Species Community Structure and Functional Redundancy in Swedish Headwater Streams

Local versus Regional Control

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Abstract

Streams and rivers only contain a small proportion of the Earth's freshwater, but nevertheless harbour much biodiversity. Headwater streams are the most prevalent running water environments, but despite their wide distribution, they are often excluded from important freshwater legislation and national monitoring programmes. This thesis investigated biodiversity patterns of benthic macroinvertebrates and diatoms in headwater streams and the relative importance of local and regional control of community structure. Functional redundancy (i.e. the relative resilience) of a headwater catchment was also assessed.

Alpha and beta diversity made significant contributions to the gamma diversity of the investigated headwaters. Local control of community structure peaked in first order streams and at small spatial extents. Also, biological predictors were able to detect additional local control of diatom assemblage structure. Regional control of community structure was less consistent, and depended on macroinvertebrate dispersal abilities and diatom growth form and size. System-specific spatial variables were also able to detect additional regional control of macroinvertebrate assemblage structure. Results indicated low functional redundancy, and that community structure within invertebrate functional feeding groups was, with a few exceptions, the result of both local and regional control.

I conclude that we are likely to underestimate biological assets (including both alpha and beta diversity) if headwater streams are not included in bioassessment and management programmes. The conservation of this diversity is likely to be most effective when management targets environmental conditions across multiple local sites within relatively small catchments. However, as regional control was detected at both small and large spatial scales, it is important to manage regional conditions (e.g. landscape connectivity), in addition to local site conditions, irrespective of the scale targeted by management. This is especially important because conservation of headwater functions (in addition to biodiversity) is likely dependent on both. Finally, we can increase the accuracy and performance of predictive models by including additional local and regional predictors which are specific to the system and organism studied.

Keywords: benthic macroinvertebrates, diatoms, metacommunity, environmental factors, spatial factors, variance partitioning, β-diversity, α-diversity, stream networks

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Dedication

To my family…

Rivers know this: there is no hurry. We shall get there some day.
-Alan Alexander Milne (Winnie the Pooh)

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Göthe, E., Friberg, N., Kahlert, M., Temnerud, J., Sandin, L. Assessing the conservation value of biodiversity in boreal headwater streams across spatial extents. (manuscript).

II Göthe, E., Angeler, D.G., Sandin, L. (2013). Metacommunity structure in a small boreal stream network. *Journal of Animal Ecology.* 82(2), 449-458.

III Göthe, E., Angeler, D.G., Gottschalk, S., Löfgren, S., Sandin, L. The influence of environmental, biotic and spatial factors on diatom metacommunity structure in Swedish headwater streams. (manuscript).

IV Göthe, E., Sandin, L., Allen, C.R., Angeler, D.G. Cross scale structure, functional redundancy and spatial resilience of a boreal stream network. (manuscript).

Paper II is reproduced with the permission of the publisher.

The contribution of Emma Göthe (EG) to the papers included in this thesis was as follows:

I EG was partly involved in the design of the study and was responsible for collecting field data in the Dalälven catchment. She also did some of the macroinvertebrate identification. JT and LS were responsible for planning and collecting field data in the Lugnån and Danshytteån catchments. The original idea of the paper came from LS, EG, and NF. LS did the data analyses. LS and EG wrote the paper together with NF, with contributions from JT and MK.

II EG planned the study together with LS, was responsible for collecting field data and performed all statistical analyses. EG interpreted the data and wrote the article together with DGA and LS. EG also did some of the macroinvertebrate identification.

III EG was responsible for collecting the data (except water chemistry which SL was responsible for) and performed all statistical analyses. EG was responsible for data interpretation and wrote the article together with DGA and LS with contributions from SL and SG. EG also did some of the macroinvertebrate identification.

IV EG designed the field study together with LS. DGA conceived the idea for the paper and designed the statistical analysis approach. EG collected the field data and performed all statistical analyses. EG interpreted the data and wrote the article together with DGA, with contributions from LS and CRA. EG also did some of the macroinvertebrate identification.

Abbreviations

AEM	Asymmetric Eigenvector Maps
AEM_D	Spatial variables (eigenvectors) based on directional downstream distances, calculated through AEM analysis
AFS	Adult Flying Strength
D_O or S	Spatial variables (eigenvectors) based on Euclidian (overland) distances, calculated through PCNM analysis
DP	Drifting Propensity
D_W	Spatial variables (eigenvectors) based on watercourse distances, calculated through PCNM analysis
E	Environmental variables
FD	Female Dispersal
FFG	Functional Feeding Group
LB	Lower Branch of River Dalälven
OD	Österdalälven
PCNM	Principal Coordinates of Neighbour Matrices
pRDA	Partial Redundancy Analysis
RCC	River Continuum Concept
RDA	Redundancy Analysis
VD	Västerdalälven

1 Introduction

Biodiversity in ecosystems worldwide is decreasing at a faster rate than ever before (Heywood, 1995) largely due to human perturbation leading to degradation and loss of natural habitats (Millennium Ecosystem Assessment, 2005). Freshwater habitats cover less than 1% of the Earth's surface area, but contain approximately 10% of all known species (Strayer & Dudgeon, 2010). It is estimated that between 10,000 and 20,000 of these species are either extinct or seriously threatened, which makes freshwaters one of the most threatened ecosystems on earth (IUCN, 2007; Sala *et al.*, 2000). Such great losses in species diversity is alarming not only because of ethical reasons, but also because it can lead to a decline in ecosystem functioning which sustain important ecosystem services to humanity (Balvanera *et al.*, 2006; Chapin III *et al.*, 2000; Ehrlich & Ehrlich, 1981).

Streams and rivers contain just 0.006% of the world's freshwater (Shiklomanov, 1993), but support a high biodiversity (e.g. Allan & Flecker, 1993). The view that streams are longitudinal systems with linear patterns in environmental conditions and biodiversity has dominated since the development of the River Continuum Concept (RCC) (Vannote *et al.*, 1980). The RCC describes how small, shaded, heterotrophic headwater reaches become medium sized, largely autotrophic, reaches which flow into large rivers that depend heavily on input of processed organic matters from upstream sites. These longitudinal changes in environmental conditions also lead to distinct species communities with distinct traits in different parts of the stream network. The RCC emphasizes both the aquatic-terrestrial linkage (e.g. upstream reaches depend on input of organic matter from riparian vegetation), and the importance of longitudinal linkages (e.g. constant supply of organic matter from upstream to downstream reaches). Any disruptions in these linkages could have consequences for the structure and function of entire stream networks. Such disruptions are already widespread, since a majority of the rivers in the world are affected by human activities (Vörösmarty *et al.*, 2010). This exploitation of stream ecosystems (including habitat degradation, water pollution and flow modifications) poses large threats to the biodiversity of running waters (Dudgeon *et al.*, 2006; Malmqvist & Rundle, 2002).

The most prevalent lotic (running water) environments are headwater streams (Fig. 1). Headwater (first and second order) reaches can comprise ~70% of the total stream length in river landscapes (Leopold *et al.*, 1964). In Sweden, estimates show that streams with catchments <15 km^2 can comprise up to 90% of the total stream length (Bishop *et al.*, 2008). The definition of a headwater stream is debated, but in the literature it often includes first and second order stream reaches (see Fig. 2 for an illustration of stream order classification) (Clarke *et al.*, 2008; Gomi *et al.*, 2002; Strahler, 1957). In this thesis, the term "headwater stream" or "headwater catchment" also includes third order stream reaches (see II, IV), and all streams investigated have catchments <10 km^2.

