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Geography meets ecology: developing proxies to understand variations of stream biodiversity

Olli-Matti Kärnä

ACADEMIC DISSERTATION

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Abstract

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Keywords: stream ecosystems, biodiversity, high-latitude regions, Arctic, boreal, environmental heterogeneity, geodiversity, catchment features, environmental variables, dispersal, physical distance measures, cost distance, GIS, statistical modelling, macroinvertebrates, diatoms, bacteria

Freshwater ecosystems form unique environments with high biodiversity. However, freshwater biodiversity is increasingly threatened because of human activities, such as the ongoing climate change and land use alterations. To prevent the further decline in biodiversity, it is crucial to understand the factors that affect and modify biotic communities. For freshwater systems, information on the patterns and underlying mechanisms of biodiversity is still inadequate, which may complicate any conservation and management efforts.

Ecologists must often rely on different proxy variables in studies examining biodiversity-environment and biodiversity-space relationships due to difficulties in obtaining direct measures of numerous factors across large regions. Biodiversity patterns in streams have been shown to be structured by direct physical properties of the local habitat and by proxy features on the catchment and regional scales, but one problem has been related to only moderate explanatory power using such ‘traditional environmental variables’. The goal of this thesis was to study biodiversity patterns in northern streams by introducing the use of geographical proxy variables of environmental features (i.e. geodiversity) and dispersal (i.e. different geographical distances). More precisely, the aims were to 1) examine the effects of local environmental and geographical variables on stream biodiversity; 2) investigate how environmental and spatial distance types between stream sites affect the variation of stream insect communities; 3) compare the relative roles of habitat-scale geodiversity measures and traditional in-stream variables in explaining stream macroinvertebrate biodiversity and; 4) examine how catchment-scale geodiversity contributes to the variation in stream biodiversity in a boreal region.

According to the results, traditional environmental variables contributed most to the variation in stream biodiversity. However, geographical proxies showed a clear usefulness in understanding biodiversity-environment relationships. It was demonstrated that physical distance measures describing dispersal routes also showed a notable role affecting community compositional variation between stream sites, implying that interesting patterns are shaped by dispersal processes in stream environments.

Moreover, the results indicated that the geodiversity on local and catchment scales correlated with stream biodiversity, which underlines the value of geodiversity as a proxy to explain biodiversity variations in the freshwater realm. If further developed, similar proxy variables to those presented in this thesis could offer complementary insights to help explain the structuring of biodiversity patterns in streams. Finally, conservation efforts may also benefit from the identified cost-efficient proxy variables helping to understand the nuances in biodiversity variation.

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List of original publications

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

(I) Kärnä, O.-M., Grönroos, M., Antikainen, H., Hjort, J., Ilmonen, J., Paasivirta, L. & Heino, J. (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.

(II) Kärnä, O.-M., Heino, J., Grönroos, M. & Hjort, J. (2018). The added value of geodiversity indices in explaining variation of stream macroinvertebrate diversity. *Ecological Indicators*, 94, 420–429.

(III) Kärnä, O.-M., Heino, J., Laamanen, T., Jyrkänkallio-Mikkola, J., Pajunen, V., Soininen, J., Tolonen, K.T., Tukiainen, H. & Hjort, J. (2019). Does catchment geodiversity foster stream biodiversity? *Landscape Ecology*, 34, 2469–2485.

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	I	**II**	**III**
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Study design	O-MK, JH, HA	O-MK, JHJ, JH	O-MK, JH, JHJ
Collecting the biological data	MG, O-MK	MG, O-MK	JJ, KTT
Identification and processing the biological data	MG, JI, LP	MG	TL, JJ, KTT
Geographical variables	O-MK, HA	O-MK, JHJ	O-MK, HT, JHJ, VP
Statistical analysis	O-MK, JH	O-MK, JH, JHJ	O-MK, JH, JHJ
Manuscript preparation	JH, O-MK, HA, MG, JHJ, JI, LP	O-MK, JHJ, JH, MG	O-MK, JH, JHJ, HT, TL, JJ, VP, JS, KTT

O-MK = Olli-Matti Kärnä, JHJ = Jan Hjort, JH = Jani Heino, HA = Harri Antikainen, MG = Mira Grönroos, JI = Jari Ilmonen, TL = Tiina Laamanen, JJ = Jenny Jyrkänkallio-Mikkola, LP = Lauri Paasivirta, VP = Virpi Pajunen, JS = Janne Soininen, KTT = Kimmo T. Tolonen, HT = Helena Tukiainen.

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Olli-Matti Kärnä

1 Introduction

The effects of global changes on the Earth's environment are ongoing. Furthermore, in the past centuries, human effects on the global environment have increased exponentially (Crutzen 2002), and scientists have thus proposed that our planet may have entered a new geological era, the Anthropocene. This is because of the magnitude of human-induced changes on the environment (Crutzen 2002; Lewis & Maslin 2015). Changes in the atmosphere, land, water, oceans, ecosystems and life on Earth are associated with two major human-induced stressors, climate change and land use changes, but also pollution and overconsumption of resources have important impacts on ecosystems (Vitousek 1994; Steffen *et al.* 2015). Climate change stems from the increase in carbon dioxide in the atmosphere mainly by burning fossil fuels, which is one of the clearest signals of human modification of the Earth system (Vitousek *et al.* 1997; IPCC 2018). In addition, human-induced changes of landscapes have led to a major decline in natural ecosystems compared to increasing areas of intensive agriculture and modified areas (Foley *et al.* 2005). Land use practices provide ecosystem services for humans, but at the same time, land use changes degrade natural conditions (Foley *et al.* 2005). For instance, global changes will significantly reduce the numbers and variability of organisms, i.e. biodiversity in terrestrial, marine and freshwater environments. For example, Pimm *et al.* (1995) reported, that after the rapid growth of human populations, the extinction rates of species are now 100–1000 times higher than before. The situation for many groups of organisms is globally concerning (IUCN 2019), and the same is true at a national level in many countries (Hyvärinen *et al.* 2019).

Freshwater ecosystems are not an exception with regard to the current biodiversity crisis. They face direct and indirect pressures from changes in land cover, channel modifications, thermal alterations, species invasions and diseases (Malmqvist & Rundle 2002; Meybeck 2003; Dodds *et al.* 2013; Reid *et al.* 2019), as well as from climate change (Parmesan 2006; Heino *et al.* 2009). These negative impacts result in river ecosystem destruction, physical habitat changes, modifications to water chemistry and species additions or removals (Malmqvist & Rundle 2002) and further, these pressures form major threats to biodiversity in river ecosystems. For instance, land use changes and overexploitation of species populations have had the most severe impact on biodiversity since the 1970s (IPBES 2019). Such negative effects are seen in different organism groups occurring in freshwater environments, ranging from amphibians and fish to the smallest invertebrates and microbes (Reid *et al.* 2019). Recently, it has been estimated that declines in species diversity, distribution and abundance due to human pressure are clearly higher in freshwater ecosystems than in terrestrial environments (Abell 2002; Wiens 2016). This is alarming because overall freshwaters constitute only about 0.8% of the Earth's surface (Dudgeon *et al.* 2006) and rivers and streams cover below 0.6% of the non-glaciated land surface (Allen & Pavelsky 2018). However, biodiversity in terms of the number of species is high in freshwater ecosystems, including as much as 6% of all the recognized species of the Earth (Dudgeon *et al.* 2006). Moreover, it has been estimated that aquatic habitats associated with 65% of continental river discharge are moderately or strongly threatened by anthropogenic pressures (Vörösmarty *et al.* 2010).

In the face of global environmental change, it is crucial to determine the status of biodiversity and to predict its response to projected changes (Gaston 2000). Traditionally, the abundance and distribution of species have been thought to vary across gradients such as latitude, altitude, depth and isolation (Brown & Lomolino 1998). Of these gradients, many work as proxy variables for primary ecological or evolutionary factors, such as temperature, productivity, insolation, environmental stability, area and environmental heterogeneity (Rohde 1992; Hillebrand 2004; Stein *et al.* 2014). In terrestrial environments, geographical diversity gradients are relatively well known (e.g. Hillebrand 2004), but such information is still inadequate at various spatial resolutions and spatial extents in the freshwater realm (Heino 2011). For instance, some freshwater vertebrate taxa often obey the general rule of a decline of species richness along the latitudinal gradient (e.g. Matthews 1998), but many insect groups do not follow the same latitudinal pattern (Heino 2009). Additionally, as support for the species-energy hypothesis (i.e. higher energy should lead to higher biomass and thereby higher species richness) has been found in fish (Romanuk *et al.* 2009) and dragonflies (Keil *et al.* 2008), among many freshwater organisms, species richness-energy relationships are generally absent, which underlines the difficulties in using energy as an overall predictor of species richness. In general, the large-scale effects, drainage basin features and local variables typically determine the variation of biodiversity in river and stream environments (Heino 2009; Passy 2009). For example, in riverine systems, many environmental features such as the substratum, velocity and chemical properties of water vary between sites regardless of the latitudinal gradients. This, in turn leads to high variation in the biodiversity of those sites (Heino 2011). In addition, environmental factors in drainage areas and on local scales may override the influence of large-scale factors on riverine biodiversity, even across broad geographical gradients (Hillebrand 2004). In addition to purely environmental factors, the dispersal of species is an important process which shapes patterns of biodiversity (Campbell Grant *et al.* 2007; Grönroos *et al.* 2013; Heino *et al.* 2017; Tonkin *et al.* 2018).

Another important aspect concerning biodiversity patterns is environmental heterogeneity: physically complex habitats offer more ecological niches and variable ways of utilizing environmental resources, thus increasing biodiversity (Tews *et al.* 2004; Stein *et al.* 2014). For instance, Tews *et al.* (2004) reviewed numerous studies which showed a positive relationship between habitat heterogeneity provided by the vegetation and animal species diversity. In addition, habitat heterogeneity referring to topographic, land cover and climate heterogeneity may also promote a positive biodiversity-environmental heterogeneity relationship (Kerr & Packer 1997; Stein *et al.* 2014). Stream biodiversity may also be affected by environmental heterogeneity, which results from various physical and chemical conditions, resources and biological interactions on different spatial and temporal scales in the landscape (Frissel *et al.* 1986; Palmer & Poff 1997; Robson & Chester 1999; Allan & Castillo 2007). More precisely, environmental heterogeneity covers spatial environmental heterogeneity between adjacent sites from the regional to local-scale (Brosse *et al.* 2003; Heino *et al.* 2013). The importance of environmental heterogeneity as a predictor of biodiversity can also be seen in the situations where environmental homogenization due to channel modifications in streams (e.g. dredging or straightening streams) has led to homogenization in species composition (Zeni & Casatti 2014).

In recent years, the majority of studies on freshwater biodiversity and the environment have concentrated on hypotheses of local and regional processes in forming diversity patterns (Stendera *et al.* 2012), including a few studies addressing the role of environmental heterogeneity (e.g. Heino *et al.* 2013; Astorga *et al.* 2014). A complementary method to understanding the relationship between the physical environment and biodiversity is to use geodiversity as a more holistic variable for environment features. Geodiversity, i.e. variability in the abiotic nature of the Earth's surface, offers another perspective to explore the relationship between the environment and biodiversity. Among the multiple definitions of geodiversity, the most commonly used was probably presented by Gray (2013) who stated it as the range of geological (rocks, minerals, fossils), geomorphological (landforms, topography, physical processes), soil and hydrological features. Geodiversity elements form the basic components of ecosystems, which may enhance biodiversity. This influences biodiversity by affecting microclimates, creating a variety of habitat types, providing resources and offering shelter from unfavourable abiotic and biotic conditions (Seto *et al.* 2004; Tews *et al.* 2004; Lawler *et al.* 2015). Thus, geodiversity may offer an 'umbrella term' which covers environmental heterogeneity from local resources to the variety of habitats which are important for biodiversity (Stein *et al.* 2014). In general, geodiversity can be measured in multiple ways (see the review by Pellitero *et al.* 2015), but in this thesis a method which sums up different features of geodiversity on a local-scale is used (Hjort & Luoto 2010; Hjort *et al.* 2012). Although geodiversity is internationally recognized nowadays and increasingly referred to as a useful surrogate approach to partition natural variability (Tukiainen 2019), studies of geodiversity and biodiversity are still relatively rare and more emphasis should be placed on linking geodiversity to biodiversity in freshwaters systems (Toivanen *et al.* 2019).

