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Cross scale structure, functional redundancy and spatial resilience of a boreal stream network

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Abstract

Assessing how ecological functions are distributed within and across temporal and spatial scales is crucial for understanding the relative resilience of ecosystems, and thus how to effectively and efficiently manage them. In this study, we assess spatial cross-scale distribution of functional feeding groups of benthic invertebrates in a headwater stream network across two seasons. We evaluated functional characteristics of the system (based on Shannon diversity, richness, and evenness indexes) and the degree of redundancy within and across spatial scales for individual feeding groups. In addition, we estimated the relative importance of environmental vs. spatial factors for regulating both the distribution of functions (functional composition) and the species that comprise functional groups (functional redundancy) for each spatial scale identified. Measures of functional diversity and within-scale redundancy of functions were similar in both seasons, but cross-scale resilience was higher in autumn under hydrologically more stable conditions, compared to spring. However, both within-scale redundancy and cross-scale redundancy assessed through spatially explicit modelling was generally low, suggesting an apparent low relative spatial resilience of the stream network. This apparent low resilience was partly due to a few species explaining the spatial models. Species contributing to stochastic noise could not be included in our assessment of cross scale reinforcement but may still contribute to increase resilience. Both environmental and spatial factors were important determinants of the scale-specific functional composition and redundancy. This highlights that components of resilience, such as response diversity and adaptive capacity, need to be studied not only as a function of local disturbance regimes, but also in relation to connectivity and the potential for organisms to disperse between sites, which are also important aspects of ecological resilience.

Introduction

Ecological resilience is most simply defined as the amount of disturbance a system can tolerate before it is pushed to a different stable state (into a different domain of attraction), thereby losing its original functions and processes (Holling 1973). However, how well a system can buffer disturbances also depends on its capacity to *reorganise* during disturbance so that original structures, processes, functions and feedbacks are preserved (Walker and others 2004). An assessment of ecological resilience in multiple ecosystems globally is important, because of ongoing global change and human-induced pressures that are causing rapid declines in species diversity (e.g., Heywood 1995; Sala and others 2000). Reduction in species diversity leads to a reduction in ecosystem functions, which sustain important ecosystem services for humanity (Ehrlich and Ehrlich 1981; Chapin III and others 2000; Balvanera and others 2006).

Walker and others (1992) suggest focusing on the preservation of ecosystem function rather than species richness because an estimation of losses in ecosystem functions putatively leads to a more efficient preservation of critical processes and characteristics of an ecosystem which more than one species rely on. Functional redundancy is an aspect of ecological resilience that measures how many species play the same ecological role in an ecosystem (i.e. how many species within a particular domain of scale can be lost without a loss in ecosystem function) (e.g. Luck and others 2003). Another aspect of ecological resilience, highly related to the concept of functional redundancy, is response diversity (Elmqvist and others 2003; Chillo and others 2011). Response diversity refers to differences in the response to disturbance among species within a functional group. Functional redundancy and response diversity are essential estimates of resilience.

Organisms of different size perceive their environment at different spatiotemporal scales, and interact with different ecological structures that reflect the particular processes

dominant at a particular scale. Because there are limited numbers of structuring processes in a system there are limited numbers of scales, and this type of scale-specific hierarchical structure (i.e. nested levels of structuring variables and processes) is a critical component of the organisation of communities (Holling 1992), and the generation of resilience in those communities (Peterson and others 1998). Ecologists have developed tools (discontinuity analyses) that allow for quantifying and comparing sudden changes in ecological patterns (Allen and Holling 2008). The ability to measure and quantify discontinuities provides insight regarding the number of dominant spatial and temporal scales of processes and structures that are present in a system (Allen and others 2005; Stow and others 2007). Most research has so far inferred resilience by studying discontinuities in body mass distributions in animals, especially vertebrates (Allen and Holling 2008). However, the development of statistical methods allows us to consider biomass or abundance data in discontinuity analyses and assess the number, location and relevance of the discontinuities, and the distribution of ecological functions within and across spatial (Borcard and Legendre 2002; Borcard and others 2004) or temporal scales (Angeler and others 2009, 2011). In this case, instead of determining discontinuities in species communities on the basis of body mass (Holling 1992), assessing both spatial and temporal components of scale separately through modelling allows the assessment of community dynamics and environmental correlates at distinct spatial or temporal scales. By distinguishing species groups associated with particular spatial and temporal scales it is possible to assess within- and cross-scale redundancy of the system. Despite this having great potential to increase our understanding of resilience of landscapes (i.e. spatial resilience) (Cumming 2011), across and within scale redundancy has been described mainly theoretically (Peterson and others 1998), and tested only with limited data for a few terrestrial (Forys and Allen 2002; Allen and others 2005; Fischer and others 2007) and aquatic ecosystems (Angeler and others 2013). Here we assess cross-scale structure and

the redundancies of functions within and across spatial scales using boreal headwater streams as model systems of ecosystems that are exposed to strong natural disturbance.

Stream ecosystems represent a tiny proportion of the worlds' freshwaters (Shiklomanov 1993), but contain great biodiversity. They also provide humans with provisioning, recreational and regulating services, which in turn makes them one of the most threatened ecosystems on the planet due to various kinds of anthropogenic disturbances (Malmqvist and Rundle 2002). Thus, an assessment of the resilience of these systems is essential to be able to predict and mitigate consequences of environmental change and human perturbation. Stream networks are also very useful for assessing dynamic aspects of resilience in ecosystems. First, the natural and continuously occurring hydrological disturbance of stream networks in combination with strong temporal fluctuations is perhaps the most important factor shaping lotic environments and their communities (Resh and others 1988; Townsend 1989). These fluctuations are often related to different seasons between which not only abiotic conditions (e.g., hydrology, water chemistry, temperature, availability in food-resources) (Giller and Malmqvist 1998; Laudon and Bishop 1999; Laudon and others 2004), but also community and functional composition may differ (i.e. species and functional turnover in time) (Cowell and others 2004; Bogan and Lytle 2007). Second, species turnover in time (Bogan and Lytle 2007) can also include shifts to other species with the same ecological function (i.e. species turnover exists, but not necessarily functional turnover) due to, for example, life-cycle differences (i.e. timing of emergence and adult dispersal) between species even within the same genus (e.g., Petersen and others 1999). Thus, even though a system can appear to have a low resilience when investigated at a single snapshot in time, functional redundancy may exist over time. Third, the hierarchical and linear structure of stream networks constrain community dynamics across a wide range of spatial scales (e.g., Mykrä and others 2007; Brown and Swan 2010; Göthe and others 2012). This highlights that both environmental and

