatial variables; LC = land cover.

Total$_t$	**Local**	**Catchment**	**Climate**	**Spatial (db-MEM)**
	pH	Forest	Hydro.1	V2
	Moss cover	Slope	Hydro.6	V1
	Substratum diversity		Hydro.8	V8
	Pebble		Hydro 10	V5
	Color		Snow cover	V7
	Total nitrogen		Hydro 19	V9
			Hydro 5	V11
				V23
				V4
				V18
				V3
				V6
Replacement$_t$	**Local**	**Catchment**	**Climate**	**Spatial (db-MEM)**
	pH	Slope	Hydro.8	V2
	Substratum diversity	LC.7*	Hydro.3	V8
	Total phosphorus	Lakes	Hydro.5	V9
	Sand	LC.12**	Hydro.9	V1
		LC.6***		V3
				V12
				V18
Abundance-diff$_t$	**Local**	**Catchment**	**Climate**	**Spatial (db-MEM)**
	Moss cover	Forest	Hydro.11	V11
	Pebble		Hydro.14	V20
	Color		Snow cover	V7

* LC7= Average upstream cover of Cultivated and managed vegetation
** LC12= Average upstream cover of Open water
*** LC6= Average upstream cover of Herbaceous vegetation

Table 4. The phylogeny-based analysis in Paper II: variable selection in db-RDA (distance-based Redundancy Analysis). Abbreviations: Hydro = hydroclimatic variables denoting reginal climate; db-MEM = distance-based Moran's eigenvector Maps, V = spatial variables; LC = land cover.

Total$_p$	**Local**	**Catchment**	**Climate**	**Spatial (db-MEM)**
	Moss cover	Forest	Hydro.1	V2
	pH	Elevation	Hydro.6	V1
	Substratum diversity	Lakes	Hydro.8	V5
	Pebble	Stream order	Hydro.10	V7
	Total nitrogen	Slope	Snow cover	V6
	Color	LC.7*	Hydro.13	V8
	Substratum evenness		Hydro3	V3
			Hydro	V11
			Hydro.16	V9
				V23
				V20
				V4
Replacement$_p$	**Local**	**Catchment**	**Climate**	**Spatial (db-MEM)**
	pH	LC.7*	Hydro.8	V2
	Substratum diversity	Slope	Snow cover	V8
	Total phosphorus	Lakes	Hydro.3	V1
	Conductivity	LC.12**		V3
	Sand	LC.6***		V9
				V6
				V13
				V12
Abundance-diff$_p$	**Local**	**Catchment**	**Climate**	**Spatial (db-MEM)**
	Moss cover	Forest	Hydro.11	V11
	Pebble		Hydro.12	V20
	Color		Snow cover	V7
				V4
				V5
				V23
				V1

* LC7= Average upstream cover of Cultivated and managed vegetation

** LC12= Average upstream cover of Open water

*** LC6= Average upstream cover of Herbaceous vegetation catchment and regional (i.e., climate) factors. This finding suggests that environmental filtering is shaping species compositions, the set of traits and the phylogenetic structure of communities across sites. Thus, changes in species identities, trait composition and phylogenetic structure are exhibiting similar patterns along large environmental gradients (e.g., Weinstein *et al.* 2014). Consequently, species that are occurring locally within streams are most likely resulting from the regional pool of species that holds a similar array of traits and similar evolutionary histories (Webb *et al.* 2002; Devictor *et al.* 2010; Weinstein *et al.* 2014). If the study area had been larger, there might have been stronger effects of spatial variables on, for example, the phylogenetic structure because very large geographical areas constitute different species pools, each of which may support related species.

A significant pure spatial signal on species-, trait- and phylogeny-based beta diversity was found in the results (Tables 5, 6, and 7). Pure spatial signal on diversity patterns can result from dispersal limitation or from unmeasured environmental variables that are spatially structured (Peres-Neto *et al.* 2006). This result is in line with previous studies on species-based community patterns of macroinvertebrates across large spatial scales (Sandin 2003; Mykrä *et al.* 2007). In these studies, the authors were possibly relating this spatial effect to dispersal limitation, which has been known to have an important effect on community structuring (Leibold *et al.* 2004; Heino *et al.* 2015). Thus, this is likely to be the case in this study, given the geographical extent of the sampled area, indicating that dispersal limitation may shape the variation in macroinvertebrate species-, trait- and phylogeny-based beta diversity, at least to some extent. In addition, environmental variables are very often spatially structured inducing spatial dependence in species distributions (e.g., Tuomisto *et al.* 2003), and this can be an alternative explanation for the significant pure spatial signal leading to variation in the facets of beta diversity. However, the most influential ecological variables influencing stream macroinvertebrate community composition were used in this study (Sandin 2003; Heino *et al.* 2007; Mykrä *et al.* 2007). Thus, it is rather safe to conclude that autocorrelation of unmeasured environmental variables is unlikely to be the reason behind the importance of spatial signal on beta diversity patterns.

Catchment variables are known to affect macroinvertebrate community composition both directly and indirectly (Corkum 1992; Poff 1997; Allan *et al.* 1997; Allan & Castillo 2007). In this study, catchment variables were less influential in explaining variation in the facets than local and spatial variables. However, the potential effects of landscape features cannot be ignored because of their known effects on local features of streams (Corkum 1992; Allan & Castillo 2007). For instance, local habitat features in streams, such as pH, conductivity and stream bed composition, have previously been shown to be affected by catchment features (Corkum 1992; Soininen *et al.* 2015). In addition, climate variables were less influential than local and spatial variables in explaining variation in macroinvertebrate facets of beta diversity in this study, which may be due to small variation in these climatic factors (mean annual temperature = 2.7 °C; sum of annual precipitation = 50.550 mm; mean number of days with snow cover = 2268). However, climate has previously been shown to have indirect influence on local stream variables

Table 5. The variation partitioning table showing species-based beta diversity (i.e., total, replacement and abundance-difference) variation explained by pure and shared effects of local, catchment, climate and spatial variables. The explained variation is based on adjusted R^2. Legend: * *P* >0.05

Pure and shared fractions	Total	Replacement	Abundance-diff
Local variables	0.04*	0.05*	0.06*
Catchment variables	0.01		0.01
Climate variables	0.02*		0.04*
Spatial variables	0.03*	0.05*	0.04*
Catchment∩Climate	0.01	0.03	
Climate∩Spatial	0.01	0.01	
Local∩Climate		0.01	
Spatial∩Local	0.01	0.02	0.02
Climate∩Spatial	0.01	0.01	
Catchment∩Local			0.01
Local∩Climate∩Spatial	0.02	0.04	0.02
Catchment∩Local∩Climate		0.01	
Climate∩Spatial∩Catchment		0.01	0.01
Local∩Catchment∩Climate∩Spatial	0.03	0.02	0.02

Table 6. The variation partitioning table showing trait-based beta (i.e., total$_t$, replacement$_t$ and abundance-difference$_t$) diversity variation explained by pure and shared effects of local, catchment, climate and spatial variables. The explained variation is based on adjusted R^2 Legend: * *P* >0.05

Pure and shared fractions	Total$_t$	Replacement$_t$	Abundance-diff$_t$
Local variables	0.04*	0.05*	0.07*
Catchment variables		0.03*	0.02*
Climate variables	0.03*		0.04*
Spatial variables	0.04*	0.08*	0.03*
Catchment∩Climate		0.02	
Climate∩Spatial	0.01		
Local∩Climate	0.01	0.01	0.02
Spatial∩Local	0.02	0.04	0.01
Climate∩Spatial	0.03		0.01
Catchment∩Local		0.02	0.01
Local∩Climate∩Spatial	0.03		0.01
Catchment∩Local∩Climate			
Climate∩Spatial∩Catchment			
Local∩Catchment∩Climate∩Spatial	0.03	0.08	0.01

Table 7. The variation partitioning table showing phylogeny-based beta diversity (i.e., total$_p$, replacement$_p$ and abundance-difference$_p$) variation explained by pure and shared effects of local, catchment, climate and spatial variables. The explained variation is based on adjusted R^2. Legend: * $P > 0.05$

Pure and shared fractions	**Total$_p$**	**Replacement$_p$**	**Abundance-diff$_p$**
Local variables	0.04*	0.07*	0.06*
Catchment variables	0.01	0.02	0.01*
Climate variables	0.02*		0.04*
Spatial variables	0.03*	0.06*	0.04*
Catchment∩Climate	0.01	0.01	
Climate∩Spatial	0.01		
Local∩Climate	0.01	0.01	0.01
Spatial∩Local	0.01	0.02	0.02
Climate∩Spatial	0.01		
Catchment∩Local		0.01	0.01
Local∩Climate∩Spatial	0.02	0.02	0.02
Climate∩Spatial∩Catchment		0.01	
Local∩Catchment∩Climate∩Spatial	0.03	0.06	0.02

through the changes in temperature and precipitation (Pajunen *et al.* 2016). This, in turn, might affect the water chemistry and hydrology of streams. Although climate was a less efficient factor in explaining variation in beta diversity dimensions in this study, I presume that its influence might have been substantial if a broader geographical region had been investigated.