The goal of this thesis was to obtain complementary information on the landscape using remote sensing (RS) and geographic information systems (GIS), and to determine possible relationships between environment proxies and biodiversity in naturally heterogeneous stream ecosystems. In general, modern techniques have improved the understanding and quantification of causal linkages between the landscape and biota, including dispersal processes on a variety of scales (Johnson & Host 2010). On the other hand, the majority of studies testing such advanced variables as potential explanatory variables for stream biodiversity have focused on the influence of land use on stream ecosystems (Leland & Porter 2000; Allan 2004; Soininen 2015; Jyrkänkallio-Mikkola *et al.* 2017), whereas systematic studies on landscape heterogeneity and stream biodiversity are scarce (Stendera *et al.* 2012). Additionally, studies examining spatial connectivity in stream environments have used rather simple methods (e.g. straight Euclidean or watercourse distances) as proxies for dispersal routes, whereas more sophisticated distance measures are still under development (McRae 2006; Tonkin *et al.* 2018). Together with easily assessed environmental data, geographical variables related to dispersal processes and advanced statistical methods are expected to provide new insights and valuable perspectives for biodiversity-environment studies, complementing more traditional explorations in the freshwater realm.

1.1 Streams and their catchments

Rivers and streams with their valley systems form a central part of the landscape (Petts & Foster 1985). A stream collects its water from the drainage basin, which is the area bordered by topographical features such as mountains, hills or eskers (i.e. higher areas in the landscape) (Gregory & Walling 1973). The channel size is proportional to the amount of mean discharge, and so the valley size (or drainage basin size) eventually determines the physical size of the stream corridor (Horton 1945). The concept of the channel network will be considered after multiple stream channels inside the drainage basin intersects with each other (Strahler 1957). Inside the drainage basin, tributary streams are nested in a hierarchical order. The smallest perennial headwater streams with clearly defined valleys are designated as the first-order streams. After the confluence of two first-order streams, a second-order stream is formed and so forth. Eventually the main river channel, which receives the entire discharge of water and sediments, is given the highest order number within the drainage basin (Strahler 1957).

As Hynes (1975) states, "*In every respect, the valley rules the stream*", the relationship between the drainage basin and a stream channel is profound. The continuous movement of water and particles from upstream to downstream within the drainage basin contribute to the morphology of streams, sedimentation patterns, water chemistry, and biology of organisms in lotic ecosystems (Wetzel 1975). Also, the hydrological, chemical, and biological properties of a given stream or a river reflect the climate, geology, and vegetation of the drainage basin (Hynes 1975; Allan & Castillo 2007). The relationship between the main channel and the drainage basin makes stream ecosystems vulnerable to anthropogenic stressors because they are not only affected at one specific spot, but also include the effects of the entire catchment from which water and material enter the main channel (Hynes 1975). In runoff, materials such as sediments, human-based waste and pollutants enter and travel towards the valley bottoms and eventually flow into streams and rivers. In addition, because of their relatively small size and water volume, streams and rivers usually lack the ability to dilute contaminants or withstand other negative impacts to the environment and on the species living there (Dudgeon *et al.* 2006).

River and stream ecosystem can be classified in different ways. In a simple division, the river or stream channel can be divided in environmentally different segments of pools and riffles (Figure 1). Pools are characterized by relatively deep areas of slow velocity and a fine substratum, whereas riffles are shallower and more fast-flowing sections with a more variable substratum (Leopold 1969). In a more sophisticated classification system, streams can be categorized on different scales, ranging from the drainage basin to stream reach (or mesohabitat) and patch scales (Frissel *et al.* 1986; Figure 1). Across these scales, stream channels are structured by physical features such as the channel size, channel shape, gradient and substratum type (Maddock *et al.* 1999). A distinct pattern

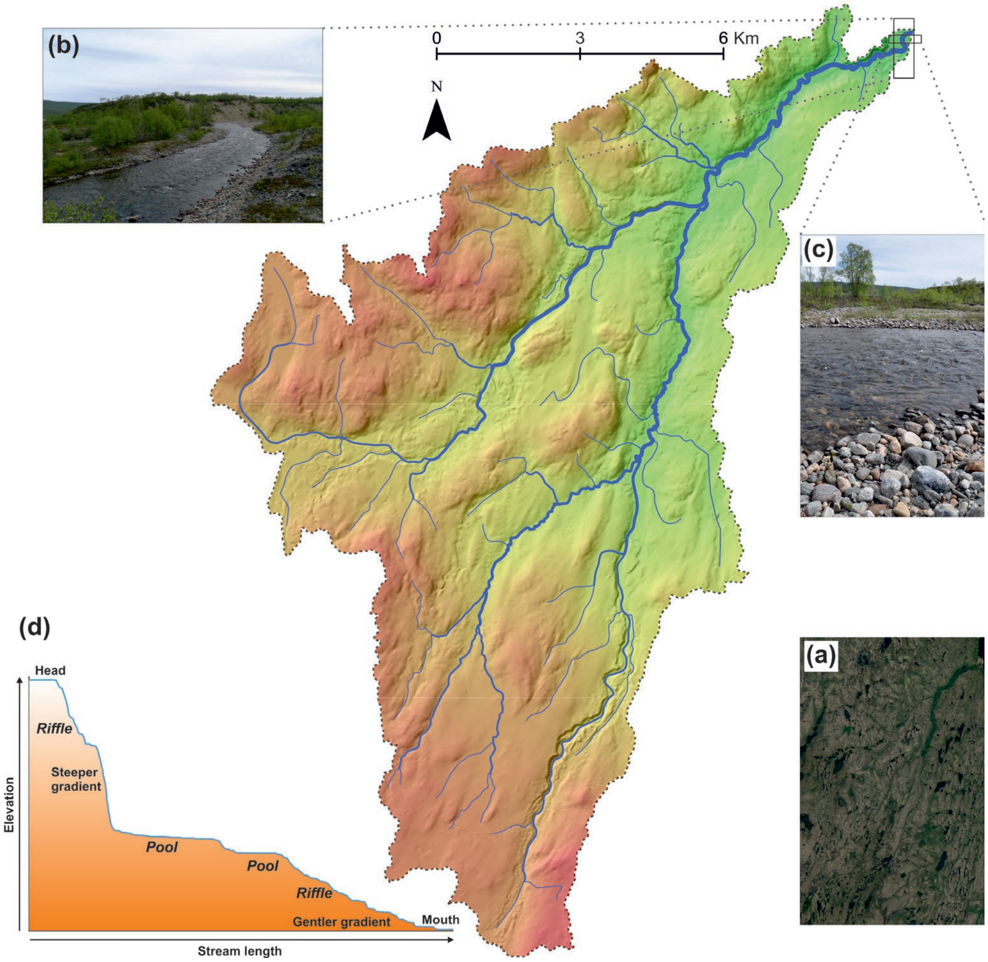

Figure 1. A simplified representation of a stream network (blue lines) within a drainage area restricted by topographical divides. Also shown are the scales of the stream environment: a) the drainage area (regional level), b) the reach level, c) the mesohabitat to patch level and, d) a representative picture of elevation gradient along the stream course from the head area to the stream mouth (data: National Land Survey of Finland; a) Google/Landsat; b–d) O.-M. Kärnä).

of hydraulic features (such as those related to stream depth and velocity), is produced when physical features are combined with a particular water discharge (Maddock *et al.* 1999; Allan & Castillo 2007). The physical habitat of a stream is spatially and temporally dynamic, with implications affecting features such as woody debris and other non-living organic materials. Typically, on the reach-scale and larger, environmental conditions are considered relatively stable, but within small sites and patches, the spatial and temporal variability of physical characteristics can be very high (Allan & Castillo 2007).

Additionally, variability is highly noticeable for headwater streams (i.e. first- and second-order streams), which have very variable physical and chemical conditions ranging from steep mountain streams to low-gradient tributaries in the swampy landscape (Meyer *et al.* 2007). Further, as they are relatively more numerous, conditions in headwater streams also have an influence downstream of the drainage network (Meyer *et al.* 2007). In addition, the river continuum concept originally presented by Vannote *et al.* (1980) predicts longitudinal patterns in the energy inputs and biological communities along river channels from the smallest first-order streams to the largest main stem river.

1.2 Organisms in stream environments

Running water environments harbour a diverse array of species, habitats and ecosystems, which is yet more remarkable in relation to the small area of the Earth they cover (Allan & Flecker 1993; Vörösmarty *et al.* 2010). Organisms in streams range from those directly associated with the substrate (e.g. bacteria, microalgae and filamentous algae, mosses, plants and macroinvertebrates) to more freely moving fish species (Hynes 1970; Allan & Castillo 2007). The focus of this thesis is mainly on macroinvertebrates because of the important roles they play in stream ecosystem processes (Covich *et al.* 1999), and because they are widely used in stream bioassessment programs (Rosenberg & Resh 1993). In addition to macroinvertebrates, benthic algae and bacteria are important groups because they are also considered as bioindicators. Furthermore, they contribute to ecosystem functions and provide of valuable ecosystem services (Hill *et al.* 2000; Palmer *et al.* 2014). Hence, algae and bacteria were also examined in this thesis.

Different types of benthic algae typically live on stones, sediment, sand, wood or on higher plants (Allan & Castillo 2007). Algae can be further categorized into diatoms (Bacillariophyceae), green algae (Chlorophyceae), red algae (Rhodophyceae), chrysophytes (Chrysophyceae) and tribophytes (Tribophyceae) (Graham & Wilcox 2000). Algal communities play an important role in lotic ecosystems. For example, they are the most important primary producers in many small to medium sized streams (Minshall 1978; Vannote *et al.* 1980) and, especially, diatoms are a species rich group which is considered to be the most important food source for benthic herbivores (Giller & Malmqvist 1998). Bacterial communities are also a vital food source for higher trophic levels, while they also drive nutrient cycling (Palmer *et al.* 2014) and stabilize sediments (Dodds & Biggs

2002). The combination of benthic algae, bacteria and fungi that occur in the extracellular matrix on the surfaces of stones, sediment and vegetation below the water surface are also called as the biofilm (Allan & Castillo 2007) and this offers an important autochthonous source of nutrition for grazing macroinvertebrates (Vannote *et al.* 1980).

Aquatic macroinvertebrates are highly diverse in most stream environments (Wallace & Webster 1996). Stream macroinvertebrates typically consist of species larger than 0.5 mm and incorporate mainly aquatic insects, but also other taxonomic groups such as crustaceans, molluscs, oligochaetes, planarians and leeches (Giller & Malmqvist 1998; Jacobsen *et al.* 2008). A general feature of most stream insects is that they spend part of their life cycle in water and typically have a terrestrial adult stage (Jacobsen *et al.* 2008; Lancaster & Downes 2013). In lotic ecosystems, macroinvertebrates contribute to nutrient cycling, primary production, decomposition, and the translocation of materials, and are themselves a vital source of food for fish species (Wallace & Webster 1996; Covich *et al.* 1999). In terms of organic material processing, macroinvertebrates can be categorized into functional feeding groups according to their food sources and food acquisition methods (Cummins & Klug 1979). Functional feeding groups range from shredders to filterer-collectors, grazers and predators (Cummins & Klug 1979). Because the abundance of the food resources for macroinvertebrates is affected by the stream size, shading and the substrate among other factors, the relative availability of food sources changes relatively predictably along the drainage network from the headwaters to the lower sections of rivers (Vannote *et al.* 1980). Shaded headwaters harbour species that consume coarse particulate organic matter, whereas grazers feeding on algae are likely to flourish in unshaded stony streams (Allan & Castillo 2007). Macroinvertebrate communities are usually dominated by a few insect orders: mayflies (Ephemeroptera), stoneflies (Plecoptera), caddisflies (Trichoptera), beetles (Coleoptera) and true flies (Diptera) (Vinson & Hawkins 1998; Lancaster & Downes 2013). Furthermore, each insect group is comprised of numerous identified species with regional variability in distribution across the world (Giller & Malmqvist 1998).

1.3 Factors affecting stream biodiversity

Running waters are hierarchically structured systems and this is strongly reflected in the biotic life, which is dependent on the effects of environmental factors acting at different scales (e.g. from large-scale geographical to local riffle and habitat-scale factors). Organisms must be adapted to the set of abiotic and biotic conditions to survive and reproduce in a given location (Biggs *et al.* 2005). These variables affect stream biodiversity on multiple spatial and temporal scales (Poff 1997; Vinson & Hawkins 1998; Townsend *et al.* 2003; Sandin & Johnson 2004) and often via complex pathways (Heino *et al.* 2007; Pajunen *et al.* 2017). More precisely, the presence of a given species in a location depends on filtering processes based on climate, geology, dispersal, channel morphology and the physical-chemical properties of local habitats (Poff 1997; Figure 2). Therefore, biodiversity in stream ecosystems result from the local environmental features and large regional processes or is determined jointly by both of them. The relative roles of local and regional factors in structuring stream communities could also result from or be associated with the spatial extent of a study sites (Mykrä *et al.* 2007; Heino *et al.* 2014). A clear environmental control of community structure is often found in studies on small scales (Horner-Devine *et al.* 2004; Mykrä *et al.* 2007), whereas regional factors, such as geographical and climatic features seem to be more important in studies on a larger spatial scale (Martiny *et al.* 2006; Heino 2009).