spatial factors are important for the distribution of species and their functions in streams (Erös and others 2012). However, explicit consideration of regional factors in empirical testing of resilience is so far lagging, although the importance of such factors has been recognised (Nyström and Folke 2001). Disentangling the effect of local vs. regional control of the cross-scale distribution of functions is important from both a theoretical and an applied perspective because the knowledge can be used as a basis for developing bioassessment tools and in environmental management when the aim is to restore and maintain resilient ecosystems (Bengtsson 2010; Heino 2012).

Benthic invertebrates are key components in stream ecosystem and can be divided into functional feeding groups (predators, shredders, scrapers, gatherer-collectors, filterers) that play important roles in multiple ecosystem processes, including secondary production, leaf litter processing, nutrient cycling, and matter and energy fluxes (e.g., Merritt and Cummins 1996; Wallace and Webster 1996). The feeding mode is thought to reflect the main food resource utilised by species and can therefore serve as an indication of the main resource base available in the system (e.g., Vannote and others 1980). Invertebrates also show strong seasonal patterns of distributions due to differences in environmental constraints and differences in the timing and magnitude of invertebrate dispersal. In addition, spatial constraints are known to vary with invertebrate dispersal capacity (e.g., Thompson and Townsend 2006; Göthe and others 2012). This makes invertebrates ideal candidates for assessing both local and regional (dispersal) processes on the spatial distribution of functions at different scales.

In this study, we use invertebrate, environmental and spatial data collected from a boreal Swedish headwater catchment in two seasons that differ in hydrological disturbance. We evaluate functional redundancy within and across spatial scales in both seasons to assess the relative resilience of the stream network. In addition, we estimate the relative influence of

environmental vs. spatial factors shaping the functional and species composition within each functional feeding group for each spatial scale identified.

We test the following hypotheses:

(1) Functional redundancy within and across spatial scales varies between seasons. We expect within- and cross-scale redundancy to be lower (i.e. for there to be lower resilience) in spring when flooding events may have disrupted the communities, and to be higher in autumn during hydrologically more stable conditions. However, as these hydrological fluctuations are naturally occurring, any seasonal variability is thought to arise from processes that operate within a single broad domain of attraction (Holling 1973), rather than from regime shifts that would entail seasonal reorganization in different alternative states.

(2) The general pattern of functional structure and redundancy is maintained across seasons despite variability in the taxonomic composition of the communities between seasons. That is, functional, but not necessarily taxonomical, composition overlaps in time and contribute to the overall functional redundancy within the stream network.

(3) The distributions of functions and their redundancies within functional groups are associated with both environmental and spatial factors, due to environmental filtering and dispersal constraints affecting community assembly in this stream network (Göthe and others 2012).

Materials and methods

Study site

The Krycklan River catchment, situated in northern Sweden (county of Västerbotten), was selected for this study (Fig. 1). Coniferous forests and wetlands dominate the catchment (Buffam and others 2007). Annual mean temperature is 1°C and annual mean precipitation is approximately 600 mm (one third of the precipitation falls as snow) (Ottosson Lövvenius and others 2003). We sampled benthic invertebrates and measured a number of local environmental factors at 52 sites (first to third order stream reaches). Sampling was performed along a 30 m stretch at each site in May and October, 2009. The sampling in May was done directly after spring flood while the sampling in October was done after a longer period of base flow conditions. Hydrological conditions at the time of our sampling were assessed by plotting daily discharge measurements from one sampling point in the catchment (data kindly supplied by Hjalmar Laudon).

Benthic invertebrate sampling

We used a Surber sampler (frame size: 14×14 cm, mesh-size: 500 µm) to sample the invertebrates along the 30 m stretch. In total 9 Surber samples and a total sample area of ~0.18 m² was collected at each site. The samples were preserved in 70% ethanol and brought back to the laboratory for sorting and identification. The benthic invertebrates were identified to the lowest possible taxonomical level, in most cases to species or genus, but some groups were identified to a higher taxonomic level, e.g., Simuliidae (identified to family level), Chironomidae (identified to subfamily level) and Coleoptera (identified to family level). Invertebrates were then divided into functional feeding groups (scrapers, filterer collectors, gatherer collectors, predators, and shredders) (Moog 1995; Merritt and Cummins 1996).

Habitat characterisation and water chemistry sampling

We measured stream width, depth, flow and canopy cover every 5 m along the 30 m stretch. Depth and flow were measured at three cross-sectional points at each transect (from each channel edge and from the middle of the stream), while width and canopy cover were measured once at each transect. We estimated canopy cover by taking digital photographs from the middle of the stream (at the surface) pointing upwards (towards the canopy). By using computer software Image-Tools (Health Science Center, University of Texas, U.S.A.), we were able to manipulate the images so that black pixels represented the canopy and white pixels represented open areas. The mean canopy cover at each site was then assessed by calculating the mean percentage of black pixels per image and site. A pebble count method (Wolman 1954) was used to estimate substratum composition. At each site, 100 stones were randomly picked up and measured. The pebble count data was then divided into eight different substratum classes based on the size of the particles after which the percentage of each substratum class could be calculated. In conjunction with the pebble count procedure we also estimated moss cover by noting the presence/absence of moss on each of the 100 substrate pebble samples. The amount of dead wood at each site was estimated by counting the number of branches and logs that measured >1 cm in diameter in the stream channel. Water chemistry samples were taken and analysed for major anions and cations, metals (Fe, Al), pH, nutrients (Total-N, Total-P, NO₂+NO₃), water colour (absorbance at 420 nm), total organic carbon (TOC) and carbon dioxide (CO₂). A drought inventory was performed on two occasions during the warmest period of the summer (late June and early July) since one characteristic of the Krycklan catchment (and headwater catchments in general) is that some upstream sites in the stream network are intermittent (i.e. they dry out during the summer months). Thus, coordinates were used to mark the point above which the stream was dry or only consisted of scattered pools without any permanent water flow and sites were classified

as affected/not affected by drought. Landuse was assessed from digital maps (shape files acquired from the Swedish forestry agency and the Swedish Land Survey), and calculated for the catchment area upstream of each sampled site in ArcGIS, version 9.3.1 (ESRI, Redlands, California, USA).