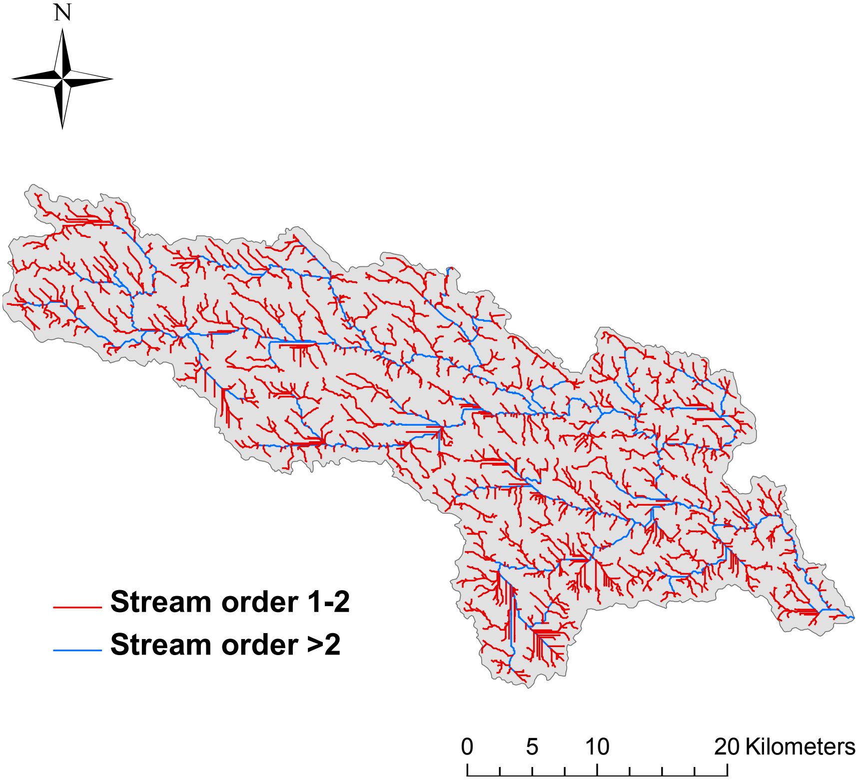

Figure 1. Map showing the wide distribution of headwater streams (first-second order stream reaches, red lines) compared to higher order streams (> second order stream reaches, blue lines) in a randomly selected Swedish catchment (Nätraån).

Headwater streams are not only abundant in the landscape, but also important for maintaining the structure and function of entire catchments. As noted above, they supply downstream reaches with key components (e.g. organic matter and organisms) (Wipfli & Gregovich, 2002) and support unique species communities contributing to regional diversity (Meyer *et al.*, 2007). They also serve as habitats for species during parts of their life cycle (e.g. spawning sites for fish) (Meyer *et al.*, 2007) and can decrease the loading of nutrients to larger streams (Peterson *et al.*, 2001).

Despite this knowledge, headwater streams are often excluded from legislation aiming to assess and conserve the ecological status of freshwaters across larger regions. For example, in the European Water Framework Directive (2000/60/EC), the recommended lower size limit for a water body to be included is 10 km^2. In Sweden's national monitoring programme the lower size limit is 15 km^2, which clearly excludes many upstream reaches in riverine landscapes (Bishop *et al.*, 2008). Also, many of the most distant, upstream reaches remain unmapped (i.e. not visible on maps with standard resolution) (Meyer & Wallace, 2001) and numerous species in these streams are therefore likely to be undescribed (Meyer *et al.*, 2007). Thus, we still know relatively little about whether headwater streams contain a high diversity that merit special conservation initiatives. It is, however, not only important to know whether these streams contain a high total (γ) diversity, but also how this diversity is distributed in the riverine landscape. That is, we need to move away from the linear perspective of streams, where much focus has been on longitudinal changes in local (α) diversity along the watercourses, and start to acknowledge and assess the importance of regional (β) diversity (Clarke *et al.*, 2008). This information is crucial to conservation planning since it will help to determine at which scale "hot-spots" of biodiversity can be found. To increase the likelihood of successful bioassessment and management of headwater streams we also need to elucidate which factors regulate this diversity, and on what spatial scale they operate (Heino, 2012; Bengtsson, 2010).

1.1 Local and regional determinants of stream communities

In this thesis, I use benthic macroinvertebrates and diatoms as study organisms because they are key organisms in stream ecosystems and frequently used as indicator species in monitoring, bioassessment and management (e.g. Battarbee *et al.*, 2010; Wright *et al.*, 1998). In the following two sections, I briefly describe local and regional determinants of stream communities and also indicate which determinants were assessed in the different papers included as part of this thesis.

1.1.1 Local determinants

The effect of local environmental factors on species community structure is one of the most studied topics in stream ecology (e.g. Hill *et al.*, 2001; Vinson & Hawkins, 1998) and there is no doubt that the distribution of both diatom and benthic macroinvertebrate communities are, to some extent, determined by factors such as water chemistry (e.g. acidity and nutrients), hydrology (e.g. stream flow and discharge), and physical habitat characteristics (e.g. substrate composition, stream-width, and shading) (e.g. Heino *et al.*, 2012; Soininen, 2007; Sandin & Johnson, 2004). Local environmental factors are therefore frequently used as predictors in bioassessment programmes (e.g. predictive modeling) aiming to assess the ecological status of stream ecosystems (Heino, 2012). They are also typically the main focus in management and conservation programmes. Local environmental control of species community structure was assessed in all four papers (I-IV) included in this thesis.

Local biotic interactions (e.g. trophic interactions and competition) have been recognized as important determinants for species community structure since the development of the niche concept (Chase & Leibold, 2003) and are also known to structure species communities in streams. However, the unique effect of biotic interactions on species community structure at large landscape scales can be hard to disentangle because they are often mediated by and strongly associated with environmental (e.g. Junger & Planas, 1993; Mulholland *et al.*, 1986) and spatial factors (Verreydt *et al.*, 2012). One way of assessing the structuring effect of trophic interactions on species community structure is to use organism groups at one trophic level as predictors of community structure at another trophic level, while correcting for both spatial and environmental control (e.g. Gray *et al.*, 2012). Diatoms may be useful as study organisms for this purpose. First, experimental studies have shown significant effects of grazing on diatom community structure (see review by Feminella & Hawkins, 1995). Second, diatoms can be divided into functional guilds that are thought to respond differently to grazing (Passy, 2007). In paper III, we assessed whether biological factors (i.e. macroinvertebrate grazers) can explain additional variation in diatom community structure at a relatively large spatial scale by doing separate analyses on different diatom guilds with different susceptibility to grazing.

1.1.2 Regional determinants

It was recognized early on that local species community structure is likely to be the result of a hierarchically nested set of structuring factors, suggesting that local factors affect only a subset of the species pool which has already been subjected to regional factors acting on larger spatial scales (Poff, 1997). Such regional factors do not necessarily have to be of environmental character (e.g. large scale climatic variation), but they can also represent spatial determinants related to dispersal and connectivity between habitats (Brown *et al.*, 2011; Wiens, 2002) (Fig. 2).

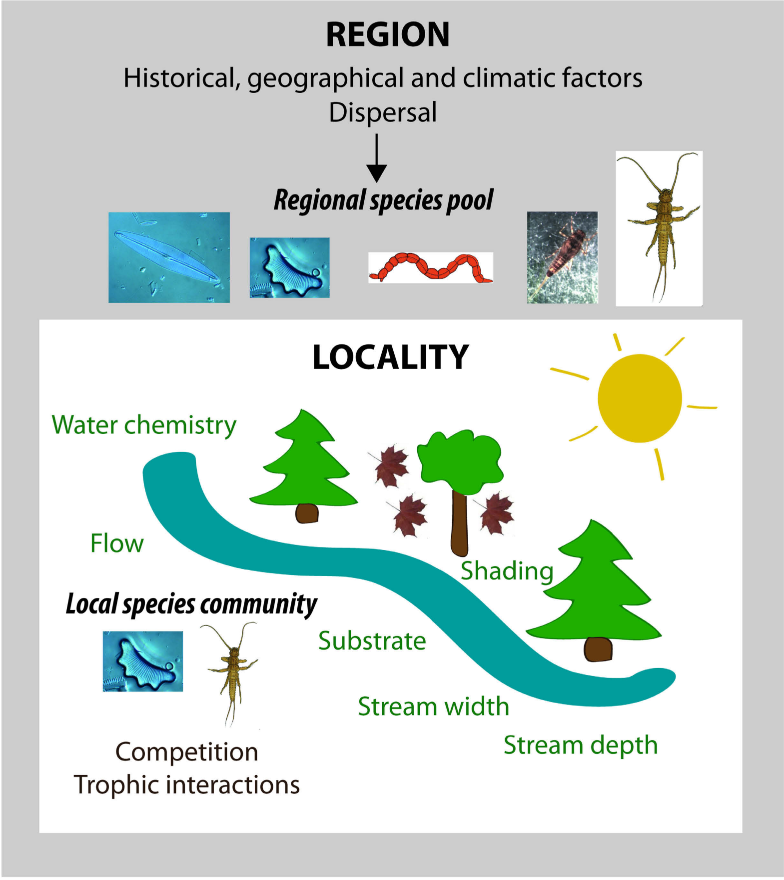

Figure 2. Illustration of how local structuring factors (white square) are nested within regional constraints (grey square). Regional constrains (e.g. historical, geographical, climatic and dispersal related factors) determine which species are available for each local site within a region (i.e. the regional species pool). These species are then subjected to different local environmental (examples are given in green text) and local biotic factors (examples are given in brown text) which ultimately determine the structure of the local species community at any given site.