Key abiotic features affecting stream communities from the reach to the habitat scales are usually those related to stream morphology, velocity, substrate and chemical properties of water (Allan & Castillo 2007). Morphological factors of streams, e.g. variables related to the stream size, have a considerable effect on biodiversity, mainly because stream corridors of varying size offer different habitats for species (Heino *et al.* 2003; Mykrä *et al.* 2007). Flow regimes along with substratum properties reflect conditions and resources for the biota, thereby adding variation to the biodiversity between sites (Minshall 1984; Biggs *et al.* 2005; Allan & Castillo 2007). In addition, the water chemistry (e.g. pH and nutrients) has been shown to considerably affect microbial (e.g. Soininen 2007) and macroinvertebrate communities (Heino *et al.* 2003). However, because of the strong relationship between the catchment and stream channel, it is difficult to distinguish whether water chemical properties reflect the soil and land use conditions on the regional-scale (Hynes 1975; Allan

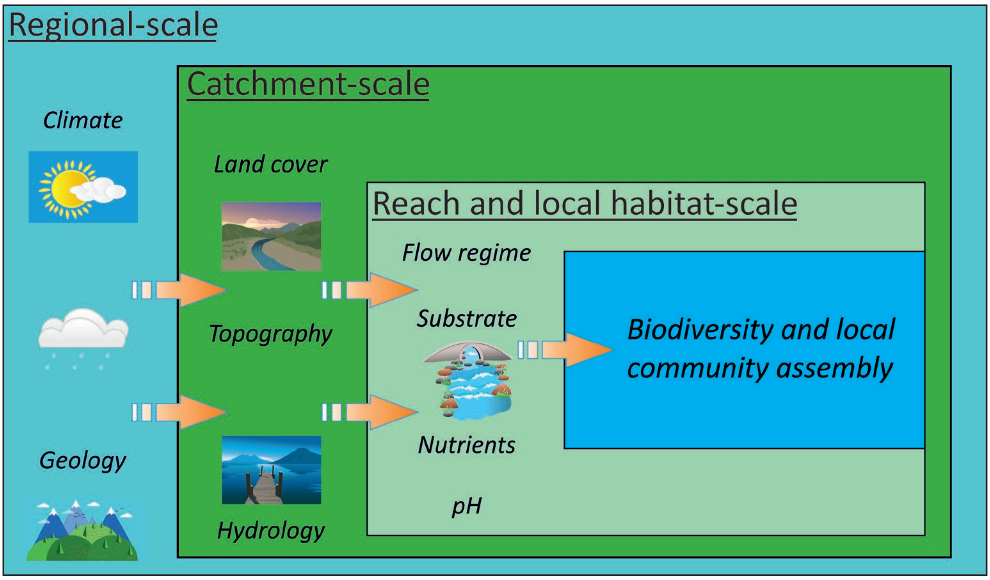

Figure 2. A representation of the geographical and ecological factors affecting stream biodiversity. The figure is modified from the information in Frissel *et al.* (1986) and (Poff 1997).

2004). It should be noted that spatial environmental heterogeneity has been acknowledged as a factor of biodiversity variation in terrestrial (Andersson & Ferree 2010; Stein *et al.* 2014) and stream ecosystems (Thienemann 1954; Heino *et al.* 2015). Spatial environmental heterogeneity in lotic environments consists of the variation in the physical and chemical features, resources and biotic processes in space and time (Palmer & Poff 1997). More precisely, the complexity of flow conditions in the different parts of the channel, and the variation in the channel morphology, substratum heterogeneity and water chemistry all contribute to environmental heterogeneity, which may affect biodiversity patterns.

On the catchment-scale, variables such as land use, soil-type, topography and geology determine the conditions of stream habitats (Hynes 1970; Frissel *et al.* 1986), which in turn affect stream biodiversity. Sometimes catchment features have been proposed to be even more effective than local stream site properties (Hynes 1975), especially for predicting the diatom community variation (Jyrkänkallio-Mikkola *et al.* 2017). Furthermore, catchment-scale characteristics may reflect environmental changes in the drainage area, thereby affecting local habitat conditions over longer time scales (Soininen *et al.* 2015). Of the large-scale geographical variables, climate has the most notable role in affecting stream microbial biodiversity (Pajunen *et al.* 2016; Jyrkänkallio-Mikkola *et al.* 2017), but also macroinvertebrate communities are shaped by climate conditions (Bhowmik & Schafer 2015; Rocha *et al.* 2018).

In addition to environmental factors, dispersal comprises an important mechanism that affects geographical distributions, community organization and, eventually, the biodiversity of all organisms (Palmer *et al.* 1996; Bilton *et al.* 2001; Bohonak & Jenkins 2003; Tonkin *et al.* 2018). In riverine systems, dispersal may meditate the processes of environmental filtering and mass effects (high dispersal rates, which may interfere with environmental filtering) in structuring biodiversity (Leibold *et al.* 2004; Tonkin *et al.* 2018). The highly branching spatial structure of stream networks can have a strong influence on community dynamics, which eventually shapes the patterns of biodiversity (e.g. Campbell Grant *et al.* 2007). For instance, headwaters tend to be more isolated in terms of dispersal than downstream locations (e.g. Brown & Swan 2010). Mass effects, on the other hand, may contribute to biodiversity variations in mid-stem sections and central parts of streams. Additionally, abiotic features such as connectivity, centrality, land cover, topography and density of the drainage network can influence the spatial patterns of biodiversity by affecting dispersal (Malmqvist 2002; Altermatt 2013; Heino *et al.* 2017; Tonkin *et al.* 2018). Dispersal in dendritic river systems is directed by stream corridors (Petersen *et al.* 1999; Malmqvist 2002) but depending on the physical features of a catchment and the biological characteristics of organisms, overland movements are also likely to take place (Malmqvist 2002; Heino *et al.* 2017). Many macroinvertebrates travel mainly through stream corridors when dispersing (Petersen *et al.* 1999), but in their flying adult stages, aquatic insects are able to move overland for considerable distances (Malmqvist 2002; Lancaster & Downes 2013).

1.4 Proxy variables for stream biodiversity

Measuring and monitoring biodiversity is often difficult due to the sampling costs and effort required (Palmer *et al.* 2002; Rocchini *et al.* 2015). Gathering reliable, large-scale, biotic data is typically challenging or sometimes even impossible. This may be because (i) species' abundance and distribution are changing over time (Robinson *et al.* 1994), (ii) it is challenging to collect every species in a region (Palmer *et al.* 2002) or (iii) there may be considerable variability in habitats (and thus species distributions) within the same stream (Gerth & Herlihy 2006). However, because of noticeable species-environment relationships, indirect measures of the environment (i.e. proxy latent variables) can contribute to providing predictive tools for species distribution and abundance patterns (Palmer *et al.* 2002; Rocchini *et al.* 2015; Table 1). Moreover, dispersal is virtually impossible to account for and ecologists must therefore rely on proxies to understand the effects of dispersal on biodiversity variations (Jacobson & Peres-Neto 2010; Heino *et al.* 2017).

Table 1. Examples of typical environmental proxies used to explain biodiversity variations in the riverine environments. Note that direct local physical-chemical variables that organisms experience, such as the flow- and chemical properties of water within the local habitat, have been excluded from the representation. *Abbreviations: RS = Remote Sensing; GIS = Geographic Information Systems.

Proxy	**Ecological mechanism**	**Measuring method***	**References**
Climatic/Biome (temperature and precipitation)	Driver for the thermal and flow regimes of streams, and thus affecting organisms.	RS, field	Poff *et al.* 2010; Dodds *et al.* 2015
Latitude	Energy- and speciation-related processes important for organisms. For instance, through the temperature, areal extent, current and past climates, and productivity effects on organisms.	GIS, RS	Jacobsen *et al.* 1997; Johnson *et al.* 2007; Feld *et al.* 2016
Altitude	Indirect indicator mainly for temperature, which in turn, is key environmental variable for metabolic rates of organisms and species distributions.	RS	Allan 1975; Jacobsen *et al.* 1997; Allan & Castillo 2007
Geology (i.e. soil and rock types)	Major influence due to the dissolution of chemical constituents which are important for the growth of organisms.	RS, field	Leland & Porter 2000
Land cover (incl. vegetation types and land use, e.g. CORINE)	Land cover affects biodiversity by acting as major variable for water chemical properties, the intensity of disturbances, shading effects and the dispersal of species.	RS, field	Johnson *et al.* 2007; Tonkin *et al.* 2016; Feld *et al.* 2016; Jyrkänkallio-Mikkola *et al.* 2017
Spatial variables (i.e. physical distances inside the drainage network)	Proxies for dispersal along stream network.	GIS	Landeiro *et al.* 2011; Grönroos *et al.* 2013; Heino *et al.* 2017
Habitat size (e.g. stream order, catchment area and stream width)	Generally related to habitat heterogeneity, resources and numbers of thermal niches.	Field, GIS	Vannote *et al.* 1980; Malmqvist & Mäki 1994; Heino *et al.* 2003
Environmental heterogeneity	Complex in-stream habitat features in terms of various local factors should offer more niche space, thus enhancing biodiversity.	RS, field, mathematical analysis	Vinson & Hawkins 2003

2 Aims of the study

The main focus of this thesis was to investigate the relationships between biodiversity variation and geographical factors in high-latitude streams. Specifically, the aim was (1) to produce GIS based accessibility measures within a stream drainage network and (2) to evaluate the geodiversity of the stream environment on the habitat and catchment scales. Furthermore, geographical proxies were tested as possible predictors of stream biodiversity along with the traditionally used variables typically measured in stream ecological studies. There were four main research questions:

Q1: What are the effects of local environmental and geographical variables on stream biodiversity in high-latitude areas (Papers I–III)?

Q2: How do environmental and spatial distances between stream sites affect the variation in the stream insect communities between subarctic streams (Paper I)?

Q3: What are the relative roles of habitat-scale geodiversity measures and traditional in-stream variables in explaining stream macroinvertebrate biodiversity in subarctic streams (Paper II)?

Q4: How does catchment-scale geodiversity contribute to the variation in stream biodiversity in a boreal region (Paper III)?

There are several hypotheses to specify the research questions mentioned above. First, I hypothesized that local environmental conditions play a central role in explaining biodiversity in the streams studied (**H1**) because physico-chemical factors have been shown to be important for stream biodiversity on the local and habitat-scale (Q1, Papers I–III; Malmqvist & Mäki 1994; Heino *et al.* 2003; Feld & Hering 2007; Soininen 2007). Moreover, a clear role for geographical proxies (i.e. spatial distances inside the drainage network, and geodiversity) is also assumed (**H2**). This is because dispersal across the landscape (Q1, Paper I; Landeiro *et al.* 2011; Heino *et al.* 2017) and environmental heterogeneity affect biodiversity variation on multiple spatial and temporal scales (Q1, Papers II–III; Vinson & Hawkins 2003; Astorga *et al.* 2014).

In Paper I, I approached the relative contributions of environmental and geographical distance variables in structuring stream insect communities (Q2) by hypothesizing that environmental distances between sites are more important for stream insects than spatial distances (**H3**; Grönroos *et al.* 2013). In addition, clear evidence of the role of geographical distances is expected for species groups showing different dispersal abilities (**H4**; Grönroos *et al.* 2013). For example, actively dispersing insect species should be better associated with environmental conditions than passive dispersers because the former can actively select suitable habitats, whereas the latter show more random dispersion patterns (Heino 2013). In Paper II, the third question (Q3) was addressed by the hypothesis: while environmental variables will probably be the most important factors for biodiversity, geodiversity will also account for substantial amount of variation in biodiversity (**H5**). This is because environmental heterogeneity is a significant driver of biodiversity (e.g. Stein *et al.* 2014), and geodiversity measures will characterize the heterogeneity of stream habitats more comprehensively than individual traditionally measured variables alone. In Paper III, the exploration of biodiversity-environment relationships was further extended to the catchment-scale (Q4) by hypothesizing that geodiversity has a considerable effect on biodiversity (**H6**). This may occur, for instance, due to the effect of surface geology on water chemistry and, further, on stream biodiversity (Leland & Porter 2000; Allan 2004).

3 Methods

3.1 Study areas

This thesis is comprised of two biological data sets covering parts of Northern and Western Finland (Figure 3). In Papers I and II, macroinvertebrate and environmental data was collected from 55 tributary streams, which all drain to the main stem of the Tenojoki River. The study area in the Tenojoki drainage area covers large areas, as the distance between the southernmost and the northernmost sites was approximately 150 km. The data set used in Paper III was based on samples from 88 tributary streams belonging to 21 major river basins in Western Finland. The spatial extent in Western Finland was considerably larger than in the first data set and the stream sites ranged 520 km in south-north and 330 km in west-east direction.