Data analyses

Data analyses focused on identifying the relevant spatial scales at which species groups of invertebrates are distributed, following the spatial modelling framework of Borcard and Legendre (2002) and Borcard and others (2004). After the identification of spatial scales we identified species (or species groups) associated with each spatial scale, and calculated functional diversity indices as well as estimates of within and across scale redundancy in the catchment. Finally, we disentangled environmental versus spatial effects on functional composition and redundancy at each spatial scale (i.e. in each species group associated with each spatial scale). Methodological details follow. All statistical analyses were carried out in R (version 2.13.2) (RDevelopmentCoreTeam 2011).

(1) Identification of spatial scales - To identify spatial scales in our data we used principal coordinates of neighbour matrices analysis (PCNM) (Borcard and Legendre 2002; Borcard and others 2004) by using the function *quickPCNM* in R package *PCNM* (Legendre and others 2010). Species data was Hellinger transformed prior to analysis (Legendre and Gallagher 2001). PCNM is based on redundancy analysis (RDA) and breaks down the overall spatial structure of species communities into independent spatial structures (significant RDA axes) shown by groups of species. First, a number of spatial variables (PCNM variables) with different sine wave frequencies are created based on geographical X, Y coordinates. The number of PCNM variables can differ depending on sampling design, but the number always

corresponds to the number of eigenvectors (PCNMs) with positive eigenvalues in the analysis (here 32 PCNMs with positive eigenvalues were created). The first PCNMs represent sine waves with low frequencies and are therefore associated with broad scale patterns in species distribution, while subsequent PCNMs represent progressively higher frequencies that model spatial patterns in species distributions at smaller scales. The PCNMs are related to the species data by means of redundancy analysis, and significant PCNMs are selected through a forward selection procedure. These PCNMs are then linearly combined to extract spatial structure in the communities at different spatial scales. These spatial structures are associated with significant RDA axes in the spatial model. The significance of each RDA axis is tested by means of permutation test. Each significant RDA axis can be interpreted as an independent spatial scale at which a subset of species is structured, and the number of significant RDA axes in the model allows quantifying the number of spatial scales in the ecosystem. For more detailed information about this modelling technique, see Borcard and Legendre (2002), Borcard and others (2004), and Dray and others (2006).

(2) Identification of species associated with each spatial scale – We correlated Hellinger transformed species raw abundance data with the modelled spatial patterns (lc scores of each significant RDA axis) to assess the taxonomic identity of species associated with each spatial scale. Species that correlated significantly ($p < 0.05$) with the lc-scores of each axis were considered to be representatives of that particular scale (Angeler and Johnson 2012) and thus retained for further analyses of functional characteristics.

(3) Estimating functional diversity, and redundancy within and across spatial scales – Based on the species groups retained for each spatial scale and season, we first calculated three estimates of functional diversity (Shannon index, evenness and richness) for each spatial scale

(i.e. for each species group associated with each spatial scale identified in PCNM analysis) in computer software PAST (Hammer and others 2001). As measures of within scale redundancy we calculated (1) the average number of species per functional group and spatial scale and (2) an index based on mean distances between sites in multivariate space *within* spatial scales. Across scale redundancy was estimated by calculating mean distances in functional composition in multivariate space *between* spatial scales. The distances were calculated by transforming functional composition data into Bray-Curtis dissimilarities. Thus, they provide an estimate of overlap in functional structure and can therefore be used as a simple and straightforward index of redundancy. That is, low average distances within or between spatial scales implies larger functional overlap and thus higher redundancy and vice versa. Mean distances within and between spatial scales were calculated using function *meandist* in R package *vegan* (Oksanen and others 2011) and visualized with an NMDS (non metric multidimensional scaling) diagram using pre-specified default arguments in function *metaMDS* in R package *vegan*. We also performed an NMDS ordination based on taxonomical composition and Bray-Curtis dissimilarities to assess taxonomical vs. functional overlap between seasons.

Note that our measures of within- and cross-scale redundancy differ from others used in previous research (following the example by Allen and others 2005). Previously, the average number of species per functional group and scale has been used as a measure of within scale redundancy, while cross-scale redundancy has been assessed by noting the presence or absence of a functional group across scales (Allen and others 2005). Here, we extend our assessment of resilience by using a multivariate approach based on measures of functional similarity between sites within or across scales. We suggest that an assessment of within- and cross-scale redundancy benefit from such an approach since it allows us to assess the similarity of functional composition across scales based on both functional identity *and*

abundance. Resilience is likely to be dependent both on (1) the redundancy of individuals within populations and functional groups (i.e. species abundances) and (2) the redundancy of species within functional groups (i.e. species richness) we believe this approach is a more comprehensive way of assessing redundancy.

Seasonal differences of measures of functional redundancy were assessed using ANOVA (type III) because of unequal sample sizes (Shaw and Mitchell-Olds 1993). These tests were performed with function *anova* in R package *car* (Fox and Weisberg 2011). Because the spatial scales identified are associated with orthogonal (i.e. independent) RDA axes, we considered each scale as an independent replicate in the analysis. However, since sample size was low (2 spatial scales in spring; 3 in autumn) our aims were to assess trends of pattern rather than a quantification of the pattern per se.