Spatial determinants are related to the spatial location of streams within a region. Depending on location, streams may be more or less connected to other sites within and across catchments which has consequences for species movements between sites within a region (Clarke *et al.*, 2008; Wiens, 2002). Therefore, spatial control of species community structure is expected to change with the scale of observation (Mykrä *et al.*, 2007) because an increase in the spatial extent will lead to the inclusion of increasingly distant sites. Spatial control of species communities is also expected to change with dispersal ability of the organisms (Brown & Swan, 2010; Thompson & Townsend, 2006) since an increased dispersal capacity will increase the likelihood of an organism reaching all sites within a region.

Spatial predictors have been recognised as important determinants of both benthic macroinvertebrate (e.g. Brown & Swan, 2010; Mykrä *et al.*, 2007) and diatom distributions (e.g. Heino *et al.*, 2010; Verleyen *et al.*, 2009; Soininen, 2004). In previous research, spatial determinants have mainly been based on Euclidian (shortest) distances between sites, representing a proxy for overland dispersal (but see Landeiro *et al.*, 2011; Brown & Swan, 2010) (Fig. 3). In streams, however, a great deal of dispersal occurs along the watercourses and some of this dispersal is largely unidirectional (e.g. drift downstream and flight upstream) (Macneale *et al.*, 2005; Petersen *et al.*, 2004; Giller & Malmqvist, 1998; Kristiansen, 1996) (Fig. 3). To be able to estimate the actual (i.e. total) regional control of stream assemblages, it is therefore important to assess whether other "system specific" spatial variables (i.e. specific to streams and stream organisms) can predict additional variation in species community structure. Spatial variables based on Euclidian distances were used to predict species community structure in papers II-IV. Spatial variables, based on watercourse and downstream directional distances, were used to predict species community structure in paper II.

1.2 Metacommunity theory and its usefulness in stream ecology

The knowledge that both local and regional factors are important determinants for the spatial organisation of stream communities has led to the incorporation of ideas from metacommunity ecology into stream ecology (e.g. Brown *et al.*, 2011). Metacommunity theory emphasises that the structure of species communities is the result of regional factors (e.g. landscape connectivity and dispersal related mechanisms) in addition to local factors (e.g. environmental conditions and biological interactions) (Holyoak *et al.*, 2005; Leibold *et al.*, 2004). In metacommunity research, systems with an insular structure, consisting of habitat patches with discrete boundaries (e.g. rock-pools, ponds, moss patches, islands etc) have been the focus of study, even though many natural ecosystems (e.g. streams, coral reefs, grasslands) have a fundamentally different structure (Logue *et al.*, 2011). Therefore, empirical studies have probably failed to assess the dominant metacommunity type in nature. To elucidate the metacommunity structure of natural ecosystems may seem interesting only from a theoretical point of view. It can, however, also be of use in applied research where the view that species communities are largely under local environmental control still prevails (Heino, 2012). Indeed, the need to acknowledge dispersal related factors and biotic interactions in applied stream research has been emphasised in a number of recent studies (Heino, 2012; Brown *et al.*, 2011; Brown & Swan, 2010).

1.2.1 Metacommunity concepts

Four metacommunity concepts can be used to describe geographical patterns of biodiversity (patch dynamics, neutral dynamics, species sorting and mass-effects) (Holyoak *et al.*, 2005; Leibold *et al.*, 2004).

Two of these, species sorting and mass-effects, both assume that there is an environmental gradient across sites within a region that species respond to. The difference between them is the relative strength of dispersal. The species sorting concept assumes that dispersal is moderate (or sufficient enough) so that species can track and be sorted along local (e.g. environmental) gradients (Holyoak *et al.*, 2005; Leibold *et al.*, 2004). Thus, species sorting will result in significant local effects on species community structure (Cottenie, 2005). On the other hand, the mass-effect concept assumes that dispersal is strong enough to alter species composition in addition to local structuring (Holyoak *et al.*, 2005; Leibold *et al.*, 2004). High dispersal can, for example, sustain maladapted or extinction-prone populations through source-sink dynamics (Mouquet & Loreau, 2003; Mouquet & Loreau, 2002). Therefore, mass-effects will also result in significant spatial (i.e. regional) structures in species communities (Cottenie, 2005).

By contrast, the neutral and patch dynamic concepts assume that patches are similar (i.e. no environmental gradient) and that dispersal is low. The neutral paradigm emphasises that community assembly is due to stochastic events, including ecological drift (Hubbell, 2001). Note that I also use the term “dispersal limitation” in this thesis which refers to spatial effects that stem from low (limited) dispersal, compared with mass-effects that originate from high dispersal (Ng *et al.,* 2009). Dispersal limitation is not a separate paradigm, but rather a key factor in neutral dynamics (Hubbell, 2001) which explains why these terms are often used as synonyms in the literature. The patch dynamic concept stipulates that empty patches are always available because dispersal is too low to compensate for local extinctions. Therefore, species community structure is, to a large degree, dictated by biological interactions between and the colonisation potential of organisms (i.e. strong dispersers are weak competitors and vice versa) (Holyoak *et al.*, 2005; Leibold *et al.*, 2004). When patch dynamics or neutrality are at play, species communities are expected to be spatially structured, but unrelated to environmental gradients (Cottenie, 2005).

1.2.2 Metacommunity structure in stream networks

Stream networks have a dendritic structure, which means that they are linearly arranged and have a hierarchical structure (Fig. 3). In addition, habitat patches have no clearly defined boundaries but are instead continuously linked to each other along watercourses. Dispersal can also occur through different pathways (Grant *et al.*, 2007). That is, dispersal can occur both along watercourses ("within/along-stream dispersal") and across catchments ("overland dispersal") depending on organism type (e.g. fish compared to winged adult aquatic insects) and life cycle stage (e.g. aquatic insect larvae compared to winged adult insects) (Fig. 3).

Environmental heterogeneity in stream networks can be substantial. For example, longitudinal changes in environmental conditions from upstream to downstream sites include changes in temperature, shading, food-resources, flow-regime and substrate composition (Vannote *et al.*, 1980). However, environmental conditions can also vary greatly across stream networks (i.e. non-longitudinal variation). This variability is known to be especially pronounced in headwater areas (Buffam *et al.*, 2007; Temnerud & Bishop, 2005). This is partly due to the dendritic and hierarchical structure of stream networks, which lead to a wider geographical distribution of headwater streams compared to downstream sites. Therefore, headwaters flow through a greater range of terrestrial environments, giving rise to disparate water chemistry and/or hydromorphological conditions (e.g. Buffam *et al.*, 2007) which ultimately affects species community composition (e.g. Petrin *et al.*, 2007). Strong environmental filtering (i.e. species sorting) is therefore expected in headwater areas.