The data analyzed in this study encompassed a relatively broad spatial extent, yet local environmental conditions were more important than large-scale factors in structuring macroinvertebrate beta diversity dimensions. Under these circumstances, it is noticeable that the details of community-environment relationships (e.g., different predictor variables) may differ among the different facets of beta diversity analyzed (Devictor *et al.* 2010; Cai *et al.* 2018). However, in this study, none of these different facets of beta diversity showed a clearly superior response compared to the traditional species-based analyses.

4.2 Insights from species-, trait- and phylogeny-based approaches

In Paper II, I explored the variation in macroinvertebrate species-, trait- and phylogeny-based beta diversity across a relatively broad spatial extent (> 500 km). Similar results were found when analyzing the responses of these different facets of beta diversity to ecological and spatial gradients (see Tables 5, 6, and 7). The three facets of beta diversity analyzed here responded similarly to variation in local environmental, catchment, climate and spatial variables. These results showed that the general patterns of macroinvertebrate community-environment relationships may not differ among the facets explored here. Therefore, different species with similar traits might respond in similar ways to environmental gradients across spatial scales, and the power of the phylogenetic approach may also depend on the spatial and environmental context (Heino & Tolonen 2017).

Here, I was able to show that species-, trait- and phylogeny-based approaches exhibit similar patterns across a study area without strong geographic barriers for dispersal (e.g., high mountains). Thus, this finding suggests that the explanatory power in phylogeny- and trait-based approaches was not superior in comparison to that in the species-based. This finding is contrary to what has been found in a previous study (Gianuca *et al.* 2018) where trait- and phylogeny-based approaches demonstrated to provide complementary insights about biodiversity patterns. However, the inference of trait- and phylogeny-based biodiversity patterns may depend on many factors, including the spatial scale of the observations, the type of information used (e.g., set of traits and phylogenetic data), the group of model organisms and the methods utilized (Gianuca *et al.* 2018). Given such complexities, it is nearly impossible to know a priori which set of traits is more informative, which methods should be employed as well as which facet of diversity is redundant or complementary. Thus, one cannot generalize that trait- and phylogeny-based analyses are always superior to species-based in terms of better detecting the responses of biotic communities to environmental and spatial gradients.

In Paper III, for both organismal groups (i.e., diatoms and macroinvertebrates), environmental distances were more important than spatial distances. Here, it is worth emphasizing that the Mantel correlation between environmental and spatial distances was not strong ($r = 0.096$), implying that the effects of the environment and space could be easily distinguished. It was also noticeable that diatom trait-based beta diversity showed stronger correlation than that of macroinvertebrates to environmental distances (Table 8). Based on my results, I also argue that diatom trait-based beta diversity responds more strongly to environmental gradients in comparison to species-based beta diversity, whereas macroinvertebrate species-based beta diversity responds better to environmental gradients in comparison to trait-based beta diversity (Table 8).

One can argue that the set of macroinvertebrate traits used in the analyses may not be strongly sensitive to environmental conditions (e.g., Mueller *et al.* 2013), which, I believe, is unlikely because it has previously showed relatively strong responses to environmental

Table 8. The results of the Mantel test and partial Mantel tests used separately for different organismal groups (i.e., diatoms and macroinvertebrates), for different beta-diversity components (Overall, Turnover and Nestedness) and for different facets of diversity (i.e., species and traits). Significant *r* values are highlighted in bold (< 0.05). Legend: Env = environmental distances; Spatial = spatial distances)

Diatoms

	Spatial		Env		Spatial/Env		Env/Spatial	
Species-based beta diversity	Mantel *r*	*p*	Mantel *r*	*p*	Partial *r*	*p*	Partial *r*	*P*
Overall	**0.177**	0.001	**0.263**	0.001	**0.163**	0.001	**0.254**	0.001
Turnover	**0.147**	0.001	**0.222**	0.001	**0.124**	0.001	**0.208**	0.001
Nestedness	0.003	0.427	0.154	0.031	-0.002	0.512	0.154	0.042
Traits-based beta diversity	Mantel *r*	*p*	Mantel *r*	*p*	Partial *r*	*p*	Partial *r*	*P*
Overall$_t$	-0.056	0.853	**0.322**	0.002	-0.064	0.916	**0.324**	0.004
Turnover$_t$	-0.020	0.686	**0.244**	0.002	-0.030	0.76	**0.245**	0.002
Nestedness$_t$	-0.050	0.836	0.247	0.010	-0.053	0.879	0.247	0.015

Macroinvertebrates

	Spatial		Env		Spatial/Env		Env/Spatial	
Species-based beta diversity	Mantel *r*	*p*	Mantel *r*	*P*	Partial *r*	*p*	Partial *r*	*p*
Overall	0.098	0.018	**0.457**	0.001	0.071	0.062	**0.453**	0.001
Turnover	0.066	0.071	**0.435**	0.001	0.026	0.256	**0.431**	0.001
Nestedness	0.028	0.238	0.186	0.014	0.017	0.315	0.184	0.018
Trait-based beta diversity	Mantel *r*	*p*	Mantel *r*	*P*	Partial *r*	*p*	Partial *r*	*P*
Overall$_t$	0.113	0.021	**0.339**	0.003	0.075	0.08	**0.329**	0.002
Turnover$_t$	-0.021	0.690	**0.240**	0.001	-0.044	0.863	**0.243**	0.001
Nestedness$_t$	**0.162**	0.004	0.309	0.006	0.137	0.005	0.297	0.007

variation across northern streams (Tolonen *et al.* 2016; 2017). Thus, it more plausible that the diatom traits are more sensitive to environmental variation than the macroinvertebrate traits used in the analyses, although I tried to explore similar functional trait groups between diatoms and macroinvertebrates (e.g., body size and substratum association). Thus, diatoms may simply be more sensitive to environmental variation because of relatively strong relationships between their traits and environmental gradients (Soininen *et al.* 2016; Vilmi *et al.* 2016; Lindholm *et al.* 2018).

4.2.1 Factors underlying variation in the facets of beta diversity

Recently, a need to understand the phylogenetic and functional composition of community variation has been stressed (Swenson 2011, and references therein). Therefore, different mechanisms may affect different facets of diversity (i.e., traits and phylogeny) in an ecologically meaningful manner, elucidating the different forces operating in community assembly (e.g., Cardoso *et al.* 2014).

In Paper II, using Podani and Schmera's (2011) approach, I found that macroinvertebrate species-based beta diversity was driven by a slight difference between replacement and abundance-difference components (0.40 and 0.42, respectively), whereas trait-based beta diversity was driven by abundance-difference and phylogeny-based beta diversity mainly by replacement (Table 9). Comparing these results with the results presented above (i.e., facets of beta diversity varying similarly across environmental gradients), I demonstrated that partitioning macroinvertebrate species-, trait and phylogeny-based beta diversity into their components revealed previously hidden and complex patterns (i.e., different mechanisms driving different facets of beta diversity). For instance, species-based beta diversity was driven by the shared proportions of species replacement and richness/abundance-difference. Hence, this finding suggests simultaneous gain and loss of species because of environmental filtering (Leprieur *et al.* 2011), and the differences in species abundance between the streams are underlying the variation in species-based community composition of macroinvertebrates in this study area.

In contrast, phylogeny-based beta diversity patterns driven by the replacement component can be due to a strong replacement (i.e., gain or loss) of lineages from one community to another, without significant difference in the amount of phylogenetic information encompassed by the different communities (Silvertown *et al.* 2005). However, the trait-based beta diversity patterns dominated by richness/abundance-difference may reflect the environmental filtering process that favors certain traits over others along environmental gradients (Kluge & Kessler 2011), suggesting that only species with a certain combination of traits are able to exist in given habitats (Poff 1997). Thus, by partitioning different facets of beta diversity into their replacement and richness/abundance-difference components, I was able to show some differences operating in community assembly that could not be explained by the analyses of total biodiversity alone (Cardoso *et al.* 2014).

Table 9. Species-, trait- and phylogeny-based beta diversity indices (i.e., total, replacement and abundance-difference) based on Podani and Schmera's (2011) approach.