(4) Environmental vs. spatial correlates of functional composition and redundancy – We estimated the relative importance of spatial versus environmental drivers of functional composition (diversity) and redundancy. Thus, Hellinger transformed abundance data (Legendre and Gallagher 2001) of our predefined species groups for each spatial scale were used as response matrices and our environmental data (water-chemistry, hydromorphology and land-use) and spatial variables (obtained from PCNM analyses, see step 1) as predictor matrices. Environmental predictor variables were log or square-root transformed where necessary to approximate normal distributions. We also performed a centred log ratio transformation on the land-use and substratum composition data as it creates linearity in the data and solves the problem of compositional data that sums to unit one (Aitchison 1983; Wang and others 2010). Then, a forward selection procedure was performed on the environmental and spatial predictors with the function *forward.sel* in R package *packfor* (Dray 2009) which retained only variables significantly ($P < 0.05$) related to functional

composition and redundancy (i.e. species composition within each functional group) at each scale. The significant environmental and spatial variables were then used in a variance partitioning analysis which was performed with the function *varpart* in R package *vegan*. The variance partitioning analyses allowed us to calculate the fraction of functional composition and functional redundancy that could be explained uniquely or by the combined fractions of two or more predictor matrices through partial redundancy analyses (pRDA). The significance of the unique fractions was estimated with function *rda* in R package *vegan*. For some scales and functional groups only one species was present. However, the R functions described above (*forward.sel*, *varpart*, *rda*) works also with single response variables, but instead of redundancy analysis (*rda*), the calculations are based on linear regression analysis.

Results

Functional diversity and richness

Our analyses identified groups of invertebrate species that were structured at two and three spatial scales in spring and autumn, respectively (Fig. 2). The average overall functional diversity within each spatial scale in the system was generally low (Shannon index: spring mean $0.62 \pm \text{SE } 0.06$, autumn mean $0.77 \pm \text{SE } 0.09$; Richness: spring mean $2.6 \pm \text{SE } 0.2$, autumn mean 3.1 ± 0.4 ; Evenness; spring mean $0.76 \pm \text{SE } 0.01$, autumn mean $0.75 \pm \text{SE } 0.04$). No significant differences in functional diversity were found between seasons ($P > 0.05$ for all diversity index).

Within and across scale functional redundancy

The average functional redundancy (number of species belonging to a feeding group) within spatial scales for shredders and filterers were slightly higher in spring (Shredder: spring mean $1.7 \pm \text{SE } 0.9$, autumn mean $1.2 \pm \text{SE } 0.5$; Filterer: spring mean $1.0 \pm \text{SE } 0.1$, autumn mean $0.4 \pm \text{SE } 0.3$) but slightly higher for predators and gathering collectors in autumn (Predator: spring mean $0.2 \pm \text{SE } 0.2$, autumn mean $1.4 \pm \text{SE } 0.3$; Gathering-collector: spring mean $1.0 \pm \text{SE } 0.9$, autumn mean $1.7 \pm \text{SE } 0.2$). However, seasonal comparisons of within-scale functional redundancy were non-significant ($P > 0.05$). On average, the mean number of species functional group⁻¹ was < 2 , highlighting low redundancy. The multivariate, distance-based measure of within scale redundancy was slightly lower in autumn (mean: $0.23 \pm \text{SE } 0.03$) compared to spring (mean: $0.28 \pm \text{SE } 0.01$), but did not differ significantly ($P > 0.05$).

The multivariate, distance-based measure of cross scale redundancy showed that cross scale redundancy was higher in autumn (i.e., mean lower value showing closer proximity in multivariate space; $0.46 \pm \text{SE } 0.05$) compared to spring (mean: $0.63 \pm \text{SE } 0.00$). Differences

in cross-scale redundancy could not be statistically evaluated because there was only one value in spring (i.e. one distance value between two spatial scales).

Functional redundancy between seasons

Functional redundancy between seasons was evaluated through visual examination of the NMDS ordination. The NMDS ordination showed overlaps in functional (but not taxonomical) composition between seasons (e.g., functional composition of RDA2 in spring overlapped substantially with RDA1 in autumn) (Fig. 3a-b).

Spatial and environmental drivers of functional composition and redundancy

Our results from the variance partitioning analysis showed that both environmental and spatial gradients shaped functional composition within each spatial scale and season. The variance uniquely and significantly explained by environmental and spatial factors ranged between 11-27% and 10-28% respectively and the shared fraction (i.e. spatially structured environmental variation) ranged between 7-42% (Fig. 4a). Our variance partitioning analyses of functional redundancy showed similar results where the majority of the analyses indicated both environmental and spatial control of taxonomical composition within each functional group. However, four species groups (or species) showed only environmental structuring, while two responded only to spatial constraints (Fig. 4b).

Discussion

We assessed the cross scale structure of functions to infer the relative spatial resilience of a headwater stream network. Despite the spatial modelling technique having been commonly used to infer scales of spatial structures in terrestrial (e.g., Lindo and Winchester 2009; Lu and others 2011; Duarte and others 2012) and aquatic environments (e.g., Landeiro and others 2011; De Bie and others 2012; Heino and others 2012), our study is the first to use this approach with a specific resilience focus. That is, we applied the approach specifically to assess how functional feeding groups of invertebrates are distributed across the spatial scales identified, in order to infer the relative spatial resilience of this stream network based on the cross-scale resilience model (Peterson and others 1998; Allen and others 2005).

Functional diversity and within-scale resilience

Stream ecosystems demonstrate large environmental heterogeneity in space and over time (e.g. Frissell and others 1986; Ward 1989; Montgomery 1999). One example of spatial environmental heterogeneity in stream ecosystems is the change in environmental conditions that occur along the watercourses, leading to characteristic communities in upstream (headwater areas) and downstream sites. For example, substantial input of coarse organic matter (e.g., leaves) in upstream areas will benefit shredders. However, poor conditions for algae growth (e.g., high shading, low temperatures) and low amounts of finer organic matter suspended in the water column will lead to lower abundances of, for example, scrapers (feeding on benthic algae) and filterers (feeding on suspended material) (Vannote and others 1980; Richardson and Daney 2007). Given the spatial segregation of resources in streams, functional feeding groups of consumer communities are patchy and functional diversity can be expected to be relatively low in headwater catchments. The findings of our study add to this body of evidence, highlighting that measures of functional diversity (Shannon index,

richness and evenness) were low, not only in both seasons but also across the spatial scales present in the stream network.