The wide geographical distribution of headwater streams not only has consequences for environmental gradients, but likely also for dispersal. This is because dispersal distances between headwater sites are deemed to be, on average, longer than those between downstream sites (Clarke *et al.*, 2008) (Fig. 3). This means that headwater streams may represent relatively isolated habitats in terms of dispersal (Brown & Swan, 2010; Clarke *et al.*, 2008). Conversely, downstream sites are thought to have a more 'beneficial' position in stream networks (in terms of dispersal) because (i) substantial dispersal can occur from many upstream sites, (ii) they are more connected to other sub-catchments within the region (via watercourses) due to their position further downstream (as discussed by Brown & Swan 2010), and (iii) they are situated closer together in space (Clarke et al. 2008) which facilitates dispersal (along all possible pathways) between similar sites. The spatial structuring of species communities is therefore expected to increase with an increasing stream order due to high dispersal (i.e. mass-effects), whereas dispersal between upstream sites is thought to be, at most, moderate or sufficient enough to allow species to track environmental gradients (i.e. species sorting) (Brown & Swan, 2010). The relative importance of environmental and spatial control of species community structure in upstream and downstream sites was assessed in paper II.

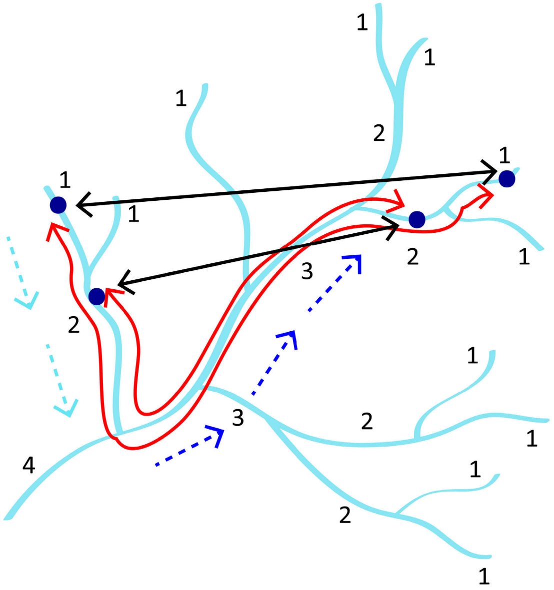

Figure 3. Illustration of a stream network. Numbers represents different stream orders (1-4). Black arrows represent Euclidian distances between two stream reaches (proxy for overland dispersal), red arrows represent watercourse distances (proxy for dispersal along the stream channels) between two stream reaches, and dotted light and dark blue arrows indicate directional downstream and upstream dispersal, respectively. Because first order sites have a wider geographical distribution, the distances between them (length of black and red arrows) are deemed to be, on average, longer than those between further downstream reaches.

1.2.3 Headwater biodiversity

The distinction between different metacommunity concepts is interesting simply from a purely theoretical point of view, but what do the differences mean in terms of biodiversity patterns? First, there are different, and scale dependent, components of biodiversity. Gamma (γ) diversity is defined as the total diversity in a region, beta (β) diversity is defined as the diversity between localities, and alpha (α) diversity is defined as the diversity within a locality (Whittaker, 1972). More precisely, β-diversity is defined as the effective number of distinct communities (stream reaches or catchments) in a region in paper I. Metacommunity theory can help us to make predictions about different diversity components in any system. For example, high dispersal (mass-effects) can lead to higher α-diversity since it may sustain populations that have a negative growth rate (Loreau & Mouquet, 1999; Pulliam, 1988). That is, without high dispersal rates such populations would go locally extinct. However, the similarity between communities on a regional scale may increase (i.e. lead to a homogenization of communities and lower β-diversity) with increasing levels of dispersal (Mouquet & Loreau, 2003). By contrast, dispersal limitation may decrease α-diversity but can lead to a differentiation between communities on a regional scale (high β-diversity). For example, speciation (on longer time scales) and spatial turnover of species communities (on shorter time scales) can be expected to lead to higher β-diversity. Finally, sufficient levels of dispersal accompanied with strong environmental gradients (i.e. species sorting) is also known to lead to high species turnover (β-diversity) (Cottenie & De Meester, 2004; Leibold & Norberg, 2004).

As discussed in section 1.1.2, headwaters represent relatively isolated habitats and the species communities present are likely to be subject to strong environmental gradients. We can therefore hypothesize that they are characterized by high β-diversity and relatively low α-diversity. In paper I, this prediction was tested by partitioning the gamma (γ) diversity (i.e. the total diversity in a region) across a set of headwater streams into its α- and β-diversity components at two spatial scales (within- and supra-catchment scale).

1.2.4 Ecological resilience

To conserve biodiversity may seem important only because of ethical and moral reasons. However, an assessment of ecosystem function can help to determine the ‘value’ of species diversity (Walker, 1992) since human society relies heavily on the services provided by ecological systems (Ehrlich & Ehrlich, 1981).

Ecological resilience is most simply defined as the level of disturbance a system can tolerate, before it is pushed to an alternative stable state and thereby lose its original functions and processes (Holling, 1973). The definition also includes a system’s capacity to reorganize during disturbances so that original functions and processes are maintained (Walker *et al.*, 2004). One aspect of ecological resilience is functional redundancy. Functional redundancy describes how many species can go extinct before an entire functional guild disappears and function is impaired (e.g. Loreau, 2004). Because organisms may perceive their environment at different spatial scales, the hierarchical structure of the landscape (i.e. nested levels of structuring variables and processes) is normally also reflected in the organization of species communities (Holling, 1992). Therefore, it has been recognized that functional redundancy exists, and should preferably be assessed, both within and across such spatial scales (Allen *et al.*, 2005; Peterson *et al.*, 1998). In paper IV, we estimated functional redundancy in a headwater catchment within and across spatial scales.

Another important aspect of ecological resilience is response diversity. Response diversity refers to whether functionally similar species respond differently to disturbances (Elmqvist *et al.*, 2003). Because disturbances are often related to environmental degradation, research has focused mainly on differences in species responses to local environmental change (Elmqvist *et al.*, 2003). In paper IV, however, we assessed the importance of both environmental and spatial factors for structuring taxonomic composition within functional groups and spatial scales.

2 Objectives of the thesis

The overall objective of this thesis was to increase our understanding of biodiversity patterns in headwater streams and investigate what factors regulate community composition in these systems. The specific objectives were to investigate the following:

1. The relative contribution of α- and β-diversity to γ-diversity in headwater streams (I)

2. The importance of different local (environmental and/or biotic) and regional factors (proxies for overland and/or watercourse and/or directional dispersal) controlling community composition in headwater streams (I-IV)

3. Whether the relative importance of local and regional control of community structure depends on organism traits (macroinvertebrate dispersal ability, diatom growth-form and size) (II-III)

4. Whether the relative importance of local and regional control of community structure differs between upstream (first order) and downstream (second and third order) sites (II)

5. The degree of functional redundancy within and across spatial scales in a headwater catchment and the relative importance of local vs. regional factors controlling taxonomic composition within each functional group and spatial scale (IV)

3 Materials and methods

3.1 Study catchments

All study catchments included in this thesis (Krycklan, Dalälven, Danshytteån and Lugnån) are located in the boreal region of Sweden (Fig. 4). All sampled sub-catchments are dominated by forests while the remaining parts consist mainly of wetlands and lakes. The amount of agricultural land in each sub-catchment is small (<10%) as well as the amount of recent forestry activities (amount of clear-cuts <26%).

3.2 Sampling of biota and local environmental variables

3.2.1 Dalälven catchment (I, III)

In total, 30 riffle-sites were selected in the Dalälven catchment. At each riffle-site, a 50 m long representative stretch was selected for habitat characterization, benthic macroinvertebrate, diatom, and water sampling. All sampled sites in the Dalälven catchment were used in paper III. The Dalälven catchment consists of three smaller subcatchments (Österdalälven [OD], Västerdalälven [VD] and the Lower Branch of River Dalälven [LB]). Six randomly selected sites within each sub-catchment were used in paper I.