3.1.1 The Tenojoki River basin

The Tenojoki River basin drains large wilderness areas in northernmost Finland and Norway. The main stem of the Tenojoki River begins after the confluence of the two large tributaries, the River Karasjohka and the River Anarjohka just north of the municipality of Karigasniemi. The other large tributary rivers are Utsjoki, Veitsijoki, Pulmankijoki, Valjohka, Iesjohka and Maskejohka. The main River Tenojoki flows north through a U-shaped valley rounded by glacial erosion (Mansikkaniemi 1970), eventually flowing into the Arctic Ocean at Tanafjord (a large fjord in Northern Norway). The total size of the Tenojoki River basin is 16,386 km^2, of which areas on the Finnish side of the border cover approximately 5,153 km^2. The lake percentage in the drainage area is only 3.10% (Ekholm 1993), and the discharge at the downstream location of the main stem varies temporally between <100 m^3 in the mid-winter to even 2,000 m^3 during spring floods (Finland's environmental administration 2019). Unfortunately, there are no discharge data for the majority of the smaller tributary streams, but temporal variations can be expected to be similar as in the main river. However, discharges in the tributary streams likely respond more strongly and faster to weather variations, such as rainfalls and drought (Dettinger & Diaz 2000).

In terms of climate, the study area belongs to the northern boreal regions (Kersalo & Pirinen 2009) with a snowfall-dominated climate, with fully humid and cool summers (Kottek *et al.* 2006). The mean annual air temperature varied between -1°C and -2°C, and the mean annual precipitation ranged from 400 mm to 550 mm between 1980 and 2010. However, spatio-temporal variations of temperature and precipitation are relatively large because of variations in elevation and the vicinity of the warmer Arctic Ocean in the north (Pirinen *et al.* 2012).

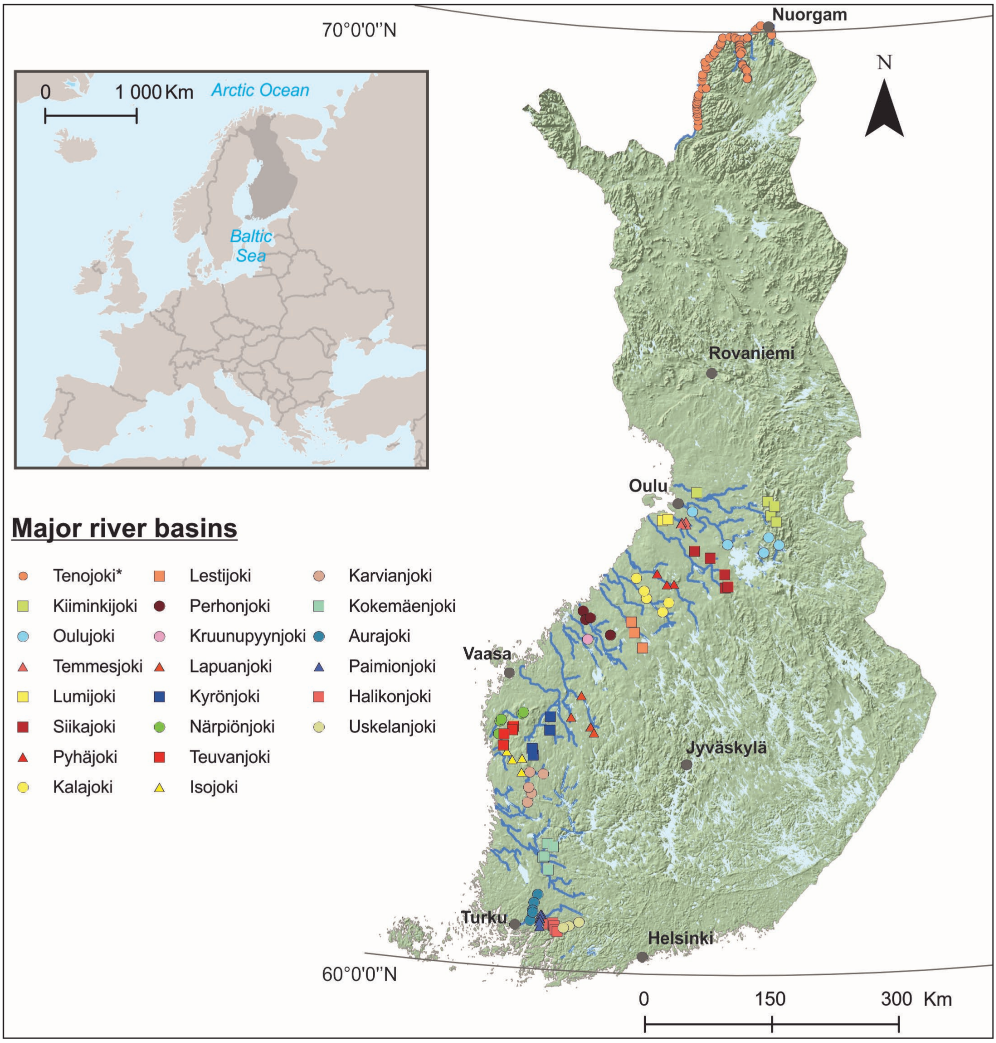

Figure 3. A map of the study areas located in Northern and Western Finland. Shown are also the locations of the 55 stream sampling sites belonging to the Tenojoki River basin (Papers I–II) and 88 stream sampling sites belonging to 21 major river basins in Western Finland (Paper III). *Note that all 55 study sites in the Tenojoki River basin are located in tributary streams outside the main stem (data: National Land Survey of Finland; Finnish Environment Institute).

The landscape in the Tenojoki River basin is mountain (i.e. fell) dominated, and altitude varies between 10 and 640 meters above sea level. However, the tributary streams flow into the main river in rather deep valleys, and relative variations in elevation in the river valleys are considerable, ranging from 200 to 400 meters. Variations in elevation, together with nearby located sub-drainage basins separated by geographical features such as ridges, eskers and fells are typical for the landscape in the Tenojoki River basin. Furthermore, because of these landscape and hydrological features, stream networks within the drainage basin are locally very dense, with a minimum distance of a few hundred meters between single stream channels. The bedrock in the northern part of Finland consists of common rock types, such as granites, gneisses, gabbros and diorites (Aro *et al.* 1990). Locally the bedrock is often exposed in stream riffles, but usually stream channels flow over surfaces characterized by sorted glaciofluvial and fluvial material (Figure 4; a–c). In the study area, peatlands are relatively rare, but in some valleys between the fells as well as close to the stream channels, peat surfaces may be present.

The study area is part of the subarctic deciduous region (Hustich 1961), where mountain birch woodland is the most common vegetation type. However, the tops of the fells and the highest regions of the north-easternmost stream sites are covered by barren tundra, with vegetation consisting of shrubs, lichen and moss (Mansikkaniemi 1970). Scattered Scotch pine woodlands are found in the southernmost parts of the study area, forming a clear boundary for terrestrial vegetation (Mansikkaniemi 1970).

Figure 4. Pictures shows the gradients of different stream types from the Tenojoki River basin (a–b; credit: O.-M. Kärnä and c; credit M. Grönroos) and in Western Finland (d–f; credit: J. Jyrkänkallio-Mikkola).

Overall, human activities, such as agriculture and forestry in the Tenojoki river basin are minor, and the human population is concentrated mainly in a couple of villages near the River Tenojoki. Owing to the minor human activity, the streams in the study area are typically in a pristine or near-pristine condition, providing excellent circumstances for studying biological communities across spatially and topographically interesting environments.

3.1.2 Western Finland

In Paper III, the study streams belonged to 21 major river basins and covered geographically extensive areas in Western Finland, the study area being much larger and environmentally more heterogeneous than that of the Tenojoki River basin. Western Finland is an area where land uplift has caused notable changes in flow directions, and it still affects aquatic systems (Hyvärinen & Kajander 2005). The river basins in this area flow mainly to the northwest into the Gulf of Bothnia in the Baltic Sea (Figure 3). Coastal rivers in the southern and western parts of this area are mostly small, with some lakes in their drainage basins. Variations in elevation are relatively small, as the rivers drain an area of gentle slopes with minor gradients along their routes. The northern rivers in the study area are larger and they flow across a more undulating landscape with the highest points being approximately 200 m a.s.l. The lake percentage of the drainage basins varies from 0 to approximately 15% in the area (Ekholm 1993). Furthermore, the discharges of the main river channels fluctuate from a few cubic meters per second to over 250 m^3/s (Korhonen 2007). There are large variations in the size of the studied catchment areas as they cover areas from 2.5 km^2 to over 700 km^2.

Western Finland belongs to the snow-dominated climate, with a fully humid climate, cool summers and cold winters being the dominant climate characteristics (Kottek *et al.* 2006). In addition, the climate shows features of both a continental and oceanic climate, resulting from the location between the Atlantic Ocean and the main Eurasian continent (Tikkanen 2005). The mean annual air temperature varied between +2°C and +6°C and mean annual precipitation ranged from 500 mm in the northwest to over 700 mm in the southern part of the study area between 1980 and 2010 (Kersalo & Pirinen 2009; Pirinen *et al.* 2012).

The bedrock of the study area was formed during the period of the Precambrian orogenies and is mainly composed of Precambrian rocks. The majority of the bedrock is composed of igneous and metamorphic rocks (Aro *et al.* 1990). In addition, the soils in Western Finland were formed during and after the latest glacial period (Aro *et al.* 1990), and the most common soil types are till (35%), peat (31%) and clay (8%). In the landscape, the stream channels sampled flow mainly through ground moraine, but in the larger valleys and coastal regions streams have eroded through deposits of sorted materials. Visible bedrock is quite rare, except in Southwestern Finland where till-covered bedrock hills are common (Fogelberg & Seppälä 1986). Irrespective of the seemingly homogenous surface soil properties in the study area, there was notable variability in local stream habitat characteristics partly because of differences in the vegetation features and land use in the study catchments (Figure 4; d–f).

The landscape in the study area is dominated by boreal vegetation with mixed and coniferous forests (Ahti *et al.* 1968). Wetlands with different types of peat deposits are relative rare in the southernmost catchments but are more and more common northwards (Hämet-Ahti *et al.* 1988). For instance, a few northern streams drain catchments where peat deposits cover over 60% of the total catchment area, whereas in some of the southwestern catchments peat deposits are very limited (0–10% of total catchment area). Furthermore, the land use of the southernmost streams comprises mainly human-dominated rural landscapes whereas the northernmost streams are typically situated in forest areas.

3.2 Biological data

In Papers I and II, stream macroinvertebrate data was collected from 55 stream sites over a period of two weeks in early June in 2012 (Table 2). This is the period when species can be best detected as larvae in northern streams (Heino *et al.* 2003), and this is also the time the snowmelt runoff and harsh flood conditions have mostly ended. For sampling stream macroinvertebrates, we used a three-minute kick-net sampling effort, comprising six 30-second and 0.3 m^2 subsamples that covered most visible microhabitat conditions (e.g. based on visual estimations of depth, current velocity, substrate size and moss cover) within a reach section of ca. 50 m^2. Six subsamples were immediately pooled into composite boxes and preserved in 70% alcohol. In the laboratory, insect individuals were extracted from the samples and were thereafter identified at the species level (excl. some individuals of early larval stages that were identified at the genus level). For simplicity, in Papers I and II, taxa are referred to as species.

In Paper I, information on the maximum body size and dispersal type (passively by the wind vs. actively flying) classes for stream insects were used as a proxy for species dispersal models. In Paper II, we used species trait information to further examine macroinvertebrate data. Specifically, we divided stream macroinvertebrates into three grouping features, each covering numerous traits (Schmera *et al.* 2015). First, functional feeding groups (FFGs) provided information about how species obtain food. These comprised filterers, gatherers, shredders, scrapers and predators (Cummins & Klug, 1979; Merrit & Cummins 1996). In Moog's (2002) 10-point system each species is given 1 to 10 points for each of the possible feeding classes. If a species got ≥ 5 points for a certain FFG, it was assigned to that FFG. If a species was missing from Moog's (2002) categorization, information from Merritt & Cummins (1996) or our expert judgment based on related species was used. Second, for habit trait groups (HTGs), species were divided into categories based on their substratum associations, mobility and where their

Table 2. A summary of the studied organism groups, response and explanatory variables and statistical methods used in the three papers. Abbreviations: BIO-ENV = Best subset of environmental variables with the maximum (rank) correlation with community dissimilarities; LR = Linear regression analysis; BRT = Boosted regression trees.

Paper	Organism group	Response variables	Environmental variables	Geographical variables	Statistical analyses
I	Insects	Community composition (entire data, active and passive species dispersal and five different classes based on maximum body size)	Water chemistry and physical habitat variables on a local-scale	Spatial distance types (i.e. watercourse-, overland- and cost-distance)	Mantel test, partial mantel and BIO-ENV
II	Macroinvertebrates	Species richness, functional diversity (different indices)	Water chemistry and physical habitat variables on a local-scale	Geodiversity measures on a mesoscale	LR, commonality analysis
III	Macroinvertebrates, diatoms and bacteria	Species richness	Water chemistry and physical habitat variables on a local-scale; catchment environmental features	Geodiversity measures on a catchment-scale	BRT

food was obtained. This categorization included burrowers, climbers, clingers, sprawlers and swimmers (Merrit & Cummins 1996). For a third categorization, species were classified into one of six different categories based on the maximum larval body length: >0–0.25, 0.25–0.5, 0.5–1, 1–2, 2–4, or 4–8 cm. The body size categorizations were based mainly on information from personal communication with S. Dolédec (Université Lyon 1, France), Jari Ilmonen (Metsähallitus, Finland), Lauri Paasivirta (Salo, Finland), or on our own information.