Similarly, an examination of individual feeding groups of invertebrates revealed that the functional redundancy for each feeding group was very low (mean < 2 species). Based on the findings of low within-scale redundancy, we can conclude that the resilience at single spatial scales is low (Allen and others 2005). As the likelihood of functional loss, and the consequence of that loss, is expected to increase with decreasing species richness (Fonseca and Ganade 2001) these results are not unexpected considering the ecosystem under study. That is, headwater streams are generally thought to be characterised by low alpha (but not necessarily low beta) diversity (e.g., Clarke and others 2008; Finn and others 2011) largely due to the substantial environmental heterogeneity across sites in upstream areas and their relatively isolated position in the river network. Isolation (preventing species to colonise/recolonise an area) in combination with strong environmental filters (preventing the establishment and maintenance of sensitive species and populations) is therefore likely to lead to relatively low resilience of these habitats. Also, recovery and reorganisation after disturbances may be slow in comparison with downstream reaches where the magnitude of dispersal (and thus colonisation rates) can be considerably higher (Brown and Swan 2010; Brown and others 2011).

Cross-scale resilience

Given that an assessment of resilience at a single scale does not adequately capture overall system resilience, ecologists have begun to explicitly consider the distributions of functions at multiple scales. Understanding how functions are distributed not only within, but also across scales, is critical for understanding and assessing ecological resilience (Fischer and others 2007; Wardwell and others 2008; Sundstrom and others 2012).

The invertebrate community was structured at two and three spatial scales in spring and autumn, respectively. We hypothesized that within and cross scale redundancy would vary between seasons, and that redundancy in general would be lower in spring due to stronger (but natural and continuously occurring) hydrological disturbance. Although our results regarding within-scale redundancy did not support the hypothesis, there was one more significant spatial scale detected in autumn compared to spring, and the overlap in functional composition between spatial scales was higher in autumn compared to spring (i.e. indicating higher cross scale redundancy). These results provide some support for our first hypothesis, regarding seasonal differences in cross-scale redundancy.

Given that many previous studies have assessed dominant scales in ecosystems without a spatially explicit approach (i.e. discontinuities in body mass distributions) in, for instance, bird, mammal, and herpetofauna communities (Forys and Allen 2002; Fischer and others 2007), comparison of cross-scale resilience between the Krycklan stream network and other ecosystems may be difficult. For example, our approach addresses the spatial aspect of resilience clearly, but it does not consider the temporal scales of habitat. Approaches based on determining discontinuities in body mass distributions utilize body mass because it is allometric to spatial and temporal scales of animals' use of the environment, but the particular spatial extents and temporal frequencies associated with particular body masses are not identified. . The approach described here explicitly identifies spatial scales. The low number of spatial scales identified in our study system (i.e. \leq half of what has been found in previous studies) may be viewed as an indication of a low spatial cross-scale reinforcement of functions in the stream network (Allen and others 2005; Fischer and others 2007). We note, however, that the spatial extent of our study area is relatively small. As our methods are applied to areas of greater extent, larger-scale spatial patterns will become apparent. It is likely that cross scale redundancy also occurs at these larger scales, and that we have thus

underestimated the actual cross scale reinforcement present in this system, which clearly consists of additional stream networks.

We suggest three non-mutually exclusive explanations to the relatively low number of spatial scales, and apparent low resilience in our study system. First, the importance of spatial factors shaping ecological communities is expected to increase with spatial extent since dispersal distances (and thus dispersal limitation of the organisms), on average, increases with an increasing scale of observation (e.g., Mykrä and others 2007; Declerck and others 2011). As stated above, because the size of the Krycklan stream network is small (study area extent: $\sim 20\text{km}^2$), we may not have captured significant ecological scales that extend beyond our scale of observation. Second, differences in spatial structuring between species within the aquatic invertebrate community may simply not be as pronounced as, for example, between terrestrial bird, mammal and herpetofauna communities (Forys and Allen 2002; Fischer and others 2007). Third, approximately half of the species in our data set were unrelated to the dominant spatial scales identified for each season. These species were rare and occurred only in low abundances (16% and 3% of the total abundance in spring and in autumn, respectively). This suggests that the detected spatial patterns are due to a few dominant species and that the abundances of the remaining species were too low for being associated with significant spatial patterns, thereby leading to stochastic noise. This may not be surprising given that species distributions in streams are generally characterized by having a few dominant species and a relatively long tail of numerically rare species (Resh and others 2005; Arscott and others 2006; Siqueira and others 2012). Focusing our evaluation of the relative resilience of the Krycklan stream network on significant patterns only may therefore have resulted in a conservative estimate of resilience since rare species, occurring in low abundances, may to some extent increase the buffering capacity of a system against disturbance (Walker and others 1999), facilitating its maintenance in a specific basin of attraction.

We also detected an overlap in functional, but not taxonomical, composition between seasons, providing some support for our second hypothesis. Such patterns are expected because of life cycle differences between invertebrate species within the same functional group (e.g., Petersen and others 1999), a component of response diversity. In addition to the potential contribution to resilience of “stochastic” species, seasonal maintenance of functions by different species may also add to the overall resilience of the system. This finding (i.e. that functional, but not necessarily taxonomical overlap exists over time) emphasises that both spatial and temporal species turnover needs to be considered when assessing the overall resilience of similar systems.