Benthic macroinvertebrates were sampled with a Surber sampler (14×14 cm) and a total area of ~0.30 m^2 $site^{-1}$ was sampled. Diatoms were sampled according to the European/Swedish standard method (SS-EN 13946; CEN 2003). Stream width, stream depth, flow and canopy cover (shading) was measured and the number of items of coarse and fine dead wood was counted at each site. Water samples were analysed for major anions and cations, total organic carbon (TOC), pH, alkalinity, total phosphorous (Tot-P), total nitrogen (Tot-N), and water colour (absorbance at 420 nm).

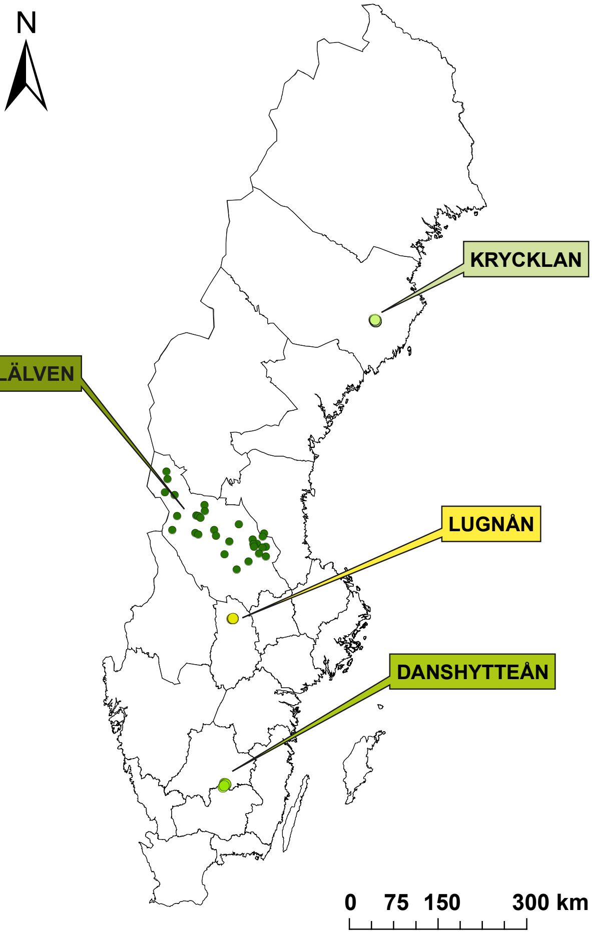

Figure 4. Location of the four study sites (Krycklan, Dalälven, Lugnån and Danshytteån catchment) in Sweden.

3.2.2 Danshytteån and Lugnån catchments (III)

Six sites were selected in each catchment. The selection of sites was restricted to first and second order stream reaches. At each site a 10 m representative stretch was selected for habitat characterization, macroinvertebrate, diatom and water sampling.

Benthic macroinvertebrates were sampled with a Surber sampler (25×25 cm) and a total area of ~0.30 m^2 $site^{-1}$ was sampled. Diatoms were collected according to the European/Swedish standard method (SS-EN 13946; CEN 2003). Stream width and depth was measured at each site and water samples were analysed for pH, Tot-N, Tot-P, TOC and water colour.

3.2.3 Krycklan catchment (II, IV)

In total, 52 sampling sites were selected in the Krycklan catchment. Of these, 30 were first order sites (upstream sites) and 22 were second-third order sites (downstream sites). Upstream sites did not have a stream node (confluence) situated upstream, while downstream sites were always situated below at least one node. Stream-order groups were analysed separately in paper II. In each stream segment, at least two sites were sampled to assess the importance of directional downstream processes (see section 3.3.2). At each site a 30 m representative stretch was selected for macroinvertebrate and water sampling, and habitat characterization.

Benthic macroinvertebrates were sampled with a Surber sampler (14×14 cm) and a total area of ~0.18 m^2 $site^{-1}$ was sampled. Stream width, stream depth, flow, canopy cover (shading), substratum composition and moss-cover was measured and the number of items of dead wood was counted at each site. A drought inventory of the sites during the warmest period of the summer was also performed. Water samples were analysed for major anions and cations, metals (Fe, Al), pH, Tot-N, Tot-P, CO_2, NO_2+NO_3, water colour, and TOC.

3.3 Description of data

3.3.1 Species data

Diatoms and macroinvertebrates were identified to the lowest possible taxonomic level. Normally individuals were identified to species or genus level, with the exception of e.g. Simuliidae (identified to family level), Chironomidae (identified to subfamily level) and Coleoptera (identified to family level). Thus, species (response) matrices consisted of site and taxon specific abundance data of the organism group of interest. In papers II-IV, the response data was further divided into groups of taxa with different traits.

Dispersal ability groups (II)

In paper II, the species data was divided into groups of macroinvertebrates with different dispersal abilities following Poff *et al.* (2006). We focused on three different types of dispersal (drifting propensity [DP], adult flying strength [AFS] and female dispersal [FD]) and assigned taxa to one of three dispersal ability groups: (1) no (only DP), (2) low and (3) high dispersal ability. No DP are genera that rarely occur in drift samples (i.e. mainly found during catastrophic drift), low DP are genera that commonly occur in drift samples, and high DP are genera that are dominant in drift samples. Low FD are genera that fly <1 km before laying eggs, and high FD are genera that can fly >1 km before laying eggs. Low AFS are genera that cannot fly into light breeze (weak flyers), and high AFS are genera that can fly into light breeze (strong flyers).

Diatom growth-form and size (III)

In paper III, diatom taxa were divided into different growth-form (low, high, motile) and size (small or large) guilds. Species within the low-growth guild grow in the boundary layer of the biofilm, close to the substrate (Passy, 2007). The high-growing guild includes species that can grow above the boundary layer of the biofilm and species within the motile guild can actively move relatively fast (Passy, 2007). Species within the small guild have a length of single cells ≤ 15 µm, and a volume of single cells ≤ 100 μm^3, while species within the large guild have a length of single cells > 15 µm, and a volume of single cells > 100 μm^3.

Functional feeding groups (IV)

In paper IV, the species data was divided into macroinvertebrate functional feeding groups (FFGs) (scrapers, filterer-collectors, gatherer-collectors, predators, and shredders) (Merritt & Cummins, 1996; Moog, 1995). Scrapers scrape material from organic and mineral surfaces (mainly feeding on biofilm and attached algae), filterer-collectors filter suspended material in the water (mainly feeding on fine particulate organic matter), gatherer-collectors collect their food from sediment or loose surface films (mainly feeding on fine particulate organic matter and/or biofilm), predators feed on other animals, and shredders chew and feed on coarse particulate organic matter (Merritt & Cummins, 1996).

3.3.2 Explanatory data

Environmental predictors (I-IV)

The environmental predictor matrix consisted of all relevant local environmental variables measured in each study. The environmental variables were always checked for normality and log or square-root transformed when necessary.

Biotic predictors (III)

The biotic predictor matrix consisted of site-specific abundance data of macroinvertebrates known to feed on diatoms (grazer-collectors) (Lancaster *et al.*, 1996; Merritt & Cummins, 1996; Moog, 1995). Taxa within the grazer-collector guild were grouped into orders (Ephemeroptera, Trichoptera, Plectoptera and Coleoptera) and Hellinger transformed prior to statistical analyses. The Hellinger transformation makes data that contain many zeros suitable for linear methods (e.g. redundancy analysis [RDA]) (Legendre & Gallagher, 2001).

Spatial predictors (II- IV)

All data analyses used to calculate spatial predictors were performed in R (R Development Core Team, 2011). Principal Coordinates of Neighbour Matrices (PCNM) analysis (Borcard *et al.*, 2004; Borcard & Legendre, 2002) was used to create spatial predictor variables based on Euclidian distances and watercourse distances. Euclidian distances represent the shortest distance between each pair of sites and can therefore be viewed as a proxy for overland dispersal. Watercourse distances represent the distance between each pair of sites following the stream channel and can therefore be viewed as a proxy for dispersal occurring along the watercourses. The PCNM analysis creates a number of spatial variables (PCNMs) with different sine wave frequencies. The first PCNMs represent sine waves with low frequencies and are therefore associated with broad scale spatial patterns, while subsequent PCNMs represent increasingly higher frequencies and are associated with spatial patterns in species distributions at smaller scales. PCNMs based on Euclidian distances (D_O, S) were used to predict species community structure in papers II-IV, and PCNMs based on watercourse distances (D_W) were used in paper II.