Based on the data described above, we calculated eight different measures of biodiversity, of which four portrayed species diversity and four described functional diversity: (1) Species richness (i.e. the number of species), (2) Shannon diversity, (3) Simpson diversity, (4) Pielou evenness, (5) functional richness, (6) functional evenness, (7) functional dispersion and (8) Rao's quadratic entropy. For computing functional diversity indices, we first constructed a species-by-traits matrix based on the FFGs, HTGs and size classes.

The biodiversity information for Western Finland (Paper III) consisted of 88 stream site samples for macroinvertebrates, diatoms and bacteria that were collected in the autumn of 2014. Autumn is also a suitable time of the year for biological sampling of boreal streams because of high species diversity and usually more stable natural conditions than in the early spring season (Heino *et al.* 2013). The sampling procedure for macroinvertebrates was otherwise similar to that used in the River Tenojoki basin data, but this time a two-minute kick sample and 1 m subsamples were taken covering a riffle site of ca. 50 m^2 (Heino *et al.* 2018). After sampling, macroinvertebrates were preserved in ethanol, and samples were taken to the laboratory for extraction and identification of individuals. Identification of individuals was done to the lowest possible taxonomic level.

The same 88 stream sites sampled for macroinvertebrates were also surveyed for diatoms and bacteria. At each site, 10 cobble-sized stones were collected from a depth of 20 cm from different locations of the riffle site. Diatoms were scraped from the stones. Subsequently, the samples were preserved in dark and cool boxes and delivered to the laboratory. In the laboratory, diatom frustules were prepared by cleaning off the organic material. Eventually, at least 500 frustules per sample were counted and identified at the species level. Bacteria samples were wiped off from the different cobble-sized stones as diatoms. Next, bacterial samples were frozen in the field until they were thawed in the laboratory for further processing and identification of operational taxonomic units (OTUs). For supplementary details of the field sampling of bacteria, see Vilmi *et al.* (2016) and Jyrkänkallio-Mikkola *et al.* (2017). More detailed laboratory methods for the processing and analysis of bacterial samples can be found in Heino *et al.* (2015) and Jyrkänkallio-Mikkola *et al.* (2017).

3.3 Local environmental variables

In Papers I–III, we measured several in-stream variables at each site, which have previously been found to be important in studies of macroinvertebrate communities in boreal and subarctic areas (Malmqvist & Mäki 1994; Heino *et al.* 2014). First, the current velocity and stream depth were measured at 30 random-selected spots in a riffle site. In the River Tenojoki study area, the mean width of the stream site was determined based on five cross-channel measurements, and in Western Finland, the mean values of 10 cross-channel measurements were used in the analysis. For Paper I, the moss cover was visually estimated for 10 1 m^2 grids at randomly selected locations on a riffle site. In both study areas, the pH and conductivity were measured at locations a few meters upstream from the sampling sites using a YSI device model 556 MPS (YSI Inc., Yellow Springs, OH, USA). In Papers I and II, water samples to measure the total nitrogen, colour, iron and manganese were taken in the field and analyzed subsequently in the laboratory following national Finnish standards (National Board of Waters and the Environment 1981). For Paper III, water samples were collected to determine the total phosphorous, total nitrogen and water colour with the same standards as used in Papers I and II.

3.4 Catchment environmental variables

In Paper III, the upstream catchment area was delineated with a digital elevation model (DEM, grid resolution 10 × 10 m, National Land Survey of Finland 2013) using the ArcGIS 10.5 software. Land use data was acquired using the CORINE Land Cover data (20×20 m, Finnish Environment Institute 2013) and the geodiversity was calculated for each study catchment separately. In practice, two land use classes (artificial and agricultural areas) were used to define the potential human pressures in the catchment areas (Jyrkänkallio-Mikkola *et al.* 2017).

3.5 Geographical variables

3.5.1 Between-site geographical distances

For the geographical distances (I), the topographic information for the entire drainage area (the River Tenojoki basin area on the Finnish side of the border) was computed using the ArcGIS 10.1 software. The data was again obtained from the National Land Survey of Finland, and it was composed of a DEM (grid resolution 25×25 m, with a vertical accuracy of two meters). To calculate the watercourse distances, data on the watercourses was collected from the Topographic database (NLS), further edited, and complemented manually in order to build the full network based on connected rivers and streams in the study area. Further, to simulate the potential dispersal routes of the stream insects, three types of between site distances (Figure 5) were calculated using the ArcGIS 10.1 software (Esri Redlands, USA). First, the shortest overland distances were simply Euclidean distances between sites. Second, the shortest distance from one site to another within the stream network was calculated using the Network Analyst extension tool in ArcGIS. As a third distance type, the cumulative cost distance between the sites was quantified. It was supposed that in the Tenojoki study area, the cost of overland movement was dependent mainly on the surface topography plus relief and not so much, for example, on land cover (i.e. vegetation). This is because the study area is characterized by the subarctic landscape with vast regions of treeless tundra, areas of low-statured trees, minor variations in natural landscape types and very little alteration of the landscape by humans. The cost distance was calculated using the Path Distance calculation tool in ArcGIS. This tool enables the gradient of the environment to be used as an effective factor for movement through landscape. The cost distance tool represents the paths of the least effort in the landscape avoiding topographically challenging areas. The cost distance tool calculates the distance in cost units of pixels, not in geographic units, as in the cases of Euclidean distance and watercourse distance.

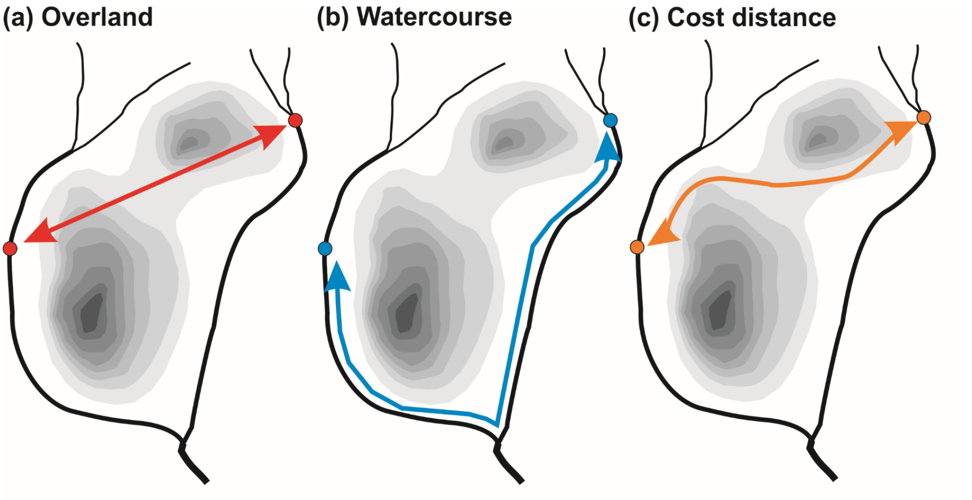

Figure 5. The types of geographical distances (coloured arrows) utilized in Paper I. The black lines represent a part of the stream network within the drainage area. For more information, see Heino *et al.* (2017) and Tonkin *et al.* (2018).

3.5.2 Geodiversity information

For studying the effects of the riverscape geodiversity on the stream biodiversity, two approaches were used (Papers II and III). First, habitat-scale geodiversity information for the stream sites was acquired from photographs taken during the field surveys in 2012 (II). Specifically, based on a visual estimation of the photographs, it was possible to determine different surface flow types (Wadeson & Rowntree 1998) and geomorphological landforms and processes (Hjort & Luoto 2010) present at each study site. Because of difficulties to estimating the benthic substratum classes from the photographs, information on the substrate size measured during field observations was used. For the benthic substratum, a slightly modified Wentworth (1922) scale was used. In addition to the different aspects of a stream site's geodiversity, a measure of the total geodiversity was calculated by summing the stream surface flow types, substrate classes and geomorphological richness.

In Paper III, geodiversity variables on the catchment-scale contained geomorphological, soil- and rock-type richness at a grid cell resolution of 1-km^2. Geomorphological data was computed using landform observations, GIS-based environmental features and generalized additive modelling (Hjort & Luoto 2012). The landform observations were based on work by an expert geomorphologist who surveyed aerial photographs (~30 cm resolution) and geomorphological maps (1:50,000). Later, a geomorphological distribution modelling method was used to predict the number of landforms in each 1-km^2 grid cell covering Finland. The landform observations and GIS-based environmental variables were used in generalized additive modelling to produce geomorphological richness values for the grid cells (Hjort & Luoto, 2012, 2013; Tukiainen *et al.* 2017).

The soil and rock-type richness on the catchment-scale were calculated by summing the number of soil and rock types in a 1-km^2 grid cell. The calculations were based on digital bedrock and soil maps covering the whole of Finland (GSF 2010a, 2010b). The soil types considered in the classification were: (1) rock (bare rock or thin soil cover; < 1 m), (2) till (glaciogenic deposits), (3) stony areas and block fields, (4) sand and gravel, (5) silt, (6) clay, (7) gyttja (lake and sea sediments; > 6% organic material), and (8) peat. The rock-types were classified by an expert into 16 genetically and geochemically distinct classes (for more detailed information see: Tukiainen *et al.* 2017 and Table 1 in Paper III). Additionally, the geodiversity measures were calculated for the whole of Finland and afterwards reduced to match the catchment boundaries in the ArcGIS 10.5. software environment.

3.6 Statistical techniques

Statistical methods that have been widely used in ecological studies comprise different multivariate analyses, which allow the studying of the relationships between species and environmental characteristics (Dray *et al.* 2012). Multivariate methods used in the context of community-environment studies can be categorized into two types. First, in canonical analysis, raw species-based information serves as the response to be explained and environmental variables act as predictor variables. Second, distance-based methods operate with biological dissimilarities and distances calculated from scaled and standardized environmental variables or with spatial distances.

In Paper I, a Mantel test (Mantel 1967) and its modifications (Clarke & Ainsworth 1993) were used to explore biological dissimilarities between sites along with spatial and environmental distances between them. Prior to the statistical testing, biological dissimilarity matrices based on presence-absence or abundance data using Sørensen (presence-absence) and Bray-Curtis (abundance) coefficients, respectively, were used to examine the differences in species composition between the streams and, further, the dissimilarity matrices created previously were used in Mantel test and partial Mantel test. Both dissimilarity coefficients are widely used in ecology (Faith *et al.* 1987; Legendre & Legendre 2012). For all habitat variables, standardized values with zero mean and unit standard deviation were used to construct Euclidean distance matrices, describing the environmental distances between stream sites. In addition, the environmental matrices were reduced related to each response matrix (e.g. for the entire community and separately for each body size class or each dispersal mode group) removing unwanted noise in the environmental distance matrices as much as possible, using a BIO-ENV (Best Subset of Environmental Variables with Maximum (Rank) Correlation with Community Dissimilarities) analysis (Clarke & Ainsworth 1993). The method starts with a community dissimilarity matrix and environmental distances, then selects all the possible subsets of environmental variables and subsequently calculates Euclidean distances for each subset. Finally, BIO-ENV finds the correlation between the community matrices and environmental distances, and uses the best combination of environmental variables, which correlates most strongly with the biological dissimilarity matrix (Clarke & Ainsworth 1993). Subsequently, the obtained environmental distance matrices and spatial distance matrices were used with all types the biological dissimilarity matrices using Mantel tests and, when controlling for the spatial distances, partial Mantel tests were used.

In Paper II, biodiversity-environment relationships were examined using linear regression and a regression-based commonality analysis (Ray-Mukherjee *et al.* 2014). Linear regression models with forward selections were run for all the environmental and geodiversity variables. The selection of the set of final predictors was based the lowest possible AIC (Akaike information criterion) value (Akaike 1973; Johnson & Omland 2004). A regression-based commonality analysis improves the interpretation of the output of linear regression models because it decomposes basic regression effects (R^2) into unique and common effects. Unique effects describe the proportion of variance explained by one predictor, whereas common effects express the proportion of variance explained by a larger set of predictors (Nathans *et al.* 2012; Ray-Mukherjee *et al.*, 2014).

In Paper III, boosted regression trees (BRTs) were used to explain the variation of species richness and to measure the relative influences of the predictors. BRT is machine learning method that can be understood as an advanced type of regression modelling (Elith *et al.* 2008). Machine learning methods have many benefits such as their robustness to collinearity and missing values in the data. Furthermore, their ability to handle non-linear relationships and variable interactions offer many benefits over the more traditional statistical methods (Elith *et al.* 2008). In recent years, related methods of decision trees have been used in many fields, including ecology (Thuiller *et al.* 2003; Feld *et al.* 2016; Jyrkänkallio-Mikkola *et al.* 2017) and biodiversity-geodiversity explorations in the terrestrial environment (Bailey *et al.* 2017; Tukiainen *et al.* 2017).