Spatial and environmental drivers of functional composition and redundancy

The third aspect of resilience evaluated in this study relates to response diversity. That is, different responses to disturbances of members within a single functional group (Elmqvist and others 2003). Given that response diversity is intrinsically related to disturbances, environmentally deterministic processes have been so far emphasized as regulators of response diversity (e.g., Chillo and others 2011). Because community assembly in streams is dependent on both environmentally deterministic and spatial processes, we expected community composition within functional feeding groups of invertebrates to be regulated by both factors. With a few exceptions, our variance partitioning analyses found that functional feeding groups were significantly related to both environmental and spatial factors. This finding not only supports our third hypothesis, but also corroborates a previous study focusing on drivers of species community composition (diversity patterns) (Göthe and others 2012). We acknowledge that we did not strictly assess the taxonomic changes within functional feeding groups before and after disturbance, which limits an assessment of response diversity *per se*. However, our results clearly demonstrate that species within functional groups are

sorted along both environmental and spatial gradients. This finding suggests that a management approach focusing on restoring and conserving both landscape features and local habitat conditions is necessary to preserve functional diversity and maintain the inherent resilience of headwater catchments. Thus, response diversity within functional groups should be considered not only in terms of environmental responses (local response diversity), but also in terms of spatial responses (Nyström and Folke 2001) (here called regional response diversity). That is, to withstand disturbances, the dispersal capacity of the organisms (and connectivity in the landscape) may be equally important as differences in organism's response to changes in local environmental conditions. For example, regional response diversity (e.g., differences in species dispersal capacity) can significantly influence the local buffering capacity through high dispersal effects (mass-effects) (e.g., Leibold and others 2004) since it can lead to the maintenance of species with negative growth rates in unsuitable habitats (Pulliam 1988).

As discussed above, some rare taxa (with low abundances) were not related to any spatial scale and thereby not included in our assessment of resilience. However, we acknowledge that in any assessment of response diversity, numerically rare species may have a significant role as they may increase in abundance following disturbance and thereby sustain important functions when dominant species are removed or novel conditions introduced (Walker and others 1999). These rare species may provide a critical component of resilience, adaptive capacity. The importance of rare species is easy to overlook, because the strength of ecological function is related to the abundance of the members of a particular functional group. However, when environmental conditions change rare species may become abundant, because they may respond differently to a disturbance even when compared to members of their own functional group (i.e., there is response diversity within functional groups), or because the common member of a functional group is especially vulnerable to a particular

disturbance, or because novel environmental conditions have arisen. Therefore the ability of a system to absorb novel perturbations – its adaptive capacity – may reside as much in the identity of its rare species as in the within and across scale distribution of function of common species.

Conclusion

Headwater streams are the most prevalent lotic environments on the planet (Leopold and others 1964), and known to inhabit distinct communities as well as being vital for the health (structure and function) of entire watersheds (Peterson and others 2001; Wipfli and Gregovich 2002; Meyer and others 2007). Yet, they are disappearing from the landscape at a relatively high rate largely due to human perturbation (Meyer and Wallace 2001) and are not included in important legislations aiming to preserve and assess biodiversity in freshwater ecosystems. Our results suggest that the consequences of anthropogenic disturbance in these systems may have substantial impact on the structure and function of local habitats, but acknowledge that the apparent low resilience assessed in this study may partly be due to our approach, which was based on the consideration of species that contributed significantly to the spatial models, and ignoring those contributing to stochastic noise. Notwithstanding, species within functional groups were shown to be structured both by local and regional factors. Therefore, any local habitat degradation or habitat loss may have consequences also for the regional maintenance of ecological functions (resilience) as it will increase isolation of the remaining habitats, which in turn decreases the possibility for species to colonise and thereby maintain community structure in these habitats. Finally, as the capability to reorganise from disturbance is expected to depend on both local and regional factors (Nyström and Folke 2001) it stresses the importance of managing landscape features in addition to local environmental conditions (Bengtsson 2010) or else, recovery after restoration of local conditions may not happen or take longer than expected (Palmer and others 2010).

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Fig. 1 Location of the Krycklan catchment in Sweden (top right) and location of the 52 sampling sites within the catchment.

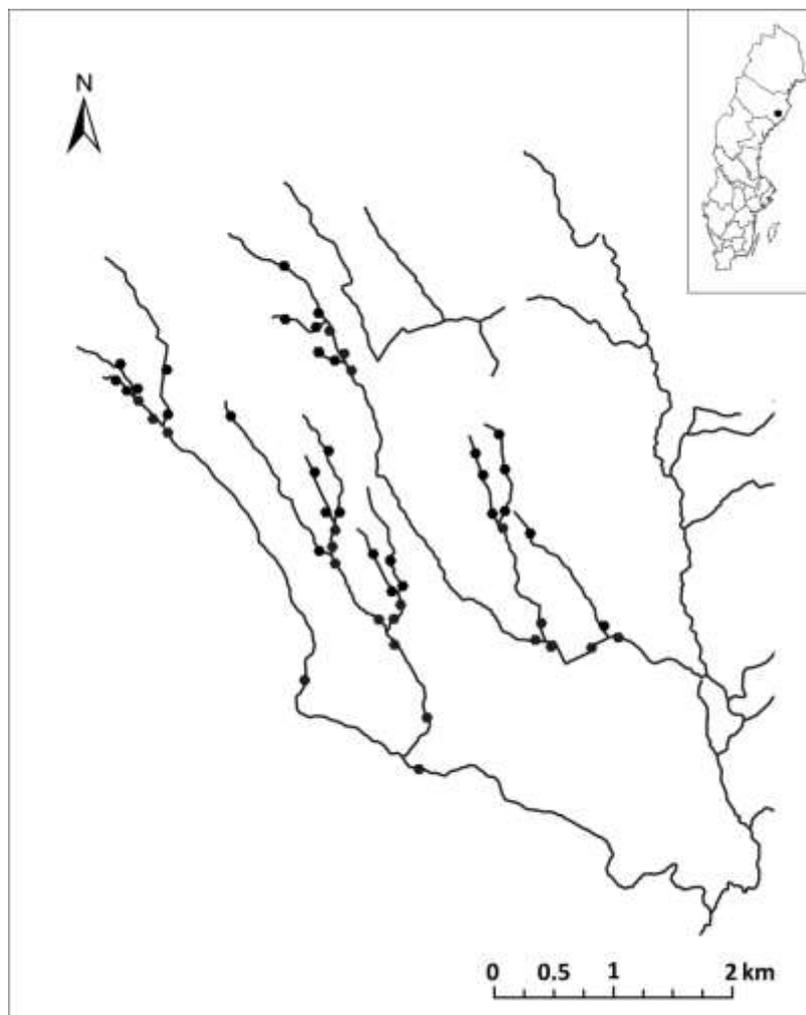
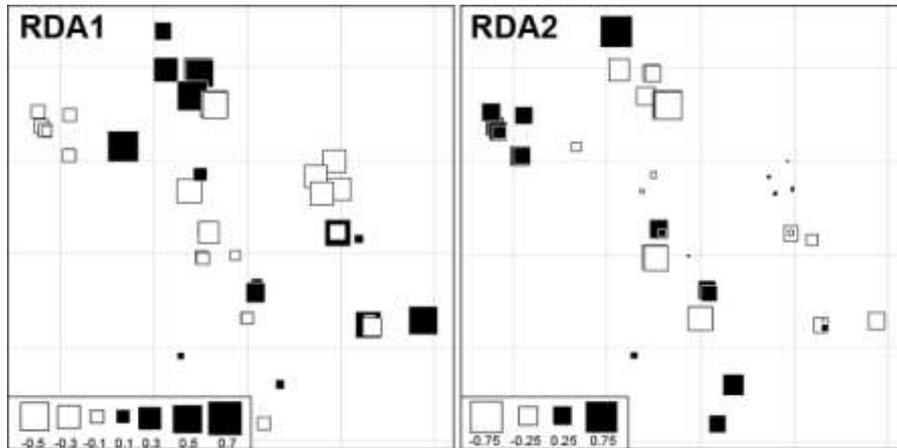