	Species	**Traits**	**Phylogeny**
Total	0.83	0.22	0.48
Replacement	0.40	0.09	0.30
Abundance-diff	0.42	0.12	0.18

In Paper III, through partitioning species-based and trait-based beta diversity using Baselga's (2010) approach, I found similar patterns for diatoms and macroinvertebrates. In general, species-based beta diversity was largely driven by the turnover component, whereas the contribution of the nestedness component was minor (Figure 6). However, the nestedness component was slightly more important than the turnover component in the trait-based analyses (Figure 6). Concurring with what has been previously found in freshwater ecosystems, changes in species composition between pairs of sites lead to the dominance of the turnover component in species-based beta diversity (Gianuca *et al.* 2017; Soininen *et al.* 2017). However, the nestedness component was slightly more important than the turnover component in the trait-based analyses, although the difference was minor. It is reasonable to infer that one possible reason for this result may be the effect of environmental filtering benefiting some specific traits over others, resulting in the low trait-diversity assemblages being subsets of the high trait-diversity assemblages (e.g., Si *et al.* 2016).

To conclude, it is possible that natural variations in stream habitat conditions should lead to the dominance of turnover on overall species-based beta diversity, whereas nestedness is driving overall trait-based beta diversity in this high-latitude study system. Thus, low levels of trait-based beta diversity found here may result from the fact that traits are shared between different species, and thus some species occurring in different streams sites are sharing the same traits and leading to a low functional complementarity between stream sites (Statzner *et al.* 2004; Villéger *et al.* 2013; Heino & Tolonen 2017).

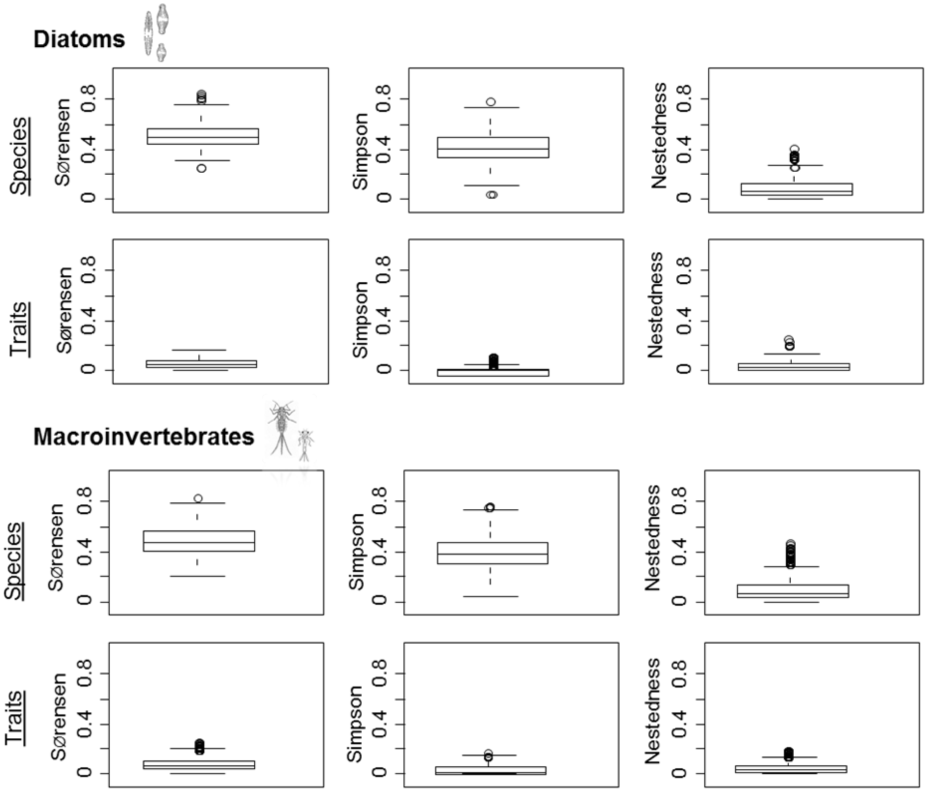

Figure 6. The boxplots of different components of average pairwise dissimilarities for each facet (i.e., species and traits) and each organism group (i.e., diatoms and macroinvertebrates). The bottom and the top of the boxplot are the 25th and 75th percentiles, and the band is the median.

5 Conclusions and implications

In summary, in this thesis, I clearly answered the study question (i) showing the importance of local environmental variables and spatial factors in explaining large-scale biodiversity patterns in stream ecosystems. Albeit of less importance, the findings also indicated that large-scale variables (i.e., catchment and climate) were also important, although less important than local environmental and spatial variables. The results in this thesis, along with those of others (Hawkins *et al.* 2000; Johnson *et al.* 2004; Sandin & Johnson 2004), suggest that local environmental variables were better correlates of changes in community structure than regional-scale variables. These findings imply that a combined understanding of both local and large-scale factors is needed to fully evaluate the mechanisms influencing the biodiversity and ecosystem processes of northern streams as well as to improve biomonitoring and conservation of running waters, in general.

Previous studies have suggested that accounting for traits and/or phylogenetic information among species could provide more accurate predictions of environmental and spatial drivers of biodiversity patterns. Overall, I answered the study question (ii) by presenting evidence that the trait-based approach may show different results between organism groups, and the inference of trait and phylogenetic biodiversity patterns may depend on many factors that are complex and difficult to define and forecast before analyzing the actual data. Hence, one cannot generalize that trait-based and phylogeny-based analyses are always superior to species-based analyses in terms of better detecting species and community responses to environmental changes. In the same vein, the present findings contribute to the small body of studies examining species-, trait- and phylogeny-based information at the same time. However, a multifaceted biodiversity approach could help to improve the evaluation, assessment and conservation of biodiversity through generating increased understanding of current patterns and environmental determinants of biodiversity variation in a changing world.

The exploration of different components of beta diversity increased the knowledge of stream biodiversity by adding trait-based and phylogenetic views into the study of biodiversity patterns and thus allowing one to understand the different mechanisms associated with different facets of the biological communities across northern streams. The different components of beta diversity may also be valuable assets in biodiversity assessment because different forces may operate in community assembly when using trait-based or phylogenetic approaches. Thus, species identities alone do not enable the detection of detailed patterns and mechanisms that require information on how species exploit and share environmental resources, and how species are phylogenetically related in biotic communities.

References

Allan. J.D. & M.M. Castillo (2007). *Stream Ecology: Structure and Function of Running Waters*. Springer, New York.

Allan, J.D., D.L. Erickson & J. Fay (1997). The influence of catchment land use on stream integrity across multiple spatial scales. *Freshwater Biology* 37: 149–161.

Anderson, M.J & P. Legendre(1999). Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs* 69: 1–24.

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J., Stegen, J.C. & N.G. Swenson (2011). Navigating the multiple meanings of biodiversity: a roadmap for the practicing ecologist. *Ecology Letters* 14: 19–28.

Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* 19: 134–143.

Baselga, A. (2012). The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography* 21: 1223–1232.

Beven K.J. & M.J. Kirkby (1979). A physically based, variable contributing area model of basin hydrology. *Hydrological Science Bulletins* 24:43–69.

Blackburn, T.M., Gaston, K.J. & R.D. Gregory (1997). Abundance-range size relationships in British birds: is unexplained variation a product of life history? *Ecography* 20: 466–474.

Burnham, K.P. & D.R. Anderson (2002). *Model selection and multi-model inference: a practical information-theoretic approach*. Colorado State University, Fort Collins.

Borcard, D. & P. Legendre (2002). All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling* 153: 51–68.

Borcard, D., Legendre, P., Avois-Jacquet, P. & H. Tuomisto (2004). Dissecting the spatial structure of ecological data at multiple scales. *Ecology* 85:1826–1832.

Brown, J.H. (1984). On the relationship between abundance and distribution of species. *American Naturalist* 124:255–279.

Cai, Y., Zhang, M., Xu, J. & J. Heino (2018). Geographical gradients in the biodiversity of Chinese freshwater molluscs: Implications for conservation. *Diversity and Distributions* 24: 485–496.

Cardoso, P., Rigal, F., Carvalho, J.C., Fortelius, M., Borges, P.A.V., Podani, J. & D. Schmera (2014). Partitioning taxon, phylogenetic and functional beta diversity into replacement and richness difference components. *Journal of Biogeography* 41: 749–761.

Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & S.W. Kembel (2009). The merging of community ecology and phylogenetic biology. *Ecology Letters* 12: 693–715.