To assess directional spatial processes, Asymmetric Eigenvector Maps (AEM) analysis was used (Blanchet *et al.*, 2008). A binary connection diagram (showing how streams were connected in a downstream direction) and weights (based on the geographic distance of each connection) were used to model directional eigenvectors (AEM_D) (Blanchet *et al.*, 2008). These predictor variables can be viewed as a proxy for downstream directional dispersal and were used as predictors of macroinvertebrate community structure in paper II.

3.4 Statistical analyses

All statistical analyses described below were performed in R (R Development Core Team, 2011). Only the methods that are relevant to the main and specific aims of the thesis are described here. For a description of other statistical analyses used, see descriptions in the individual papers.

3.4.1 Assessing γ-, α- and β-diversity (I)

In paper I, the γ-diversity of diatoms and macroinvertebrates was partitioned into its α- and β-diversity components at two different spatial scales (within- and supra-catchment level). This was done by using the multiplicative partitioning method by Jost (2007). In this method, α is the average value of the diversity index (number equivalents) of the samples, β is the effective number of distinct communities (reaches at the within-catchment scale and catchments at the supra-catchment scale), and γ is the total diversity (α×β) of the region analyzed (Jost, 2007).

3.4.2 Local and regional control of species communities (I-IV)

In paper I, local environmental control of macroinvertebrate and diatom community structure was assessed by using an approach (bioenv) which finds the best subset of environmental variables representing the maximum (Spearman rank) correlation between species community dissimilarities (here based on Bray-Curtis index) and environmental dissimilarity (here based on Euclidian distances) (Clarke & Ainsworth, 1993).

In papers II-IV, redundancy analysis (RDA) (Legendre & Legendre, 1998) was used to assess the relative importance of local versus regional control of species communities. Species (response) data was always Hellinger transformed prior to statistical analyses to make it suitable for RDA (Legendre & Gallagher, 2001). First, explanatory variables (environmental, spatial and/or biotic) were selected with a forward selection procedure (Dray, 2009). Variables that were significantly related to species community structure ($p<0.05$) were then compiled into explanatory matrices (environmental, biotic, and spatial) for further analyses. The relative amount of variation in species community structure that could be explained by each explanatory matrix was assessed through variance partitioning analysis (Legendre & Legendre, 1998; Borcard *et al.*, 1992). Variance partitioning analysis uses partial redundancy analysis (pRDA) to calculate how much of the variance in species community structure that can be explained uniquely by each explanatory matrix after removing the effects of all other explanatory matrices (covariables). The fraction explained jointly by explanatory matrices (shared variance) and the unexplained variation was also calculated. The significance of each testable fraction in the variance partitioning analysis was obtained by permutation tests (Oksanen *et al.*, 2011). These analyses were performed in the same way for each stream-order group (II), macroinvertebrate dispersal ability group (II), diatom growth-form and size guild (III) and each functional feeding group associated with each spatial scale (IV).

4 Results and Discussion

4.1 Diversity in headwater streams (I)

The total (γ) richness in the five catchments was 111 benthic macroinvertebrate taxa and 271 diatom taxa. This value is lower than what has been recorded over larger spatial scales and in larger streams. For example, Heino & Soininen (2007) found 153 invertebrate taxa and 364 diatom taxa in seven catchments across whole Finland, and Stendera & Johnson (2005) found 175 invertebrate taxa in the most taxon rich ecoregion in Sweden. Our estimate of total macroinvertebrate richness is, however, in the upper range (or higher) of what has been recorded in other studies that have included similar stream sizes as we (Clarke *et al.*, 2010; Clarke *et al.*, 2008).

Alpha diversity made a significant contribution to the total (γ) diversity in the headwater streams included in this study. We estimated that, on average, 48% of the total macroinvertebrate taxon richness, and 73% of the total macroinvertebrate Shannon diversity, could be found in local stream reaches within each catchment. For diatoms, that same estimate was 34% of the total richness and 44% of the total Shannon diversity.

β-diversity was also relatively high. On average, 35% of the stream reaches within each catchment comprised distinct macroinvertebrate communities when partitioning was based on taxon richness, with a corresponding average turnover rate per stream reach of 0.22. Diatom β-diversity was consistently higher compared to macroinvertebrate β-diversity. On average, 48% of the stream reaches comprised distinct diatom communities when partitioning was based on taxon richness, with a corresponding turnover rate per stream reach of 0.38. β-diversity was lower for both organism groups when partitioning was based on Shannon index, suggesting that a high occurrence of rare taxa (‘unique’ to individual sites and catchments) contributed to the observed β-diversity patterns. The occurrence of a high number of ‘unique’ taxa in headwater streams has been observed also in previous studies (Danehy *et al.*, 2007). That β-diversity was relatively high is in line with the findings from a global study by Finn *et al.* (2011) who found higher taxonomical (and genetic) β-diversity in low order streams (first to second order reaches) in comparison to higher order streams (third to fourth order reaches). Our estimates of the relative contribution of α- and β-diversity to γ-diversity is also similar to what was found in a study of first order stream reaches in Australia (Clarke *et al.*, 2010).

4.2 Local and regional control of species communities (I-IV)

Local environmental factors were consistently related to macroinvertebrate and diatom community structure in all papers included in this thesis. That is, even though the magnitude of local control (i.e. the amount of variance explained) varied in our analyses, environmental factors were, in most cases, *significantly related* to community structure (I-IV). Thus, species communities in the headwater streams included in this study are clearly subject to some degree of environmental filtering (species sorting) which is consistent with previous studies (e.g. Heino *et al.*, 2012; Heino & Mykrä, 2008). However, environmental control peaked at small spatial extents (I) and in upstream sites (II), emphasizing that local control is scale dependent (Mykrä *et al.*, 2007) and dependent on stream-order type (see section 4.2.3). A unique (and additional) fraction of the variation in diatom community structure could also be explained by local biological predictors (macroinvertebrate grazer abundances) (III). However, the detection of a significant biological relationship between grazer abundances and diatom community structure was dependent on diatom growth form and size (see section 4.2.2).

Regional (spatial) factors also predicted unique and significant fractions of macroinvertebrate and diatom community structure, over both large (III) and small (II, IV) spatial extents, but were less consistently related to community structure compared to environmental factors. For example, the detection of a significant relationship between spatial factors and community structure was dependent on macroinvertebrate dispersal capacity (see section 4.2.1), diatom growth form and size (see section 4.2.2) and the spatial location of sampling sites in the stream network (i.e. stream order) (see section 4.2.3). Further, all spatial variables used in paper II could explain unique and significant portions of macroinvertebrate community structure. In general, however, spatial predictors based on Euclidian (D_O) and downstream directional distances (AEM_D) were more consistently related to community structure compared to those based on watercourse distances (D_W) (II). This suggests that D_O and

AEM_D may be better predictors of macroinvertebrate distributions compared to D_W, whereas D_W may instead be more suitable for predicting the distribution of species that are more restricted to the stream channel (e.g. fish) (Landeiro *et al.*, 2011).

4.2.1 Macroinvertebrate dispersal capacity (II)

In agreement with previous studies (e.g. Brown & Swan, 2010; Thompson & Townsend, 2006), our analyses of macroinvertebrate dispersal capacity groups showed changes in the degree of spatial structuring between low and high dispersal communities (II, Table 1a-b). That spatial structuring changed with dispersal capacity of organisms at a small spatial extent (minimizing the effect of other regional determinants) suggests that the unique spatial structures found are likely to be the result of dispersal related factors. Interestingly, spatial structuring of macroinvertebrates during spring decreased with increasing dispersal capacity for spatial variables based on Euclidian and watercourse distances (D_O and D_W), but increased with an increasing dispersal capacity for our spatial variables based on directional downstream distances (AEM_D) (II, Table 1a-b). Although the results were not consistent between seasons, this finding indicates that both dispersal limitation and mass-effects can occur simultaneously, but through different dispersal pathways. That dispersal limitation can be evident at this small spatial scale could be dependent on the stream type investigated. Some of our sites were intermittent and species may have to constantly recolonize these areas. Species with low dispersal abilities may therefore not have enough time to establish at all sites. As pointed out by Townsend (1989), mass-effects may also be evident through, for example, high downstream dispersal (drift) of abundant species present in, and adapted to, environmental conditions in upstream areas. This finding also deviates from what is expected for more commonly investigated systems in metacommunity research, that often have a more insular structure (e.g. ponds, rock-pools and islands) and therefore fewer potential dispersal pathways.