Using the 'gbm.step' function allowed to calibrate BRT models with three parameters to identify. First, tree complexity means the model complexity in terms of allowed interactions between independent variables. Second, bag fraction divides the input data into calibration and evaluation data. Third, the learning rate can be specified. Additionally, the competence of the models was estimated using the percent of explained deviance. To understand the effects of specific variables on species richness, the relative influence of each predictor variable was acquired from 'gbm.step'. In addition, partial dependency plots were created to explore the effect of the predictor variables on species richness (Müller *et al.* 2013; Mouchet et. al. 2015). The final models were validated by 10-fold cross-validation by subsampling the data 10 times according to the bag fraction used. Finally, the assumption of spatial independence of the response and predictor variables as well as residuals of the final BRT models were tested using Moran's I correlograms (Legendre & Legendre 2012).

4 Results and discussion

4.1 Summary of the results

The results of this thesis are structured based on the three Papers (I–III; Table 3). Overall, the goals were to test (i) how well stream biodiversity can be explained with traditional environmental variables and (ii) if there is a relationship between geographic proxy variables and biodiversity indices. According the results of Papers I–III, the biotic variation were best explained by traditional variables, thus clearly supporting hypothesis **H1,** where it was expected that local environmental features are important for biodiversity. Additionally, promising results were obtained on the role of geographical variables, especially when the relative influences of geodiversity on biodiversity were compared to traditionally used environmental variables. This supports hypothesis **H2** about the usefulness of variables based on geographical proxies to explain variation in stream biodiversity.

In Paper I, the effect of different distance types on the structure of the stream insect community for 55 stream sites within the River Tenojoki drainage basin was examined. Apart from the more commonly utilized overland and watercourse distances in the studies of the distance-decay relationship, the objective was to measure the effect of the least-cost above surface path measurements between sites and correlate them with community dissimilarities. The focus was also to study how the classification of stream insects by their maximum body size and dispersal mode would affect the community structure of the stream sites. According to the main results of the Mantel tests, the community structure was more strongly correlated with environmental aspects than the physical distances between sites. On the other hand, the community structure was also significantly associated with physical distances between sites, thus clearly supporting the geographical approach used in the study.

In Paper II, we examined the power of mesoscale geodiversity variables in explaining the variation of macroinvertebrate biodiversity, in comparison to the traditionally used environmental variables. In this study, photographs taken during the field work were used in a novel way to define the geodiversity for stream reaches. Although traditionally used environmental variables remained the most important predictors of biodiversity, the results of a commonality analysis indicated the feasibility of using geodiversity variables in the evaluation of stream habitats and as a predictor of stream biodiversity. Most importantly, a significant relationship between surface flow-type or total geodiversity and biodiversity was detected.

Paper III explored the effects of three geodiversity variables, two land use variables and four local habitat variables on the richness of macroinvertebrates, diatoms and bacteria. According to the results, a substantial effect of the catchment geodiversity on stream biodiversity was detected, although the local habitat variables remained the strongest predictors of biodiversity variation. Of the geodiversity measures, the soil-type richness

Table 3. Summary of the key results from the three Papers I–III.

Paper I	Paper II	Paper III
Stream insect communities corresponded to the environmental and geographical variables used.	Biodiversity correlated strongly with traditional habitat variables.	The role of the local habitat conditions and land use variables related to biodiversity was evident.
Community structure was better explained by the environmental than physical distances between sites.	The relative importance of geodiversity, e.g. flow richness, on macroinvertebrate diversity was also shown.	A notable relationship between the soil-type richness and biodiversity was detected.
The importance of physical distance was also noted. Especially the cost distance showed its novelty value.	The total geodiversity on the mesohabitat level seems to be a relevant variable for stream biodiversity.	The indirect effect of geodiversity on biodiversity was probably through water chemistry.

correlated best with the biodiversity of stream organisms (Table 3; see also Figure 4 in Paper III).

4.2 Linkages between environmental or geographical distances and community dissimilarities

According to the results of Paper I, the environmental variables selected in the BIO-ENV analysis varied slightly between subsets of species groups as well as between the abundance and presence-absence data used in the analysis. In general, several habitat and water chemistry variables were selected for the best environmental distance matrices, although moss cover seemed to be the most important one because it was included in all environmental distance matrices. For the presence-absence data, more variables were included in the environmental distance matrix compared to the abundance data. Otherwise, environmental variables were selected for both dissimilarity matrices (presence-absence and abundance data). Correlations of each response matrix to the environment distance matrices varied slightly. The variables selected from the BIO-ENV were used in Mantel tests, and according to the main results of Paper I, environmental distance matrices correlated more to the community structure than geographical distance types (Figure 6). Thus, the results supported **H3**, and this was generally true for all subsets of insects, although entire communities and passive dispersal groups differed from the others, showing the strongest correlation with the environmental distance matrices. Similar results on the relationships between environmental distances and communities have been found in a few other studies of aquatic environments (Brown & Swan 2010; Grönroos *et al.* 2013; Cañedo-Argüelles *et al.* 2015), which also supports the idea that the presence of a species in a location is dependent on environmental filters on multiple spatial scales from the catchment to habitat (Poff 1997). We also detected clear, albeit variable support for **H4**, where it was expected that different geographical distance types (i.e. overland, watercourse and cost distances) within the drainage area may act as proxies for dispersal effects for stream insect species. This is because all the three distance matrices were correlated significantly with some biological dissimilarity matrices. In general, groups of passive dispersers, as well as the size class of 0.50–1 cm, and all species appeared to be the most responsive to geographical distances, and there were only minor changes in correlations after controlling for the environmental distance. This was because environmental and spatial distances were weakly correlated across the study area.

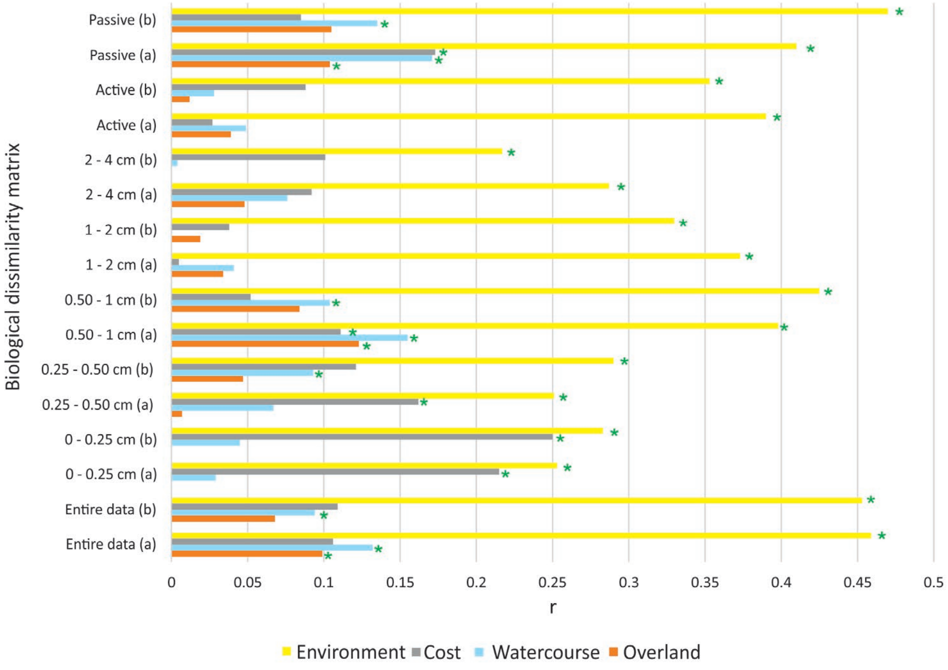

Figure 6. The results of the Mantel test for abundance data based on Bray-Curtis biological dissimilarity matrices (a) and presence-absence data based on Sørensen biological dissimilarity matrices (b). Shown are only positive values, and the correlations between biological dissimilarities and physical distances are shown after controlling for environmental differences. * $p < 0.05$.

The reasons for the stronger role of environmental differences explaining the biological dissimilarities may lie in the time of the sampling or the nature of sampling sites. On the one hand, the time of the sampling period in the River Tenojoki drainage basin (late spring – early summer) is also the time when there may still occur high melt-water discharge which in turn causes the unlimited drift of species from the upper sections of streams and thus weakens the possible detectable environmental signals (Göthe et. al. 2013). On the other hand, the prevailing environmental features of the study sites may represent more headwater (i.e. smaller stream order) than midstream (i.e. larger stream order) conditions. Thus, it appeared that the community structure was, on average, unaffected by the used distance measures, and biological communities were structured mainly by local environmental factors (Brown & Swan 2010). However, even the weak relationships between the physical distances and biological dissimilarities could indicate that biological communities were affected by the joint influences of local environmental features and the spatial location, i.e. the geographical distances between sites (Thompson & Townsend 2006; Göthe *et al.* 2013).

Of the spatial distance types, the biological dissimilarities were slightly better explained by the watercourse distances than by the overland distances. This only partly supports the traditional approach, which assumes that most of the dispersal of stream insects occurs along stream corridors (Malmqvist 2002; Petersen *et al.* 2004). This finding may stem from the fact that the study sites were situated close to each other without longer sections of stream reaches between the main channel and stream sites. In fact, the observed pattern was shown as a high correlation between the overland and watercourse distances (Mantel r = 0.901). Additionally, including the sections of larger rivers within the potential dispersal routes via watercourses may have hindered the importance of the stream corridors compared to the overland distances (Grönroos *et al.* 2013). On the other hand, a considerable role of overland distance may be that the topographic heterogeneity of landmasses was not enough to represent a greater obstacle for dispersal. For instance, Tonkin *et al.* (2017) found a clearer dispersal role along the river network in relation to overland dispersal in Himalayan streams, which may highlight the role of overall topographic variation and the landscape complexity on dispersal through different routes (Tonkin *et al.* 2018). An interesting exception was that the cost distance measures, which represent the force of resistance faced by an organism according to topographical factors (McRae 2006), differed greatly from the simple spatial measures between sites. Actually, there were no clear correlations between the cost distances and the other two spatial distance measures.

Moreover, although we did not include highly sophisticated cost distance measures, such as the properties of the land cover or the effects of wind, the results were nevertheless encouraging. In our study, the group of the smallest size class of insects were more related to the cost distances, which suggests a different role for the least cost paths in structuring the distributions of the smallest members of stream insect communities. While overland and watercourse routes are assumed to be the most used dispersal routes of stream organisms (Malmqvist 2002), the least cost path approach could work even better, especially if the landscape resistance to organisms' dispersal is considerable.

4.3 The relationship between geodiversity and stream biodiversity

In Papers II and III, the geodiversity at multiple scales was tested as a proxy variable for environmental heterogeneity and as a predictor of stream biodiversity variation. In general, measures of geodiversity had a noticeable contribution to the biodiversity of stream organisms in both study areas. Scaling the stream geodiversity to the mesoscale (II) showed that the flow type richness (i.e. observable water surface variability) in particular was related to species richness and the functional richness of the stream macroinvertebrates. Of the catchment geodiversity (III), the soil-type richness was the most important geodiversity measure for the variation of stream biodiversity.

4.3.1 The relative roles of habitat-scale variables and mesoscale geodiversity on stream macroinvertebrate diversity

Paper II found a notable relationship between biodiversity indices and the measures of geodiversity and traditional environmental variables, supporting **H1** and **H5**. Of the traditionally used environmental variables, the most important variables related to the diversity of macroinvertebrates were depth, width, pH and current velocity. Among the geodiversity indices, the flow richness emerged as the most important variable for the different measures of biodiversity. Additionally, the influences of the geodiversity indices were dominantly positive across the biodiversity measures. The main results of the commonality analysis revealed in more detail that the flow richness had the highest unique power of explanation on species richness (82% relative independent contribution). In addition, the Shannon diversity, Simpson diversity and functional evenness responded positively to the flow richness on stream sites. An interesting finding was the clear positive relationship between total geodiversity and species richness or the functional richness (Figure 7; see also Figure 4 in Paper II for the main results), although the former relationship was not detectable in the results of commonality analysis.