Chapin III, F.S., Sturm, M., Serreze, M.C., McFadden, J.P., Key, J.R., Lloyd, A.H., McGuire, A.D., Rupp, T.S., Lynch, A.H., Schimel, J.P., Beringer, J., Chapman, W.L., Epstein, H.E., Euskirchen, E.S., Hinzman, L.D., Jia, G., Ping, C-L., Tape, K.D., Thompson, C.D.C., Walker, D.A. & J.M. Welker (2005). Role of Land-Surface Changes in Arctic Summer Warming. *Science* 310:657–60.

Clarke, K.R. & R.M. Warwick (1998). A taxonomic distinctness index and its statistical properties. *Journal of Applied Ecology* 35: 523–531.

Clark, R. & M. Ainsworth (1993). A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series* 92: 205–219.

Connell, J.H. (1978). Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310.

Corkum, L.D. (1989). Patterns of benthic invertebrate assemblages in rivers of northwestern North America. Freshwater Biology, 21, 191–205.

Corkum, L.D. (1992). Spatial distributional patterns of macroinvertebrates along rivers within and among biomes. *Hydrobiologia* 239:101–114.

Cowley, M.J.R., D.A. Thomas, D.A., Wilson, R.J., Léon-Cortés, J.L., Gutiérrez, D. & C.R. Bulman (2001). Density-distribution relationships in British butterflies: II. An assessment of mechanisms. *Journal of Animal Ecology* 70:426–441.

Crist, E.P. & R.C. Cicone (1984) A physically-based transformation of thematic mapper data—the TM tasseled cap. *IEEE Transactions on Geoscience and Remote Sensing* 3: 256–263.

Death, R.G. & M.K. Joy (2004). Invertebrate community structure in streams of the Manawatu-Wanganui region, New Zealand: the roles of catchment versus reach scale influences. *Freshwater Biology* 49: 982–997.

Devictor, V., Mouillot D., Meynard, C., Jiguet, F., Thuiller, W. & N. Mouquet (2010). Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecology Letters* 13: 1030–1040.

Dietz, A.J., Kuenzer, C. & S. Dech (2015). Global SnowPack: a new set of snow cover parameters for studying status and dynamics of the planetary snow cover extent. *Remote Sensing Letters* 11: 844–853.

Doledéc, S., Chessel, D. & C. Gimaret-Carpentier (2000). Niche separation in community analysis: a new method. *Ecology* 81:2914–2927.

Domisch, S., Amatulli, G. & Jetz W. (2015). Near-global freshwater-specific environmental variables for biodiversity analyses in 1 km resolution. *Scientific Data* 2,150073 doi:10.1038/sdata.2015.73.

Dudgeon, D., Arthington A.H., Gessner, M.O., Kawabata, Z., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A., Soto, D., Stiassny, M.L.J. & C.A. Sullivan (2006). Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* 81: 163–182.

Dray, S., Legendre, P. & P.R. Peres-Neto (2006). Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling* 196: 483–493.

Ferrari, S.L.P. & F. Cribari-Neto (2004). Beta Regression for modelling rates and proportions. *Journal of Applied Statistics* 31:799–815.

Frissell, C.A., Liss, W.L., Warren, C.E. & M.D. Hurley (1986). A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environmental Management* 10: 199–214.

Gaston, K.J. (1994). *Rarity*. Chapman & Hall, London.

Gaston, K.J. (2000) Global patterns in biodiversity. *Nature* 405: 220–227.

Gaston, K.J. & J.I. Spicer (2004). *Biodiversity: An Introduction*. Blackwell Publishing, Oxford.

Gaston, K.J. & T.M. Blackburn (1996). Range Size-Body Size Relationships: Evidence of Scale Dependence. *Oikos* 75: 479–485.

Gaston, K.J. & J. H. Lawton (1988). Patterns in the distribution and abundance of insect populations. *Nature* 331: 709–712.

Gaston, K.J. & J. H. Lawton (1990). Effects of scale and habitat on the relationship between regional distribution and local abundance. *Oikos* 58: 329–335.

Gaston, K.J., Blackburn, T.M., Greenwood, J.J.D., Gregory, R.D., Quinn, R.M. & J.H. Lawton (2000). Abundance-occupancy relationships. *Journal of Applied Ecology* 37:39–59.

Gerhold, P., Cahill, J.F., Winter, M., Bartish, I.V. & A. Prinzing (2015). Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Functional Ecology* 29: 600–614.

Gianuca, A.T., Declerck, S.A.J., Cadotte, M.W., Souffreau, C., De Bie, T. & L. De Meester (2017). Integrating trait and phylogenetic distances to assess scale-dependent community assembly processes. *Ecography* 40: 742–752.

Gianuca, A.T., Engelen, J., Brans, K. I., Hanashiro, F.T. T., Vanhamel, M., van den Berg, E. M., Souffreau, C. & L. De Meester (2018). Taxonomic, functional and phylogenetic metacommunity ecology of cladoceran zooplankton along urbanization gradients. *Ecography* 41: 183–194.

Graham, C.H. & P.V.A Fine (2008). Phylogenetic beta diversity: linking ecological and evolutionary processes across space in time. Ecology Letters 11: 1265–1277.

Gregory, R.D. & K.J. Gaston (2000). Explanations for commonness and rarity in British breeding birds: separating resource use and resource availability. *Oikos* 88:515–526.

Gower, J.C. (1971). A general coefficient of similarity and some of its properties. *Biometrics* 27: 857–874.

Hanski, I., Kouki, K. & A. Halkka (1993). Three explanations of the positive relationship between distribution and abundance of species. *In*: Ricklefs R.E. & D. Schluter (eds.): *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, pp 108–116.

Hawkins C.P., Norris, R.H., Gerritse, J., Hughes, R.M., Jackson, S.K., Johnson, R.K. & R.J. Stevenson (2000). Evaluation of landscape classifications for biological assessment of freshwater ecosystems: synthesis and recommendations. *Journal of North American Benthological Society* 19: 541–556.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guegan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & J.R.G. Turner (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84: 3105–3117.

Heino, J. (2011). A macroecological perspective of diversity patterns in the freshwater realm. *Freshwater Biology* 56: 1703–1722.

Heino, J. (2013). Environmental heterogeneity, dispersal mode and co-occurrence in stream macroinvertebrates. *Ecology and Evolution* 3:344–355.

Heino, J.& J. Soininen (2006). Regional occupancy in unicellular eukaryotes: a reflection of niche breadth, habitat availability or size related dispersal capacity? *Freshwater Biology* 5:672–685.

Heino, J., Virkkala, R. & H. Toivonen (2009). Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. *Biological Reviews* 84: 39–54.

Heino, J. & G. de Mendoza (2016). Predictability of stream insect distributions is dependent on niche position, but not on biological traits or taxonomic relatedness of species. *Ecography* 39:001–011.

Heino, J. & M. Gönroos (2014). Untangling the relationships among regional occupancy, species traits, and niche characteristics in stream invertebrates. *Ecology and Evolution* 4:1931–1942.

Heino, J., Grönroos, M., Ilmonen, J., Karhu, T., Niva, M. & L. Paasivirta (2013). Environmental heterogeneity and beta diversity of stream macroinvertebrate communities at intermediate spatial scales. *Freshwater Science* 3:142–154.

Heino, J., Muotka, T. & R. Paavola (2003). Determinants of macroinvertebrate in headwater diversity streams: Regional and local influences. *Journal of Animal Ecology* 72: 425–434.

Heino, J., Melo, A.S., Siqueira, T., Soininen, J., Valanko, S. & L.M. Bini (2015). Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshwater Biology* 60: 845–869.

Heino, J. & K.T. Tolonen (2017). Ecological drivers of multiple facets of beta diversity in a lentic macroinvertebrate metacommunity. *Limnology and Oceanography* 62: 2431–2444.

Heino, J. & K.T. Tolonen (2018). Ecological niche features override biological traits and taxonomic relatedness as predictors of occupancy and abundance in lake littoral macroinvertebrates. *Ecography* 41: 1–12, in press.

Heino, J., Mykrä, H., Kotanen, J. & T. Muotka (2007). Ecological Filters and Variability in Stream Macroinvertebrate Communities: Do Taxonomic and Functional Structure Follow the Same Path? *Ecography* 30: 217–230.

Hjort, J. & M. Luoto (2006). Modelling patterned ground distribution in Finnish Lapland: an integration of topographical, ground and remote sensing information. *Geografiska Annaler* 88:19–29.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & A. Jarvis (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978.

Hoeinghaus, D.J., Winemiller, K.O. & J.S. Birnbaum (2007). Local and regional determinants of stream fish assemblage structure: Inferences based on taxonomic versus functional groups. *Journal of Biogeography* 34: 324–338.