4.2.2 Diatom growth-form and size (III)

Environmental control of diatom assemblage structure was consistently high. The detection of a significant biological relationship between grazer abundance and diatom assemblage structure was, however, dependent on diatom growth-form and size. That is, biotic factors explained a significant portion of diatom taxonomic composition within all guilds, except within the motile and large-sized guild (Fig. 5). Results from previous experimental studies provide some support of this finding. For example, grazers have been shown to frequently ingest diatoms growing in the upper layer of the biofilm, decreasing their abundance (Hill & Knight, 1988; Hill & Knight, 1987). Diatom species growing closer to the substrate may instead increase in abundance (Hill & Knight, 1987), probably due to release from competition. Moreover, motile diatoms have been shown to be less selectively grazed compared to other guilds (Tuchman & Stevenson, 1991). It is important to note, however, that our analysis does not allow us to determine mechanistic causes behind the observed patterns. Despite this limitation, the biotic predictor matrix could explain additional variation in diatom community structure, most likely reflecting the detection of additional local control. This finding is consistent with results from previous studies in both lakes (Gray *et al.*, 2012) and streams (Johnson & Hering, 2010).

Pure spatial gradients (regional effects) were also dependent on diatom growth-form and size. Significant spatial structures were evident in all diatom guilds, except the motile and large-sized guild (Fig. 5). Because very little is known about diatom dispersal, we can only speculate about the underlying mechanism behind this finding. However, we do not exclude the possibility that it could reflect differences in diatom dispersal capacity. For example, it has been suggested that locally abundant species are also globally abundant and therefore represent taxa that are more easily/frequently dispersed, while the opposite would be true for locally rare species (Soininen & Heino, 2005; Finlay *et al.*, 2002). In our study, the motile and large-sized guild generally comprised taxa with lower abundances in comparison with the small-sized, high- and low-growth guild. Interestingly, size has been suggested to be a possible important trait which may influence diatom dispersal capacity (Heino & Soininen, 2006; Kristiansen, 1996).

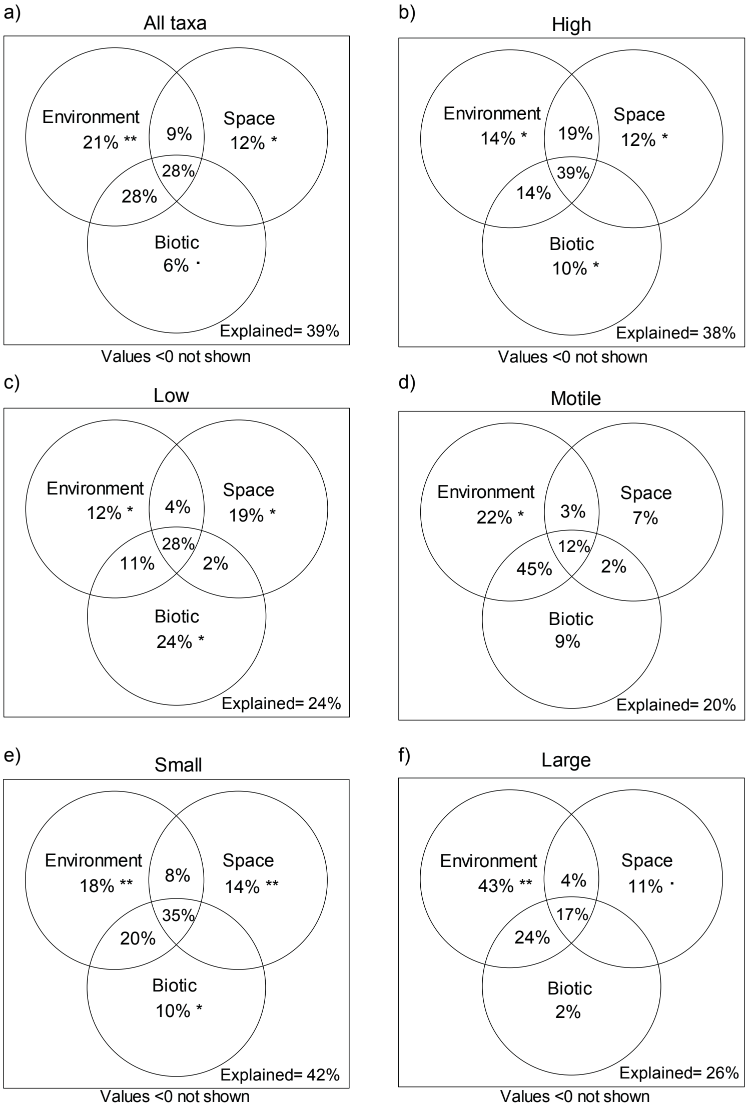

Figure 5. Venn-diagrams showing the unique fraction of taxonomic composition explained (i.e. % fraction explained/ % total variance explained) by environmental (environment), spatial (space) and biotic (biotic) factors (III). Diagrams show variances explained of a) total diatom assemblage structure (i.e. all taxa were analyzed together) and of taxonomic composition within the b) high-growth, c) low-growth, d) motile, e) small-sized, and f) large-sized diatom guild. The significance of each fraction explained is indicated in the figures (** $p<0.01$, * $p<0.05$, $^{\cdot}$ $p<0.10$). Shown is also the variance explained jointly by all three explanatory matrices, environmental and biotic factors, biotic and spatial factors, and environmental and spatial factors (overlapping parts of the circles). The number of replicates (n) is 30 in all analyses. The percentage of total explained variance in each analysis is reported in the lower right hand corner.

4.2.3 Upstream vs. downstream sites (II)

Macroinvertebrate community structure in upstream sites was more consistently and strongly related to environmental factors compared to downstream sites in both spring and autumn. However, the difference was more pronounced during spring when environmental factors explained 22% ($p<0.01$) and 7% ($p<0.1$) of community structure in upstream and downstream sites, respectively (Fig. 6). In autumn, spatial variables based on downstream directional distances (AEM_D) explained 5% of community structure in upstream sites. However, after removing the effect of AEM_D, upstream sites were completely unrelated to spatial variables based on Euclidian (D_O) and watercourse distances (D_W) in both spring and autumn (Fig. 6). This is consistent with a previous study, covering a larger spatial scale, where no significant relationship was found between overland or watercourse distances and species community dissimilarity in first order streams (Brown & Swan, 2010).

Downstream sites showed less consistent patterns. In spring, neither environmental nor spatial factors could explain unique and significant fractions of macroinvertebrate community structure. In autumn, however, both environmental and spatial factors explained some fraction of community structure (E: 16%, D_O: 5%, AEM_D: 6%) (Fig. 6). The autumn result agreed with our predictions and is also consistent with a previous study suggesting that mass-effects prevail in downstream sites (Brown & Swan, 2010). The spring result was puzzling but could be explained by the stronger spatial structuring of macroinvertebrate communities at the whole network scale during spring (i.e. all spatial factors were significant) (Fig. 6). This finding suggests that dispersal may be pronounced at this time of year. For example, high flows associated with spring flood can mediate downstream drift (e.g. Waringer, 1992). Also, many common stoneflies in our study hatch during spring and aerial dispersal along the watercourses may be pronounced (Macneale *et al.*, 2005; Petersen *et al.*, 1999). It is therefore likely that high dispersal may have masked both environmental and spatial signals in our downstream sites during spring, while moderate dispersal coupled with strong environmental gradients caused species sorting dynamics to prevail in the more isolated upstream sites.