A well-known fact is that stream macroinvertebrate biodiversity is affected by local habitat conditions, such as the stream width, stream depth, velocity and water chemical properties (e.g. Malmqvist & Mäki 1994; Poff 1997; Vinson & Hawkins 1998). The current velocity and the size of the stream channel (i.e. depth and width) are closely associated with the conditions of the streambed. Macroinvertebrates must be adapted to the balance between physical drag forces and the profits owing to the import of food and nutrients

(Allan & Castillo 2007), and different species usually respond differently to these features (e.g. Hildrew & Giller 1994). While our results corroborate previous studies about the role of traditional in-stream variables, we also obtained positive signals of the effect of hydraulic variations on the stream biodiversity (e.g. Reid & Thoms 2008). The surface flow richness may indirectly affect the conditions on the streambed and above it, and hence macroinvertebrates must be adapted to such conditions. For instance, a stream reach with flow types associated with high velocities may be too homogenous for most of macroinvertebrate species. On the other hand, stream reaches with heterogeneous flow types (i.e. variable flow conditions on the streambed) could offer variable habitat settings and, for instance, shelter from harsh current conditions (Biggs *et al.* 2005). In fact, the positive relationship between total geodiversity and biodiversity found for the functional richness indices is in line with this assumption. Functional richness shows the trait space that is occupied by the species present in a certain habitat (Mason *et al.* 2005) and, thus, the total sum of geodiversity measures may better reveal the variation in habitat conditions than the traditionally used environmental variables.

In spite of the quite clear relationship between geodiversity and some of the biodiversity indices, there was no perceived relationship between the substratum richness or geomorphological richness and biodiversity. Especially, the weak role of the substratum was surprising because substratum has been noted as one of the key variables in structuring stream habitats mainly due to its effect on environmental heterogeneity (e.g. Vinson & Hawkins 1998). One potential reason for this finding may stem from the problems of using overly simple classifications to characterize the stream bottom units, or it may be that the variation in terms of substratum particles in the Tenojoki River basin is not large enough to show the relationship between the variability of the substratum and biodiversity. Additionally, the minor role of geomorphological types in the macroinvertebrate richness was somewhat unexpected. This is because it has been previously proposed that channel

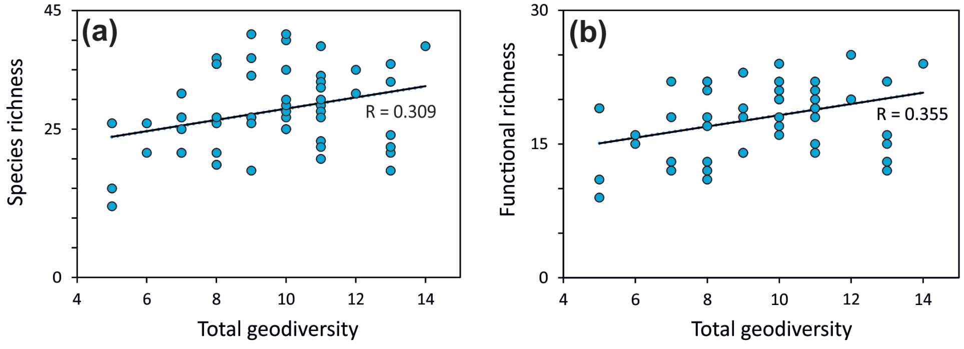

Figure 7. The relationship between total geodiversity and species richness (a) or total geodiversity and functional richness (b).

types within geomorphic typologies may harbour diverse physical characteristics, which in turn, would lead to biotic differences (Braaten & Berry 1997; Milner *et al.* 2015). Additionally, the geomorphological typology in this study encompassed a wide variety of features that can be related to the habitat preferences of different organisms (Giller & Malmqvist 1998). Again, a potential reason for an absent relationship may lie in the overly homogenous habitat conditions of the study sites. Additionally, geomorphological features, such as sand and gravel bars and depositions of fine sediments may be too small in size to affect macroinvertebrate distributions. For instance, Milner *et al.* (2015) classified whole stream reaches based on geomorphological typology and found stronger relationships between the macroinvertebrate community structure and geomorphology.

4.3.2 The effects of local environmental, land use and catchment-scale geodiversity variables on variation in stream biodiversity

The data analyzed in Paper III illustrated the importance of local-scale environmental and catchment-scale land use variables in explaining the species richness of different organismal groups. This is consistent with many studies, where the roles of local environmental (Hildrew & Giller 1994; Malmqvist & Mäki 1994; Soininen 2007; Wang *et al.* 2017) and land use (Tonkin *et al.* 2016; Pajunen *et al.* 2017) variables on stream organisms have been observed. Additionally, using the geodiversity measures to a wide spatial extent, showed that the geodiversity-based approach could capture some variation in macroinvertebrate, diatom and bacteria species richness. Thus, this finding partly supports **H6**. The relationship between geodiversity and biodiversity has been recognized especially in terrestrial ecosystems (Andersson & Ferree 2010; Stein *et al.* 2014; Tukiainen *et al.* 2017), but similar results are largely lacking in the freshwater realm (but see Toivanen *et al.* 2019).

According to the results, the performance of the BRT models was the highest for macroinvertebrates (53% of the explained deviance) and diatoms (50%), whereas the model performance for bacteria richness (38%) was considerably lower (Figure 8). Further, the BRT models showed that the most important local habitat variables affecting macroinvertebrate biodiversity were those that presented variations in physical-morphological aspects of streams (e.g. width, depth) and variables related to the stream water chemistry (e.g. pH). The variables based on land use were less important, whereas geodiversity variables connected to the soil-type and geomorphological landforms showed a higher relative influence on the macroinvertebrate richness. Variation in bacterial richness was explained by physical (i.e. current velocity) and chemical (i.e. pH) variables, whereas depth and width were less important. Similarly to macroinvertebrate richness, variables related to land use were relatively weak predictors of bacterial richness. On the other hand, the soil-type richness of the drainage areas showed a higher importance in explaining bacterial richness. Different from the two previous organismal groups, the model for diatom richness was distinct, as the variables with the highest relative influence

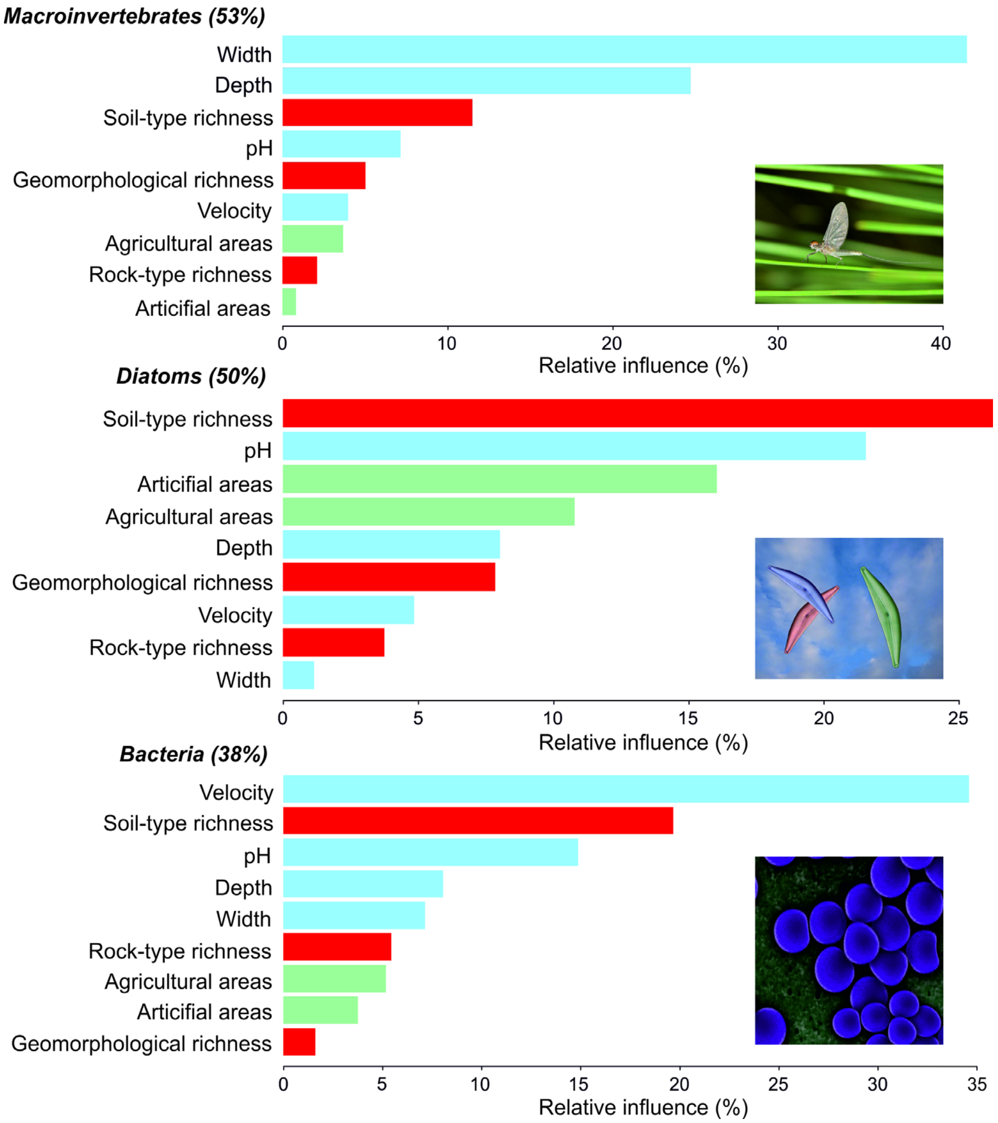

Figure 8. A boosted regression tree summary showing the relative importance of each variable on the richness of different biotic groups. Numerical values after a biotic group's name shows the percentage of deviance explained (%) by the respective model.

on species richness were those directly or indirectly related to the catchment properties. In fact, the soil-type richness had the highest effect on diatom richness before pH and land use variables.

The physical variables of the streams were the main factors accounting for variation in macroinvertebrate richness. One possible reason for this may lie in the 'area effect', whereby larger streams should offer more habitats for macroinvertebrates than smaller streams (Vannote *et al.* 1980; Heino *et al.* 2003). In fact, this is a plausible reason because the size of study streams varied from rather small headwater streams to larger mid-order rivers. In the mid-order rivers, the autochthonous primary production and organic transport from upstream to downstream direction could offer more resources for species and thus the macroinvertebrate richness may be higher than in headwater streams (Vannote *et al.* 1980). In addition, depth may be related to the amount of sunlight that reaches the stream bottom and, therefore, is essential to autotrophs, which in turn acts as energy sources for higher trophic levels in streams (Allan & Castillo 2007). The relative influence of the current velocity in controlling stream diatom and bacteria richness has been found in previous studies (Bere *et al.* 2016; Wang *et al.* 2017). High stream velocities may act as disturbance factor for microbes (Schneck *et al.* 2017), or it can be related to high turbidity, that may reduce light availability for stream organisms. This possible effect of high velocities was shown especially for bacteria whose richness decreased in velocities over 0.3 m/s.

Catchment-level characteristic are known to affect stream environments in complex ways (Allan 2004). In this study (III), the effects of catchment-level variables, including land use and geodiversity were noted for both diatoms and bacteria groups. The contribution of land use to microbial richness was not surprising, as many recent studies have obtained similar results of the combined role of land use and water quality in explaining the structure of stream communities (Tonkin *et al.* 2016; Pajunen *et al.* 2017; Jyrkänkallio-Mikkola *et al.* 2017). The reason behind the relatively high influence of agricultural and artificial land use on diatom richness may stem from the fact that slightly modified areas may maintain higher diatom richness than highly impacted or pristine areas (Jyrkänkallio-Mikkola *et al.* 2017). Moreover, the effect of anthropogenic land use can be related to their role as a proxy variable for water chemistry, especially the pH (Varanka & Luoto 2012) and nutrients, which have been noted as important variables for microbial communities (Soininen 2007). On the other hand, the minor role of agricultural and artificial land use in structuring macroinvertebrate diversity may be explained by the overall relatively pristine catchment conditions across Western Finland. Macroinvertebrate communities may remain in good condition until the extent of agriculture is very high, typically more than 30%–50% (Allan 2004), whereas the average amount of the human affected landscape in the stream catchments remained well below 20% in Western Finland.

An interesting finding was that soil-type richness showed a rather strong positive effect on the richness of macroinvertebrates, diatoms and bacteria. Similarly to the land use variables, the soil-type richness may reflect the water quality of entire catchments. This result is partly in line with the previous studies on species richness-soil-type richness studies. For instance, Passy (2010) reported that diatom richness increased as dissolved organic carbon (DOC) and iron concentrations increased owing to the presence of wetlands in the catchment. Moreover, a recent study found a similar positive relationship between aquatic plant richness and soil-type richness (Toivanen *et al.* 2019). The weathering of different rocks and ground materials contributes to the dissolution of essential nutrients into streams, which in turn may benefit stream organisms (Leland & Porter

2000). Although the reasoning behind the importance of the soil-type richness is yet speculative, soil-type richness may describe the variability of catchment conditions in a more comprehensive way than the percentage of land cover (Leland & Porter 2000). It may also be that the soil-type richness reveals information about the water sources (e.g. springs and peatlands) or it could also be possible that catchment-scale geodiversity is a more robust proxy for water quality than in-stream water samples. Thus, a measure of soil-type richness may offer a more persistent variable to explore water quality with little effect of spatial-temporal variation due to factors such as atmospheric deposition (Likens 2013). On the other hand, as both the soil-type richness and geomorphological richness were explained the richness of macroinvertebrates and diatoms, it appears that the diversity of catchment features (i.e. environmental heterogeneity) may support species richness in freshwater ecosystems (Soininen *et al.* 2015; Toivanen *et al.* 2019).