Hoffsten, P.O. (2004). Site-occupancy in relation to flight morphology in caddisflies. *Freshwater Biology* 49:810–817.

Holyoak, M., Leibold, M.A. & R.D. Holt (2005). *Metacommunities: spatial dynamics and ecological communities*. University of Chicago Press, Chicago.

Hynes, H.B.N. (1970). *The Ecology of Running Waters*. University of Toronto Press, Toronto.

Hynes, H.B.N. (1975). The stream and its valley. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 19:1–15.

Johnson, R.K., Goedkoop W. & L. Sandin (2004). Spatial scale and ecological relationships between the macroinvertebrate communities of stony habitats of streams and lakes. *Freshwater Biology* 49:1179–1194.

Jyrkänkallio-Mikkola, J., Meier, S., Heino, J., Laamanen, T., Pajunen, V., Tolonen, K.T., Tolkkinen, M. & J. Soininen (2017). Disentangling multi-scale environmental effects on stream microbial communities. *Journal of Biogeography* 44: 1512–1523.

Kampichler, C., van Turnhout, C.A.M., Devictor, V. & H.P. van der Jeugd (2012). Large-Scale Changes in Community Composition: Determining Land Use and Climate Change Signals. *PLoS ONE* 7(4): e35272.

Keddy, P.A. (1992). Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science* 3: 157–164.

Kelly. M.G., Cazaubon, A., Coring, E., Dell'Uom, A., Ector, L., Goldsmith, B., Guasch, H., Hürlimann, J. & A. Jarlman (1998). Recommendations for the routine sampling of diatoms for water quality assessments in Europe. *Journal of Applied Phycology* 10: 215–224.

Kluge, J. & M. Kessler (2011). Phylogenetic diversity, trait diversity and niches: species assembly of ferns along a tropical elevational gradient. *Journal of Biogeography* 38: 394–405.

Kärnä, O-M., Gönroos, M., Antikainen, J., Hjort, J., Ilmonen, J., Paasivirta, L. & J. Heino (2015). Inferring the effects of potential dispersal routes on the metacommunity structure of stream insects: as the crow flies, as the fish swims or as the fox runs? *Journal of Animal Ecology* 84: 1342–1353.

Legendre, P. (2014). Interpreting the replacement and richness difference components of beta diversity. *Global Ecology and Biogeography* 23: 1324–1334.

Legendre, P., Borcard, D. & P.R. Peres-Neto (2005). Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecological Monographs*, 75, 435–450.

Legendre, P. & L. Legendre (2012). *Numerical ecology*. Elsevier, Amsterdam.

Leibold, M.A. & J.M. Chase (2018). *Metacommunity Ecology*. Princeton University Press, USA.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D.,Shurin, J.B., Law, R., Tilman, D., Loreau, M. & A. Gonzalez (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters* 7: 601–613.

Leprieur, F., Tedesco, P.A., Hugueny, B., Beauchard, O., Dürr, H.H., Brosse, S. & T. Oberdorff (2011). Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. *Ecology Letters* 14: 325–334.

Lindholm, M., Grönroos, M., Hjort, J., Karjalainen, S-M., Tokola, L. & J. Heino (2018). Different species trait groups of stream diatoms show divergent responses to spatial and environmental factors in a subarctic drainage basin. *Hydrobiology* 816: 213–230.

Logue, J.B., Mouquet, N., Peter, H. & H. Hillebrand (2011). Empirical approaches to metacommunities: a review and comparison with theory. *Trends in Ecology & Evolution* 26: 482–491.

Losos, J.B. (2008). Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters* 11: 995–1003.

Malmqvist, B. & S. Rundle (2002). Threats to the running water ecosystems of the world. *Environmental Conservation* 29, 134–153.

Mantel, N. (1967). The detection of disease clustering and a generalized regression approach. *Cancer Research* 27: 209–220.

McGill, B.J., Enquist, B.J., Weiher, E. & M. Westoby (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* 21: 178–185.

Merritt, R.W. & K.W. Cummins (1996). *An introduction to the aquatic insects of North America*. Kendall/ Hunt Publishing Company, Iowa.

Merritt, R., Cummins, K. & M. Berg (2008). *An introduction to the aquatic insects of North America*. Dubuque, Iowa: Kendall/ Hunt Publishing Company.

Meynard, C.N., Devictor, V., Mouillot, D., Thuiller, W., Jiguet, F. & N, Mouquet (2011). Beyond taxonomic diversity patterns: How do α, β and γ components of bird functional and phylogenetic diversity respond to environmental gradients across France? *Global Ecology and Biogeography* 20: 893–903.

Moog, O. (2002). *Fauna Aquatica Austriaca – a comprehensive species inventory of Austrian aquatic organisms with ecological notes*. Bundesministerium für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft, Vienna.

Mueller, M., Pander, J. & J. Geist (2013). Taxonomic sufficiency in freshwater ecosystems: effects of taxonomic resolution, functional traits, and data transformation. *Freshwater Science* 32: 762–778.

Mustonen, K-R., Mykrä, H., Martilla, H., Sarremejane, R., Veijalainen, N., Sippel, K., Muotka, T. & C.P. Hawkins (2018). Thermal and hydrologic responses to climate change predict marked alterations in boreal stream invertebrate assemblages. *Global Change Biology*, in press.

Mykrä, H., Heino, J. & T. Muotka (2004). Variability of lotic macroinvertebrate assemblages and stream habitat characteristics across hierarchical landscape classifications. *Environmental Management* 34: 341–352.

Mykrä, H., Heino, J. & T. Muotka (2007). Scale-related patterns in the spatial and environmental components of stream macroinvertebrate assemblage variation. *Global Ecology and Biogeography* 16: 149–159.

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. & R.M. Woodfin (1994). Declining biodiversity can alter the performance of ecosystems. *Nature* 368: 734–737.

National Board of Waters and the Environment (1981). Vesihallinnonanalyysimenetelmät. *Publications of National Board Waters of Finland Report* 213:1–136

National Land Survey of Finland (2010a). Basic map 1: 20 000. PaITuli spatial data service. In: https://research.csc.fi/paituli.

National Land Survey of Finland (2010b). Topographic database 1: 10 000. PaITuli spatial data service. In: https://research.csc.fi/paituli.

National Land Survey of Finland (2000c). Digital elevation model. PaITuli spatial data service. In: https://research.csc.fi/paituli.

Pavoine, S. & M.B. Bonsall (2010). Measuring biodiversity to explain community assembly: A unified approach. *Biological Reviews* 86: 792–812.

Pajunen, V., Luoto, M. & J. Soininen (2016). Climate is an important driver for stream diatom distributions. *Global Ecology and Biogeography* 25: 198–206.

Passy, S.I. (2007). Differential cell size optimization strategies produce distinct diatom richness–body size relationships in stream benthos and plankton. *Journal of Ecology* 95:745–754

Passy, S.I. (2012). A hierarchical theory of macroecology. *Ecology Letters* 15:923–934.

Peres-Neto, P. R., Legendre, P., Dray, S. & D. Borcard (2006). Variation partitioning of species data matrices: Estimation and comparison of fractions. *Ecology* 87: 2614–2625.

Podani, J. & D. Schmera (2011). A new conceptual and methodological framework for exploring and explaining pattern in presence–absence data. *Oikos* 120: 1625–1638.

Poff, N.L. (1997). Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* 16:391–409.

R Core Team (2017) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. Available at: http://www.R-project.org/. Accessed October 2017.

Richards, C., Haro, R.J., Johnson, L.B. & G.E. Host (1997). Catchment and reach-scale properties as indicators of macroinvertebrate species traits. *Freshwater Biology* 37: 219–230.

Rimet, F. & A. Bouchez (2012). Life-forms, cell-sizes and ecological guilds of diatoms in European rivers. *Knowledge and Management of Aquatic Ecosystems* 406:1–14.

Round, F.E., Crawford, R.M. & D.G. Mann (1990). *The diatoms, Biology, morphology of the genera*. Cambridge University Press, Cambridge and New York.

Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.

Sala, O.E., Chapin III, F. S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F.,. Jackson, R.B, Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L,Sykes, M.T., Walker, B.H., Walker, M. & D. H. Wall (2000). Biodiversity: global biodiversity scenarios for the year 2100. *Science* 287: 1770–1774.

Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V. & G.Woolmer (2002). The Human Footprint and the Last of the Wild: The human footprint is a global map of human influence on the land surface, which suggests that human beings are stewards of nature, whether we like it or not. *BioScience* 52: 891–904.

Sandin, L. (2003) Benthic macroinvertebrates in Swedish streams: community structure, taxon richness, and environmental relations. *Ecography* 26: 269–282.