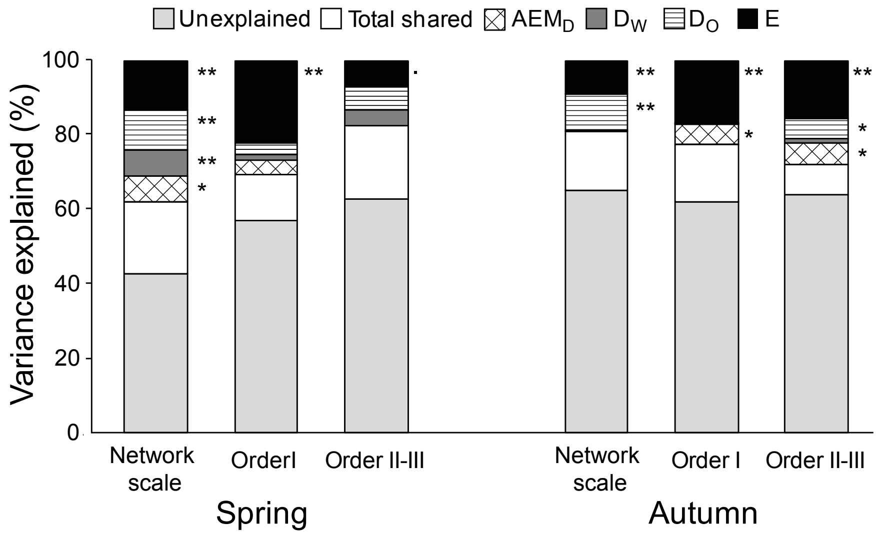

Figure 6. Results of the variance partitioning analyses between explanatory variables and the species data (II). The figure shows the amount of variation (%) in the species data explained by local environmental variables (E), Euclidian distance eigenvectors (D_O), watercourse distance eigenvectors (D_W) and downstream directional eigenvectors (AEM_D). The unexplained variation and the total shared variation (i.e. the sum of all pairwise shared components + the shared variation explained between all four explanatory matrices). The tests are divided by season (spring vs. autumn) and hierarchical levels (i.e. whole network scale vs. upstream (order I) vs. downstream (order II-III) sites). The level of significance is indicated next to the bars (** p<0.01, * p<0.05, ˙ p<0.10). The figure is reproduced from Göthe *et al.* (2013).

4.2.4 Functional redundancy (IV)

Our results indicated low relative resilience of the Krycklan catchment. First, our analysis identified a low number of significant spatial scales (two-three) in each season (Fig. 7). Second, few taxa were, on average, present within each functional group and scale (mean number of taxa per functional group <2). Some taxa (occurring in low abundances) were, however, unrelated to the spatial scales detected and could therefore not be included in the functional redundancy assessment within and across scales. It is important to acknowledge that such numerically rare species may contribute to the resilience of ecosystems if they respond differently to disturbances compared to functionally similar dominant species (Walker *et al.*, 1999). The relative resilience of this headwater catchment may therefore be underestimated.

Despite this limitation, our results clearly showed that community structure within macroinvertebrate functional feeding groups (at all spatial scales) was, with a few exceptions, structured by a combination of environmental and spatial factors (Fig. 7). This suggests that functionally similar taxa not only differ in their response to local factors, but also to regional factors.

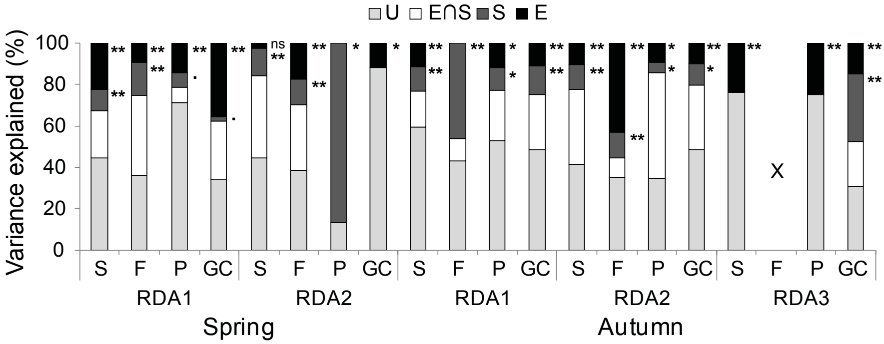

Figure 7. Results of the variance partitioning analyses. The figure shows the amount of variance in taxonomic composition within each functional group explained (%) by local environmental factors (E) and spatial eigenvectors (S) (IV). Shown are also variances explained jointly by environmental and spatial factors (E∩S) and unexplained variation (U). X indicates that no taxa were associated with that particular scale and FFG. S = Shredder, F = Filterer-Collector, P = Predator and GC = Gathering-Collector. The tests are divided by season (spring vs. autumn) and spatial scale (RDA1, RDA2, and RDA3). The level of significance is indicated next to the bars (** p<0.01, * p<0.05, $^{\cdot}$ p<0.10, ^{ns} p>0.10).

5 Conclusions

- Both α- and β-diversity contributed significantly to γ-diversity in the headwater streams included in our assessment (I). No simple conclusion, based on this result, can be drawn considering whether we can conserve most of this biodiversity by preserving a few local sites, or if we have to conserve many sites with different species communities. Nevertheless, the results suggest that we are likely to exclude a significant amount of biodiversity by not considering them in bioassessment and management. To elucidate the contribution of headwater stream biodiversity to the total diversity in riverine landscapes, future assessments should also include other stream-types (i.e. downstream reaches) within the same catchments.

- Local environmental control increased with decreasing spatial extent (I) suggesting that conservation of headwater biodiversity is likely to be most effective when management targets environmental conditions across multiple local sites within relatively small catchments.

- Local environmental control peaked in the most upstream sites (II), most likely due to greater environmental variation and an increased isolation in terms of dispersal. Different stream-types may therefore differ in their sensitivity to environmental change and ability to recover after disturbances. If upstream species communities are more isolated, their recovery may be substantially slower compared to downstream reaches where high dispersal can potentially mitigate the negative effects of local disturbances. However, future studies are needed to assess the generality of our findings since the study was performed over a limited spatial scale and only in one catchment.

- Additional variation in diatom assemblage structure could be explained by including biotic predictors (III), reflecting the importance of local control. The accuracy of predictive models is therefore likely to increase by including biotic predictors. Our results also suggest that guilds vary in their response to spatial and biological factors and that guild-specific management approaches may be required. Our approach does not, however, allow us to assess the underlying cause(s) of the observed differences. Therefore, small scale experiments with controlled manipulations of diatom dispersal, environmental conditions and grazing pressure could be used to shed light on some of the underlying mechanisms behind our results.

- Spatial factors explained significant fractions of community structure over both large (III) and small (II, IV) spatial extents. This suggests that bioassessment will not improve substantially by using predictive models based on small geographical areas (e.g. within catchments or bioregions). That is, it may be important to incorporate spatial factors in predictive models irrespective of the spatial scale of observation. This finding also emphasizes the importance of managing regional conditions (e.g. landscape connectivity), in addition to local site conditions, irrespective of the scale targeted by management.

- Spatial factors differed in their ability to predict macroinvertebrate community structure (II) which emphasizes the importance of using spatial predictors that are specific and relevant to the system and organism studied. However, we have not assessed all relevant spatial determinants in the studies herein. Although downstream directional dispersal is important in stream networks, much dispersal is also directed upstream (e.g. adult macroinvertebrates). In addition, landscape characteristics may significantly influence dispersal processes in streams (e.g. steep slopes, land cover). Therefore, the use of available spatial modeling techniques that can assess directional spatial structures, as well as incorporate landscape characteristics, are likely to improve the results further.

- Taxonomic composition within macroinvertebrate FFGs was, in most cases, the result of both local and regional control (IV). Therefore, the maintenance of headwater functions most likely requires management of both local and regional conditions. Moreover, studies of important resilience components, such as response diversity, should consider differences in organism responses not only to local disturbance regimes, but also to spatial gradients (e.g. organism dispersal capacity).

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