Fig. 2 Eigenvector maps, showing the spatial structures identified at each spatial scale (RDA axis) in a) spring and b) autumn. Each square represents one sampling site. That is, the squares in the maps are equivalent to the spatial location of each sampling site in the Krycklan catchment (as shown in Fig. 1). The size of the symbols are proportional to the lower-order PCNM vectors that describe this spatial structure and the color represents the sign of correlation (white = negative, black = positive, number under squares are site scores).

a)



b)

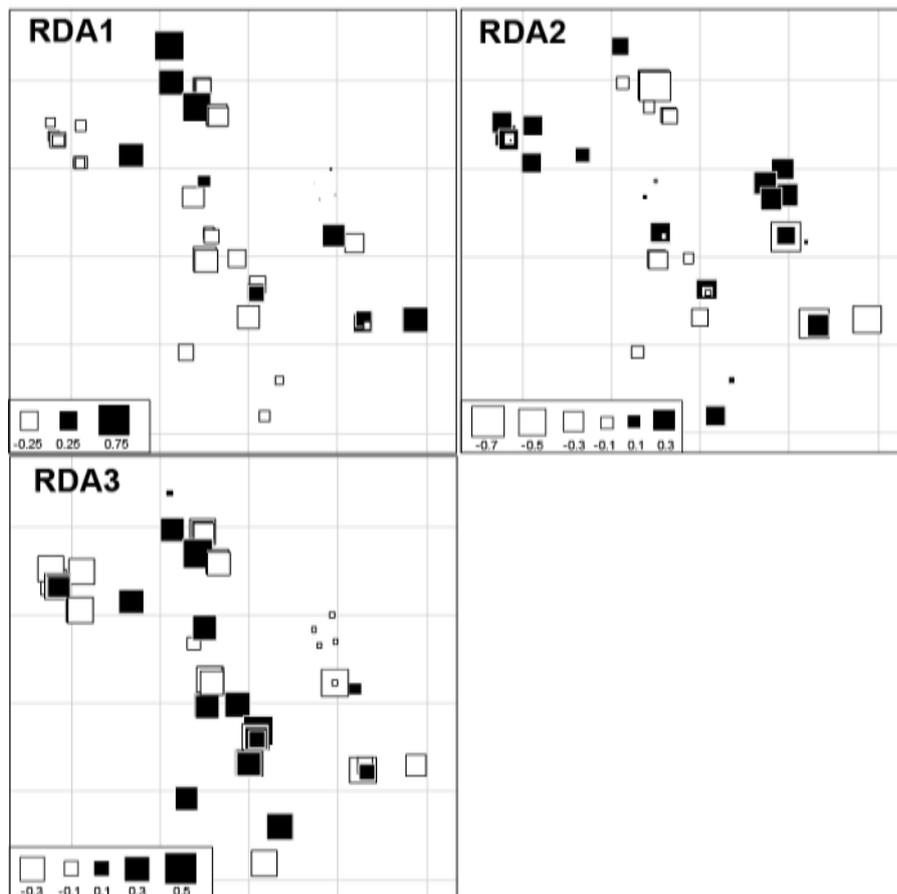
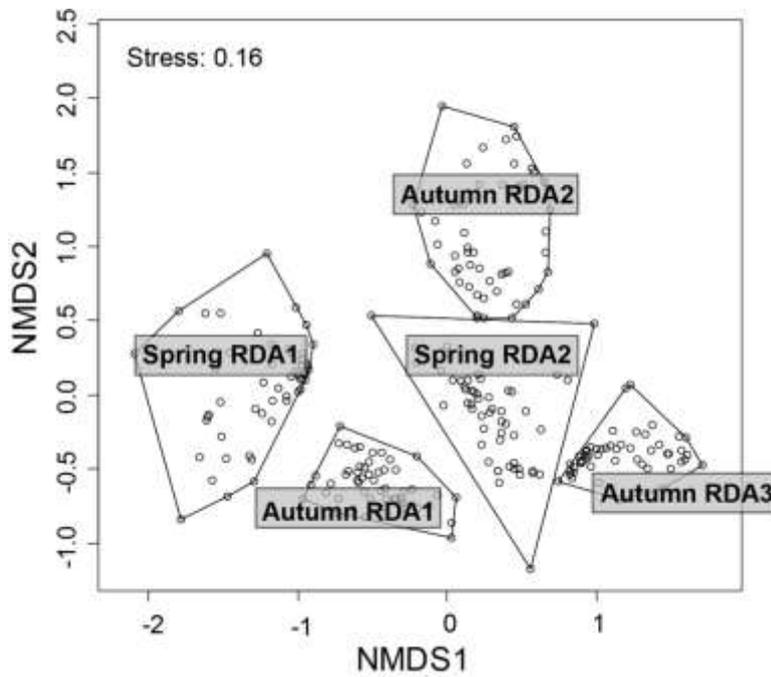