Sandin, L. & R.K. Johnson (2004). Local, landscape and regional factors structuring benthic macroinvertebrate assemblages in Swedish streams. *Landscape Ecology* 19:501–514

Sankaran, M. & S.J. McNaughton (1999). Determinants of biodiversity regulate compositional stability of communities. *Nature* 401: 691–693.

Slatyer, R.A., Hirst, M. & J.S. Sexton (2013). Niche breadth predicts geographical range size: a general ecological pattern. *Ecology Letters* 16:1104–1114.

Swenson, N.G., Anglada-Cordero, P. & J.A. Barone (2011). Deterministic tropical tree community turnover: evidence from patterns of functional beta diversity along an elevational gradient. *Proceedings of the Royal Society* B 278: 877–884.

SFS-EN 14407 (2005) *Water quality. Guidance standard for the identification, enumeration and interpretation of benthic diatom samples from running waters*. Suomen standardisoimisliitto SFS ry, Helsinki.

Si, X., Baselga, A., Leprieur, F., Song, X. & P. Ding (2016). Selective extinction drives taxonomic and functional alpha and beta diversities in island bird assemblages. *Journal of Animal Ecology* 85: 409–418.

Siqueira, T., Bini, L.M., Cianciaruso, M.V., Roque, F.O. & S. Trivinho-Strixino (2009). The role of niche measures in explaining the abundance-distribution relationship in tropical lotic chironomids. *Hydrobiologia* 636:163–172.

Silvertown, J., Ortega, J.F. & M. Carine (2005). The monophyly of island radiations: an evaluation of niche pre-emption and some alternative explanations. *Journal of Ecology* 93: 653–657.

Soininen, J., Heino, J. & J. Wang (2017). A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. *Global Ecology and Biogeography* 27: 96–109.

Soininen, J., Bartels, P., Heino, J., Luoto, M. & H. Hillebrand (2015). Toward more integrated ecosystem research in aquatic and terrestrial environments. *Bioscience* 216:1–9.

Soininen, J., Jamoneau, A., Roseberry, J. & S.I. Passy (2016). Global patterns and drivers of species and trait composition in diatoms. *Global Ecology and Biogeography* 25: 940–950.

Statzner, B., Dolédec, S. & B. Hugueny (2004). Biological trait composition of European stream invertebrate communities: assessing the effects of various trait filter types. *Ecography* 27: 470–488.

Stendera, S., Adrian, R. & N. Bonada (2012). Drivers and stressors of freshwater biodiversity patterns across different ecosystems and scales: a review. *Hydrobiologia* 696: 1–28.

Strayer, D.L & D. Dudgeon (2010). Freshwater biodiversity conservation: recent progress and future challenges. *Journal of the North American Benthological Society* 29: 344–358.

Tachet, H., Richoux, P., Bourneau, M. & P. Usseglio-Polatera (2010). *Freshwater Invertebrates, Systematics, Biology, Ecology*. CNRS Editions, Paris.

Tales, E., Keith, P. & T. Oberdorff (2004). Density-range size relationship in French riverine fishes. *Oecologia* 138:360–370.

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

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

Tonn, W.M. (1990). Climate change and fish communities: a conceptual model approach. *Transactions of the American Fisheries Society* 119: 337–352.

Tonkin, J.D., Arimoro, F.O. & P. Haase (2016). Exploring stream communities in a tropical biodiversity hotspot: biodiversity, regional occupancy, niche characteristics and environmental correlates. *Biodiversity Conservation* 25:975–993.

Townsend, C.R., Dolédec, S., Norris, R., Peacock, K. & C. Arbuckle (2003). The influence of scale and geography on the relationships between stream community composition and landscape variables: description and prediction. *Freshwater Biology* 48: 768–785.

Tilman D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & E. Siemann (1997). The Influence of Functional Diversity and Composition on Ecosystem Processes. *Nature* 277:1300–1302.

Tuomisto H., Ruokolainen K. & Yli-Halla M (2003). Dispersal, environment, and floristic variation of western Amazonian forests. *Science* 299: 241–244.

Tuanmu, M-N. & W. Jetz (2014). A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. *Global Ecology and Biogeography* 23: 1031–1045.

Verberk, W., van Noordwijk, C.G.E. & A.G. Hildrew (2013). Delivering on a promise: integrating species traits to transform descriptive community ecology into a predictive science. *Freshwater Science* 32: 531–547.

Villéger S, Manson, N.W.H & D. Mouillot (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89: 2290–2301.

Villéger, S., Grenouillet, G. & S. Brosse (2013). Decomposing functional b-diversity reveals that low functional b-diversity is driven by low functional turnover in European fish assemblages. *Global Ecology and Biogeography* 22: 671–681.

Venier, L.A. & L. Fahrig (1996). Habitat availability causes the species distribution-abundance relationship. *Oikos* 76:564–570

Vinson M.R. & C.P. Hawkins (1998). Biodiversity of stream insects: variation at local, basin, and regional spatial scales. *Annual Review of Entomology* 43:271–293.

Vilmi, A., Karjalainen, S-M., Hellsten, S. & J. Heino (2016). Bioassessment in a metacommunity context: are diatom communities structured solely by species sorting? *Ecological Indicators* 62: 86–94.

Zeileis A, Kleiber, C. & S. Jackman (2008). Regression models for count data in R. *Journal of Statistical Software* 27:1–25.

Young, H.S., McCauley, D.J., Galetti, M. & R. Dirzo (2016). Patterns, Causes, and Consequences of Anthropocene Defaunation. *Annual Review of Ecology, Evolution, and Systematics* 47:333–58.

Webb, C.O., Ackerly, D.D., McPeek, M.A. & M.J. Donoghue (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics* 33: 475–505.

Weinstein, B.G., Tinoco, B., Parra, J.L., Brown, L.M., McGuire, J.A., Stiles, F.G. & C.H. Graha (2014). Taxonomic, phylogenetic, and trait Beta diversity in South American hummingbirds. *American Naturalist* 184: 211–224.

Wentworth, C.K. (1992). A scale of grade and class terms for clastic sediments. *Journal of Geology* 30:377–392.

Wilson E.O. (1988). The current state of biological diversity. *Biodiversity* 521: 3–18.

Winter, M., Devictor, V. & O. Schweiger (2013). Phylogenetic diversity and nature conservation: Where are we? *Trends in Ecology & Evolution* 28: 199–204.

Whittaker, R.H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30: 280–338.

Wrona, F.J, Reist, J.D, Amundsen, A., Chambers, P.A., Christoffersen, K., Culp, J.M., di Cenzo, P.D., Forsström, L., Hammar, J., Heino, J., Heikkinen, R.K., Kahilainen, K.K., Lesack, L., Lehtonen, H.,Lento,J. Luoto, M., P. Marsh, Marcogliese, D.J., Moquin, P.A., Mustonen, T., Prowse, T.D., Power, M., Rautio, M., Swanson, H., Thompson, M., Toivonen, H., Vasiliev, V., Virkkala, R. & S. Zavalko (2013). Freshwater ecosystems. *In* Meltofte H. *Arctic Biodiversity Assessment. Status and Trends in Arctic Biodiversity*. Conservation of Arctic Flora and Fauna, Arctic Council, Iceland, pp 335–377.

Appendices

Table A1. Literature of respective species traits used in Paper II. HTG = habit trait groups; FFG = functional feeding groups; B.M = body dry mass (mg). Abbreviations: bur (burrowers), cra (crawlers), spw (sprawlers), sses (semi-sessile), swd (swimmers-divers), gat (gatherers), pre (predators), fil (filters), scr (scrapers), shr (shredders), pre (predators), pier (piercers).