The rock-type-richness was not important in explaining the variation of stream biodiversity, which was opposite to previous findings concerning a relationship to periphyton-basin geology relationship (e.g. Biggs 1990). It is likely that igneous and metamorphic rocks present in Western Finland have restricted weathering capabilities and result in smaller ionic concentrations compared to many other areas. In addition, the landscape dominated by till and other surficial sediments should restrict the weathering of bedrock in the study area (III).

4.4 Strengths and caveats of using geographical proxies to explain stream biodiversity

Based on the results of Papers I–III, it has been shown that explanation of stream biodiversity variation using geographical proxies along with more traditional local- and catchment-scale variables may provide valuable information for stream ecologists and environmental managers. In this study, the proxies for spatial and local habitat conditions included geodiversity elements on the habitat and catchment scales and three different geographical dispersal routes within a drainage basin. All these variables were measured on scales which have been widely recognized to be important for stream organisms, acting through regional and local processes (e.g. Hynes 1970; Frissel *et al.* 1986; Poff 1997; Malmqvist 2002; Heino 2009). Moreover, the variables examined in this thesis, may also provide new information and perspectives on the exploration and management of stream biodiversity. However, one must consider the strengths and limitations of the geographical variables used before explicit and far-reaching conclusions can be made.

The application of distance-based measures (Paper I) may provide opportunities for dispersal studies in aquatic ecology. This is because direct methods to quantity dispersal (e.g. mark-recapture of animals; Petersen *et al.* 1999) and indirect methods such as population genetic variation (e.g. Hughes 2007) have been shown to be rather difficult to utilize or are expensive (Heino *et al.* 2017). Instead, measures of physical distance provide valuable proxies for dispersal routes within a drainage basin (Landeiro *et al.* 2011; Göthe *et al.* 2013). Easily accessible spatial data (e.g. DEMs) and land cover data offer many possibilities to construct different dispersal route matrices which are potentially important for the dispersal of organisms. For instance, resistance maps for cost-distance calculations can be based on various features of the landscape. Including features such as information on the canopy cover, landscape curvature and elevation for resistance maps of cost distance surfaces may help to gain a better understanding of species dispersal in the complex riverine landscapes (Heino *et al.* 2017; Tonkin *et al.* 2018). In general, the importance of physical distances as proxies for dispersal and the importance of dispersal in general are highly context dependent, which emerges from variability in biological, geographical and environmental settings (Heino *et al.* 2015; Tonkin *et al.* 2018). Moreover, the spatial scale of a study may play an important role in understanding dispersal phenomena. For example, while studies conducted at local scales found random distributions of the caddisfly *Drusus discolor* (Geismar *et al.* 2015), Pauls *et al.* (2006) showed dispersal limitations in larger regions for the same species. In addition, the resolution of spatial data is critical. In our study, the grid cell size was probably too coarse (25 × 25 m) for the accurate description of dispersal routes for stream insects.

The method of using representative photographs to characterize the stream flow-richness and geomorphological features at the study sites seemed to be a cost-efficient way of measuring geodiversity on the reach-scale (II). For example, it was possible to determine the different forms and processes afterwards, independently from the choices made during the field surveys. Moreover, the use of photographs improved the reliability of the classification because special attention could be paid to the targets otherwise difficult to map and categorize in the field under challenging conditions. An interesting finding in Paper II was the positive relationship between the surface flow-richness and macroinvertebrate richness. Although surface flow features should reflect current conditions within the water column and hydraulic conditions affecting the near-bed microhabitats occupied by most of the organisms (Allan & Castillo 2007), it may suffer from being overly simplistic. For instance, different species respond differently to variability in velocity ranges (e.g. Jowett 2003) or some benthic species favour areas of boulders (Robson & Chester 1999). Therefore, it may be advisable to fine-tune measures of surface flows in an ecologically more relevant way.

Streams are naturally highly variable environments in terms of spatial and temporal scales (Frissel *et al.* 1986; Allan 2004). The role of natural disturbances (e.g. floods) has an especially strong effect on the physical environment of streams and, in turn, on biotic communities (Townsend 1989; Schneck 2017). In high-latitude regions, spring floods are known to inflict natural disturbances on stream communities (Giller & Malmqvist 1998; Göthe *et al.* 2013). Thus, it would be advisable to gather biodiversity and environmental variable data over multiple seasons. Moreover, in stream environments, the pool-riffle morphology of a reach is determined by the geologic, climatic and discharge forces acting in the contributing drainage area (Schumm & Lichty 1965; Frissel *et al.* 1986).

Thus, measuring the geodiversity of longer stream segments (e.g. 100 to 500 m) could provide more information about the effectiveness of geodiversity in explaining stream biodiversity. On the other hand, it is rather safe to argue that the water surface measures used in Paper II are more resilient to hydrological fluctuations than measured velocities on the microhabitat-scale and in a certain period of time.

The scale and contents of the used geodiversity variables in Paper III also require some attention. Geographical and climatic factors should determine stream biodiversity across broad geographical regions (e.g. Martiny *et al.* 2006), whereas a clear environmental control is often detected in local-scale studies (e.g. Heino *et al.* 2003). Thus, one can argue how well the different aspects of geodiversity (i.e. soil, rock and geomorphological landforms) on the scale of 1-km^2 are able to cover processes operating on different scales affecting stream biodiversity. This is a challenging task to cover properly. Therefore, researchers should carefully take the spatial scale into account when studying the relationship between geodiversity and biodiversity in a dendritic stream landscape. Moreover, the intermediate-scale variables would provide a lot of information about processes acting in water-land zones such as the effects of some latent variables not effectively measured by *in-situ* conditions (Soininen *et al.* 2015). In Paper III, we made a strong assumption that the soil-type richness may work as a proxy variable for stream water chemistry (Leland & Porter 2000). However, the relationship between soil-type richness and water chemistry is speculative at present and needs more research. Additionally, as the topographic features of the catchment influence soil erosion (Horton 1945) and the amount of dissolved solids in stream water (Allan & Castillo 2007), it would be advisable to include topographic variables along with geodiversity measures in stream studies. Finally, the weighting of the most relevant soil type classes could better reveal the relationship between the soil-type richness and water chemistry (Leland & Porter 2000; Passy 2010).

4.5 Management implications and future perspectives

In the face of global environmental change, there is an urgent need to define the biodiversity-environment relationship. This is especially true for freshwater environments where the biodiversity patterns remain relatively poorly studied (Heino 2011), and where conservation planning is not as developed as in the terrestrial or marine realms (Abell 2002; Darwall *et al.* 2018). Different from many spatially accumulated terrestrial and marine reserves, the conservation of stream biodiversity should take into account the complexity and connectivity of stream environments (Moilanen *et al.* 2008). For instance, the conservation of biological communities in the mid-sections of a stream network may require the protection of headwater areas (Moilanen *et al.* 2008) or even rely on catchment-scale management (Saunders *et al.* 2002). However, comprehensive knowledge of the most important areas for freshwater biodiversity (e.g. significant areas for the persistence of biodiversity or key biodiversity areas) are still lacking on different spatial scales (Carrizo *et al.* 2017).

The papers in this thesis represent basic research, although the results may have value for applied stream ecology. Catchments with higher geodiversity may offer more resilient environments for species to cope with negative environmental changes compared to more homogenous catchments following the principle of conserving nature's stage (Lawler *et al.* 2015). Furthermore, the consideration of geodiversity information could help in selecting the most important catchments for conservation efforts because measures of geodiversity have been shown to improve predictive biodiversity models (Hjort *et al.* 2012; Tukiainen *et al.* 2017). To obtain a more comprehensive picture of the potential and opportunities provided by geodiversity data, it would be necessary to study biodiversity-catchment relationships at various geographical locations and on multiple scales from habitat to regional scales.

Habitat restoration and management are important approaches to maintain stream biodiversity. Restoration programs often rely on the assumption that different species have different habitat preferences and that abiotic environmental conditions determine biodiversity in stream environments (Palmer *et al.* 2010). In addition, Heino (2013) argue that the consideration of both habitat preferences and dispersal-related processes should be the goal in bioassessment, restoration and conservation programs. In this context, ecologically relevant measures of geodiversity, especially if compiled using remote sensing-based methods (e.g. unmanned aerial system and structure-from-motion photogrammetry) may offer new insights for evaluating stream habitat features. Thus, geodiversity measures may eventually provide possible advantages for the evaluation of the success of stream restoration before and after project starts. Similarly, the failure in the efforts of restoring stream biodiversity after human-induced stressors may not necessarily mean that the projects themselves were insufficient, but it could stem from the lack of understanding of dispersal-related processes within the stream network (Tonkin *et al.* 2018). As potential proxies for dispersal, geographical distance types may increase our understanding of community assembly processes, especially if they are developed further by using more fine-tuned landscape information. To increase the applicability of cost distance measures, it would be important to include ecological knowledge and relevant data in the computation of cost surfaces. For instance, the density and height of vegetation can be derived from airborne laser scanning data (Davies & Asner 2014), or it could be possible to include meteorological wind predictions as factors affecting species dispersal (Heino *et al.* 2017).

Moreover, as shown in Paper II, the different aspects of biodiversity may respond differently to environmental variables. Thus, it would be fruitful to examine how functional and phylogenetic diversity would react to geodiversity measures on the catchment-scale. Additionally, as functional and phylogenetic diversity may respond differently to environmental changes in the freshwater realm (Alahuhta *et al.* 2019), this kind of information could reveal new insights into the efforts of stream conservation projects based on geodiversity-biodiversity connections.

5 Conclusions

In this thesis, different geographical variables for lotic environments and dispersal-related processes were used to understand biodiversity patterns of northern streams. The main goal was to compare the effectiveness of spatial distances computed by GIS and measures of geodiversity in relation to traditional environmental variables to explain stream biodiversity. The results highlighted streams as multi-dimensional environments, where local environmental drivers, as well as environmental heterogeneity and dispersal in complex landscapes affect biodiversity. In other words, the thesis confirmed that a range of factors on multiple spatial scales and through various processes shape stream biodiversity. Based on the results of this thesis, I draw the following main conclusions (according to the four original study questions):

1. Local environmental features were identified as the main determinants of stream biodiversity variation. However, geographical proxies also proved their value for exploring the relationship between stream environments and biodiversity. In Northern Finland, the spatial effect of geographical distances between the stream sites, and in a separate study, mesoscale geodiversity measures provided complementary information to explain stream biodiversity. In Western Finland, geodiversity variables on the catchment-scale contributed to the patterns of different organism groups.
2. In Northern Finland, although biological dissimilarities were more strongly connected to environmental distances, the value of different geographical distances were also highlighted. Especially, the least cost routes (resistance maps based on landscape topography) proved to be useful for studying dispersal processes in a dendritic stream network.
3. On the habitat-scale, typical local environmental features correlated with biodiversity variation. Moreover, mesoscale features of geodiversity (water flow richness and total geodiversity) were more strongly correlated with macroinvertebrate biodiversity than local environmental variables alone, which underlines the complementary value of geodiversity.
4. Specific geodiversity measures on the catchment-scale (soil-type richness, rock-type richness and geomorphological richness) captured the biodiversity in some cases better than in-stream measures and land use features. These results urge researchers to further explore biodiversity-geodiversity relationships in different types of catchments. Furthermore, relatively easily accessible geodiversity information could be used as one means to decide the most valuable areas for the conservation of stream biodiversity in human-altered landscapes.

Traditionally used environmental variables retained their role as the most important determinants of stream biodiversity; however, the rather weak explanatory powers of the models emphasized that in the field of aquatic ecology there is still room for new perspectives in explaining biodiversity. The use of GIS and RS proxies in examining the variability of stream biodiversity may be a fruitful approach in this regard. However, acquiring a better understanding of the importance of more sophisticated stream and catchment geodiversity measures in explaining biodiversity variation would require more studies in different types of stream systems, organismal groups and on various spatial scales. Additionally, as the complexity of the landscape is partly behind the same processes, consideration of geodiversity and dispersion in the same study could reveal their relative importance in shaping stream biodiversity. If the geographical variables presented in this thesis turn out to be efficient predictors of biodiversity in various situations, they would have benefits and implications for bioassessment. For instance, geodiversity measures implemented with modern techniques such as drones or other unmanned aerial vehicles may reduce the need for costly and time-consuming field sampling. Eventually, the use of GIS- and RS-based measures of stream environments along with the methods of applied ecology could improve the evaluation and conservation of biodiversity in the face of global change.

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Appendices

Errata

Paper III:

Page 2473, in the Biological sampling section is written “For macroinvertebrates …in a riffle section of approximately 100 m^2 was taken.”

It should be changed to “For macroinvertebrates …in a riffle section of approximately 50 m^2 was taken.”