Fig. 3 Non metric multidimensional scaling diagrams showing a) taxonomical and b) functional feeding group composition across and within the different spatial scales (RDA1, RDA2, RDA3) identified through PCNM analysis and between the two seasons (spring and autumn). The analysis is based on Bray-Curtis dissimilarities and n=52 in all defined groups.

a)



b)

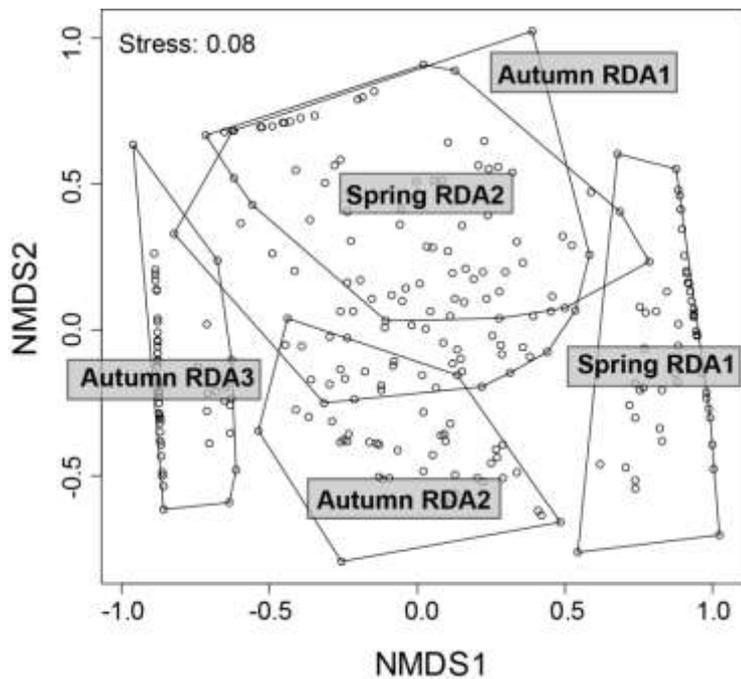
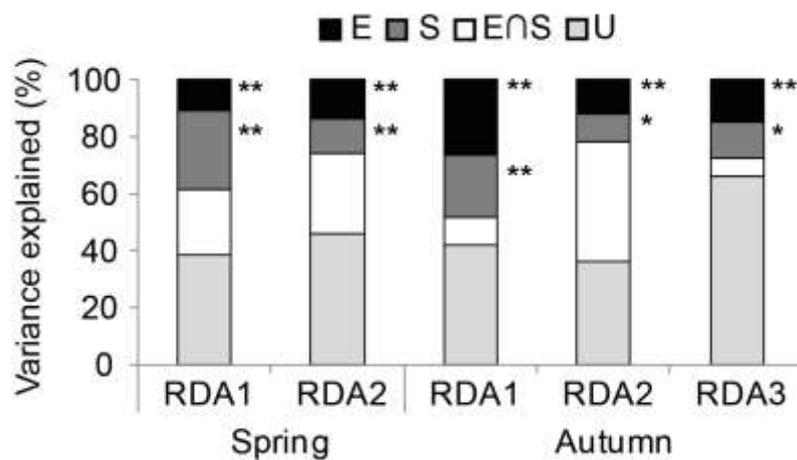
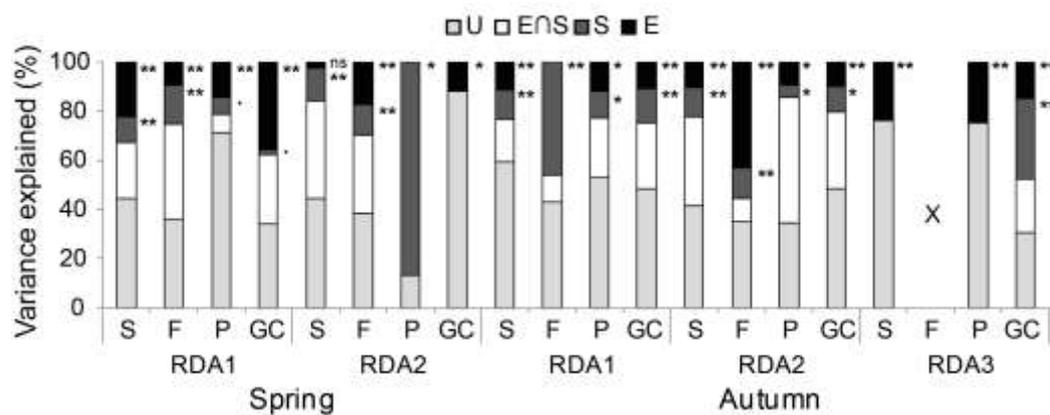


Fig. 4 Results from the variance partitioning analyses between explanatory variables and a) functional composition and b) species composition within each functional group (i.e. functional redundancy). The figure shows the amount of variation explained (%) in a) functional and b) taxonomical composition by local environmental (E) and spatial eigenvectors (S). Shown are also variances explained jointly by environmental and spatial factors ($E \cap S$) and unexplained variation (U). X indicates that no taxa were associated with that particular scale and FFG. S=Shredder, F=Filterer, 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 (ns = $P > 0.1$ ** = $P < 0.01$, * = $P < 0.05$, ' = $P < 0.10$).

a)



b)



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