Species	**HTG**	**B.M.**	**FFG**
Rhynchelmis tetratheca	bur [a]	8.36 [b, **c**]	gat [a]
Spirosperma ferox	bur [a]	4.86 [b, **c**, **d**]	gat [a]
Stylaria lacustris	cra [a]	0.31 [b, **c**]	gat [a]
Dina lineata	spw [a]	90.52 [b, **e**]	pre [a]
Erpobdella octoculata	spw [a]	231.54 [b, **e**]	pre [a]
Erpobdella testacea	spw [a]	103.57 [b, **e**]	pre [a]
Glossiphonia complanata	spw [a]	48.01 [b, **d**, **e**]	pre [a]
Haemopis sanguisuga	spw [a]	699.17 [b, **e**]	pre [a]
Helobdella stagnalis	spw [a]	4.63 [b, **d**, **e**]	pre [a]
Pisidium spp.	sses [a]	18.44 [**f**, g]	fil [a]
Pseudanodonta complanata	sses [a]	26130.40 [**f**, h]	fil [a]
Sphaerium spp.	sses [a]	584.55 [**f**, g]	fil [a]
Ancylus fluviatilis	cra [a, l]	9.92 [j, **k**]	scr [a, l]
Bathyomphalus contortus	cra [a]	6.52 [**d**, g, **k**]	scr [a]
Galba truncatula	cra [a, l]	4.25 [i, **m**]	scr [a, l]
Gyraulus albus	cra [a]	12.75 [**d**, g, **k**]	scr [a]
Myxas glutinosa	cra [a]	126.53 [**f**, g]	scr [a]
Radix auricularia	cra [a]	102.80 [i, **m**]	scr [a]
Radix peregra	cra [a]	17.98 [**d**, **m**, n]	scr [a]
Segmentina complanata	cra [a]	4.02 [**f**, i]	scr [a]
Valvata pulchella	cra [a]	6.52 [**d**, **f**, g]	gat [a]
Asellus aquaticus	cra [l]	22.61 [**d**, **m**, n]	shr [l]
Gammarus lacustris	swd [a]	31.37 [j, **k**]	shr [l,o]
Gammarus pulex	swd [a]	102.91 [j, **k**]	shr [l, o]
Amphinemura borealis	cra [l]	0.68 [**k**, p]	gat [q]
Capnopsis schilleri	cra [q]	0.35 [**d**, **k**, r]	shr [l, q]
Diura bicaudata	cra [q]	6.33 [**d**, **k**, r]	pre [l, q]
Isoperla difformis	cra [l]	5.10 [**k**, p]	pre [a]

Isoperla obscura	cra [l]	4.04 [**k**, p]	pre [a]
Leuctra fusca	cra [a, l]	1.10 [**k**, p]	gat [a]
Leuctra nigra	bur [a, l]	0.83 [**k**, p]	gat [a]
Leuctra hippopus	cra [a, l]	1.10 [**k**, p]	gat [a]
Nemoura avicularis	cra [l, q]	1.02 [**k**, p]	gat [l, q]
Nemoura cinerea	cra [l, q]	0.68 [**k**, p]	gat [l, q]
Nemoura sp.	cra [l, q]	0.84 [**k**, p]	gat [l, q]
Nemurella pictetii	cra [l]	1.02 [**k**, p]	shr [l]
Protonemura meyeri	cra [l]	3.68 [**k**, p]	shr [l]
Siphonoperla burmaisteri	cra [l]	0.66 [**k**, p]	pre [a]
Taeniopteryx nebulosa	cra [a]	5.98 [**k**, p]	gat [a]
Baetis digitatus	swd [q]	4.31 [s, **t**]	scr [l, q]
Baetis fuscatus	swd [q]	1.71 [s, **t**]	scr [l, q]
Baetis niger	swd [q]	2.80 [s, **t**]	scr [l, q]
Baetis rhodani	swd [q]	2.18 [s, **t**]	scr [l, q]
Baetis subalpinus	swd [q]	1.22 [s, **t**]	scr [l, q]
Baetis vernus	swd [q]	2.18 [s, **t**]	scr [l, q]
Caenis horaria	cra [q]	0.68 [**d**, s, **u**]	gat [q]
Caenis luctuosa	cra [q]	0.74 [s, **u**]	gat [q]
Centroptilum luteolum	swd [l, q]	4.32 [**d**, **m**, s]	scr [l, q]
Cloeon dipterum	swd [l, q]	11.22 [**d**, **m**, s]	gat [l, q]
Ephemera vulgata	bur [l, q]	27.94 [**d**, **k**, s]	shr [l, q]
Haprophlebia lauta	cra [a]	1.00 [**m**, s]	gat [a]
Heptagenia dalecarlica	cra [l, q]	15.30 [**d**, **k**, s]	scr [l, q]
Kageronia fuscogrisea	cra [l]	15.30 [**k**, s]	scr [l]
Leptophlebia marginata	cra [l, q]	5.69 [**d**, **m**, s]	gat [q]
Agapetus ochripes	cra [a]	1.20 [**t**, v]	scr [a]
Athripsodes cinereus	cra [l, q]	5.86 [**d**, **m**, w]	scr [l, q]
Beraeodes minutus	cra [a]	1.93 [**u**, w]	scr [a]
Brachycentrus subnubilus	sses [q]	5.46 [**t**, w]	fil [a]
Ceraclea annulicornis	cra [l, q]	1.51 [**d**, **t**, w]	shr [l, q]
Ceraclea excisa	cra [l, q]	3.95 [**t**, w]	pre [l, q]
Ceraclea nigronervosa	cra [l, q]	7.52 [**t**, w]	pre [l, q]
Ceraclea spp.	cra [l, q]	4.37 [**t**, w]	shr [l, q]
Ceratopsyche silfvenii	sses [q]	15.35 [**t**]	fil [q]
Chaetopteryx villosa	cra [l, q]	16.66 [**d**, **k**, w]	shr [l, q]

Cheumatopsyche lepida	sses [q]	3.99 [**t**, v]	fil [q]
Cyrnys trimaculatus	sses [l]	4.17 [**d, u, v**]	pre [l]
Glyphotaelius pellucidus	cra [a, l]	48.47 [**k**, w]	shr [a, l]
Goera pilosa	cra [l, q]	12.19 [**d, k**, w]	scr [l, q]
Hydatophylax infumatus	cra [l, q]	51.89 [**k**, w]	shr [a, l, q]
Hydropsyche angustipennis	sses [l, q]	19.95 [**t**, v]	fil [l, q]
Hydropsyche pellucidula	sses [l, q]	19.95 [**t**, v]	fil [l, q]
Hydropsyche saxonica	sses [l, q]	25.37 [**t**, v]	fil [l, q]
Hydropsyche siltalai	sses [l, q]	19.95 [**t**, v]	fil [l, q]
Hydroptila sp.	cra [l, q]	0.20 [**d**, j, **m**]	pier [q]
Ithytrichia sp.	cra [l]	0.20 [**m**, v]	scr [a]
Lepidostoma hirtum	cra [l, q]	3.52 [**t**, w]	shr [l, q]
Limnephilus extricatus	cra [l, q]	9.70 [**d, k**, w]	shr [l, q]
Limnephilus rhombicus	cra [l, q]	45.20 [**d, k**, w]	shr [l, q]
Lype reducta	sses [l, q]	3.83 [**t**, v]	scr [a, l, q]
Lype phaeopa	sses [l, q]	1.53 [**t**, v]	scr [a, l, q]
Micrasema gelidum	cra [l]	2.25 [**t**, w]	shr [l]
Micropterna lateralis	cra [a]	24.15 [**k**, w]	shr [a]
Micropterna sequax	cra [a]	31.04 [**k**, w]	shr [a]
Molannodes tinctus	cra [l, q]	7.58 [**d, k**, w]	scr [l, q]
Mystacides azurea	cra [l, q]	2.31 [**d, u**, w]	shr [l, q]
Nemotaulius punctatolineatus	cra [l, q]	127.01 [**d, k**, w]	shr [l, q]
Neureclipsis bimaculata	sses [l, q]	17.68 [**u**, v]	pre [a]
Notidobia ciliaris	cra [l]	12.36 [**k**, w]	shr [l]
Oecetis sp.	cra [l, q]	9.22 [**t**, w]	pre [q]
Oligostomis reticulata	cra [l]	30.05 [**t**, w]	shr [l]
Oxyethira sp.	sses [l, q]	0.20 [**d**, j, **m**]	pier [l, q]
Philopotamus montanus	sses [l]	10.45 [**t**, v]	fil [a, l]
Plectrocnemia conspersa	sses [l]	33.33 [**u**, v]	pre [a, l]
Polycentropus flavomaculatus	sses [a, l]	7.03 [**d, u**, v]	pre [a, l]
Polycentropus irroratus	sses [a, l]	7.03 [**u**, v]	pre [a, l]
Potamophylax latipennis	cra [l]	33.59 [**d, k**, w]	shr [l]
Psychomyia pusilla	sses [l]	1.43 [**t**, v]	scr [a, l]
Rhyacophila nubila	cra [a]	17.31 [**t**, v]	pre [a]
Sericostoma personatum	cra [a]	7.86 [**k**, w]	shr [a]
Silo pallipes	cra [l]	2.13 [**k**, w]	scr [a]

Tinodes waeneri	sses [q]	1.77 [t, v]	scr [q]
Sialis lutaria	cra [q]	27.58 [d, j, u]	pre [q]
Sisyra sp.	cra [l, q]	2.13	pre [q]
Callicorixa wollastoni	swd [a]	5.22 [j, u]	gat [a]
Glaenocorisa propinqua	swd [a]	8.04 [u, x]	pre [a]
Paracorixa concinna	swd [a]	6.22 [u, x]	gat[a]
Agapus elongatus	swd [q]	11.31 [u, y]	pre [q]
Agapus guttatus	swd [q]	16.24 [u, y]	pre [q]
Gyrinus gyrinus	swd [l, q]	9.05 [j, u]	pre [q]
Elmis aenea	cra [l, q]	0.77 [d, u, z]	scr [l, q]
Elodes sp.	cra [a]	4.89 [u, aa]	shr [a]
Helophorus sp.	cra [a]	1.76 [u, bb]	shr [a]
Helophorus arvernicus	cra [a]	1.80 [u, bb]	shr [a]
Helophorus brevipalpis	cra [a]	1.44 [u, bb]	shr [a]
Helophorus tuberculatus	cra [a]	2.06 [u, bb]	shr [a]
Hydraena britteni	cra [q]	0.73 [u, bb]	scr [q]
Hydraena.gracilis	cra [q]	0.85 [u, bb]	scr [q]
Hydraena.riparia	cra [q]	0.85 [u, bb]	scr [q]
Hydraena pulchella	cra [q]	0.40 [u, bb]	scr [q]
Ilybius fuliginosus	swd [l, q]	27.09 [u, y]	pre [q]
Ilybius guttiger quadriguttatus	swd [l, q]	25.47 [u, y]	pre [q]
Limnebius spp.	cra [a]	0.69 [u, bb]	scr [a]
Limnius volckmari	cra [l]	1.68 [u, cc]	scr [a, l]
Oulimnius tuberculatus	cra [l, q]	0.55 [d, u, z]	scr [l, q]
Orectochilus villosus	swd [a]	9.05 [u, dd]	pre [a]
Platambus maculatus	swd [a]	14.03 [u, y]	pre [a]
Scarodytes halensis	swd [a]	3.23 [u, y]	pre [a]
Atherix ibis	spw [l]	8.24 [j, k]	pre [a]
Limnophora riparia	spw [q]	6.59 [j, t]	pre [q]
Pericoma sp.	spw [l]	0.85 [j, u]	gat [q]
Ptychoptera lacustris	bur [q]	16.25 [j, u]	gat [a, q]
Ptychoptera paludosa	bur [q]	16.25 [j, u]	gat [a, q]
Tipula yamatotipula	bur [l, q]	64.25 [d, j, k]	shr [l, q]

a. Schmidt-Kloiber, A. & Hering, D. (2015). www.freshwaterecology.info – an online tool that unifies, standardises and codifies more than 20 000 European freshwater organisms and their ecological preferences. Ecological Indicators, 53, 271-282.

b. Timm, T. (1999). A guide to the Estonian Annelida. Estonian Academy Publishers, Tallinn.

c. Miserendino, M.L. (2001). Length-mass relationships for macroinvertebrates in freshwater environments of Patagonia. Ecologia Austral, 11, 3-8.

d. Tolonen, K.T., Vilmi A., Karjalainen, S.M., Hellsten, S., Sutela T. & Heino, J. (2017). Ignoring spatial effects results in inadequate models for variation in littoral macroinvertebrate diversity. Oikos, 126, 852-862.

e. Edwards, F.K., Lauridsen, R.B., Armand, L., Vincent H.M. & Jones, J.I. (2009). The relationships between length, mass and preservation time for three species of freshwater leeches (Hirudinea). Fundamental and Applied Limnology, 173/4, 321-327.

f. Stoffels, R.J., Karbe, S. and Paterson, R.A. (2003). Length-mass models for some common New Zealand littoral-benthic macroinvertebrates, with a note on within-taxon variability in parameter values among published models. New Zealand Journal of Marine and Freshwater Research, 37, 449-460.

g. www.habitas.org.uk/molluscireland/

h. Glöer, P. & Meier-Brook, C. (1994) Süsswassermollusken. Deutcher Jugendbund für Naturbeobachtung, Hamburg.

i. Glöer, P. (2002) Süsswassermollusken Nord- und Mitteleuropas. Conch Book, Hackenheim, Germany.

j. Olsen, L-H., Sunesenand J. & Pedersen, B.V. (1999). Små dyr i sø og å. G. E. C. Gads Forlag.

k. Meyer, E. (1989). The relationship between body length parameters and dry mass in running water invertebrates. Archiv für Hydrobiologie, 117, 191-203.

l. Tachet, H., Richoux, B., Bournaud, M. and Usseglio-Polatera, P. 2010. Invertébrés d'eau douce. – CNRS editions.

m. Baumgärtner, D. & Rothaupt, K. O. (2003). Predictive length-dry mass regressions for freshwater invertebrates in a pre-alpine lake littoral. International Review of Hydrobiology, 88, 453-463.

n. Martin, A.J., Seaby, R.M.H. & Young, J.O. (1994). Does body size difference in the leeches *Glossiphonia complanate* (L.) and *Helobdella stagnalis* (L.) contribute to co-existence? Hydrobiologia, 273, 67-75.

o. Kelly, D.W., Dick, J.T.A. & Montgomery, W.A. (2002). The functional role of *Gammarus* (Crustacea: Amphipoda): shredders, predators or both? Hydrobiologia, 485, 199-203.

p. Lillehammer, A. (1988). Stoneflies (Plecoptera) of Fennoscandia and Denmark. Fauna Entomologica Scandinavica, 21, 1-165.

q. Merritt, R.W. & Cummins, K.W. (1995). An introduction to the aquatic insects of North America. Kendall Hunt Publishing Company, 3rd edition.

r. Zwick, P. (2004). A key to the West Palaearctic genera of stoneflies (Plecoptera) in the larval stage. Limnologica, 34, 315-348.

s. Engblom, E. (1996). Ephemeroptera, mayflies. – In: Nilsson, A. (ed.), Aquatic insects of North Europe. A taxonomic handbook. Volume 1. Apollo Books, Steenstrup, pp. 13-53.

t. Benke, A.C., Huryn, A.D., Smock, L.A. & Wallace, J.B. (1999). Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. – J. N. Am. Benthol. Soc. 18: 308-343.

u. Smock, L.A. (1980). Relationships between body size and biomass of aquatic insects. – Freshwater Biol. 10: 375-383.

v. Lepneva, S.G. (1970). Fauna of the U.S.S.R. Trichoptera, Volume II, No. 1. Larvae and pupae of Annulipalpia. – Keter Press, Jerusalem.

w. Lepneva, S.G. (1971). Fauna of the U.S.S.R. Trichoptera, Volume II, No. 2. Larvae and pupae of Integripalpia. – Keter Press, Jerusalem.

x. Savage, A.A. (1989). Adults of the British aquatic Hemiptera Heteroptera. Freshwater Biological Association.

y. Nilsson, A.N. & Holmen, M. (1995). The aquatic Adephaga (Coleoptera) of Fennoscandia and Denmark, Volume II. Dytiscidae. Fauna Entomologica Scandinavica 32: 1-192.

z. Engblom, E., Lingdell, P-E. & Nilsson, A. (1990). Sveriges bäckbaggar (Coleoptera, Elmidae) - artbestmning, utbredning, habitat val och värde som miljöindicatorer. Entomol. Tidskr. 111: 105-121.

aa. Klausnitzer, B. (1996). Coleoptera Scirtidae, Marsh Beetles. In Nilsson, A. (ed.). Aquatic Insects of North Europe, A Taxonomic Handbook, Volume 1. Apollo Books Aps., Stenstrup, Denmark. pp. 203-208.

bb. Hansen, M. (1987). The Hydrophiloidea (Coleoptera) of Fennoscandia and Denmark. Fauna Entomologica Scandinavica 18: 1-254.

cc. Nilsson, A.N. (1996). Coleoptera Dryopoidea, Riffle Beetles. In Nilsson, A. (ed.). Aquatic Insects of North Europe, A Taxonomic Handbook, Volume 1. Apollo Books Aps., Stenstrup, Denmark. pp. 195-202.

dd. Nilsson, A.N. (1996). Coleoptera Gyrinidae, Whirligig Beetles. In Nilsson, A. (ed.). Aquatic Insects of North Europe, A Taxonomic Handbook, Volume 1. Apollo Books Aps., Stenstrup, Denmark. pp. 123-129.

ee. Chvála, M. & Ježek, J. (1997). Diptera Tabanidae, horse flies. In: Nilsson, A. (ed.), Aquatic insects of North Europe. A taxonomic handbook. Volume 2. Odonata - Diptera. Apollo Books, Steenstrup, pp. 295-309.