Citation for the published paper:
David G. Angeler, Craig R. Allen, Daniel R. Uden and Richard K. Johnson. (2015) Spatial patterns and functional redundancies in a changing boreal lake landscape. *Ecosystems*. Volume: 18, Number: 5, pp 889-902.
http://dx.doi.org/10.1007/s10021-015-9871-z.

Spatial patterns and functional redundancies in a changing boreal lake landscape

David G. Angeler[1], Craig R. Allen[2], Daniel R. Uden[3] and Richard K. Johnson[1]

[1] *Swedish University of Agricultural Sciences, Department of Aquatic Sciences and Assessment, PO Box 7050, SE - 750 07 Uppsala, Sweden*

[2] *U.S. Geological Survey, Nebraska Cooperative Fish and Wildlife Research Unit, School of Natural Resources, University of Nebraska – Lincoln, Lincoln, NE, USA.*

[3] *Nebraska Cooperative Fish and Wildlife Research Unit, School of Natural Resources, University of Nebraska-Lincoln, Lincoln, Nebraska 68503-0984, USA*

*author for correspondence:

david.angeler@slu.se

Tel: +46 (0) 18-673049

Fax: +46 (0) 18-673156

Running title: spatial resilience and boreal lakes

Author contributions: DGA, CRA, DRU and RKJ conceived the study. DGA analyzed the data and lead the writing with contributions from CRA, DRU and RKJ.

Abstract

Global transformations extend beyond local habitats; therefore, larger-scale approaches are needed to assess community-level responses and resilience to unfolding environmental changes. Using long-term data (1996-2011), we evaluated spatial patterns and functional redundancies in the littoral invertebrate communities of 85 Swedish lakes, with the objective of assessing their potential resilience to environmental change at regional scales (i.e., spatial resilience). Multivariate spatial modeling was used to differentiate groups of invertebrate species exhibiting spatial patterns in composition and abundance (i.e., deterministic species) from those lacking spatial patterns (i.e., stochastic species). We then determined the functional feeding attributes of the deterministic and stochastic invertebrate species, in order to infer resilience. Between one and three distinct spatial patterns in invertebrate composition and abundance were identified in approximately one-third of the species; the remainder were stochastic. We observed substantial differences in metrics between deterministic and stochastic species. Functional richness and diversity decreased over time in the deterministic group, suggesting a loss of resilience in regional invertebrate communities. However, taxon richness and redundancy increased monotonically in the stochastic group, indicating the capacity of regional invertebrate communities to adapt to change. Our results suggest that a refined picture of spatial resilience emerges if patterns of both deterministic and stochastic species are accounted for. Spatially extensive monitoring may help increase our mechanistic understanding of community-level responses and resilience to regional environmental change, insights that are critical for developing management and conservation agendas in this current period of rapid environmental transformation.

Key words: adaptive capacity; benthic invertebrates; functional traits; global change; landscape ecology; redundancy; spatial resilience

Introduction

Ecologists have a long-standing interest in the temporal stability of communities in aquatic and terrestrial ecosystems (Loureau and others 2001; Steiner and others 2005; Tilman and others 2006; Isbell and others 2009), especially in the current period of rapid environmental change that has prompted concern regarding potential negative consequences for biodiversity and ecosystem function (Hooper and others 2005; Millennium Ecosystem Assessment 2005). Lakes provide important ecosystem services (e.g., commercial fishing, groundwater recharge, and recreation) and contribute to local and regional biodiversity. Boreal lakes undergo abiotic and biotic change as a result of the combined effects of land use and climate change, hydrological alterations, acid deposition (Evans and others 2005; Monteith and others 2007; Angeler and Johnson 2012) and biological invasions (Angeler and others 2012).

Recent studies have documented a loss of functional diversity and homogenization of terrestrial and aquatic communities at regional and global scales due to environmental change (e.g., Clavel and others 2010; Clavero and Brotons 2010; Pool and Olden 2012). Boreal lake benthic and pelagic communities also undergo structural and functional change following environmental perturbations (e.g., Stendera and Johnson 2008; Burgmer and others 2007; Angeler and others 2011), but it is unclear how environmental change affects communities in landscapes, and how these changes affect the resilience of invertebrate communities. We address these uncertainties by evaluating spatial patterns of change of functional community attributes in response to environmental pressures over large geographic areas.

The assessment of structural community responses, followed by characterization of the functional attributes of taxa that explain structural change can help represent how ecosystem processes and services (e.g., matter and energy fluxes, and primary productivity) are affected by environmental change (Hooper and Vitousek 1997; Laliberté and others 2010; Mori and others

2013). Invertebrates are useful models for assessing functional change because they are comprised by species with different feeding modes (e.g., predators, shredders, grazers, gatherer-collectors, and filterers), and are critical for ecosystem functions in aquatic ecosystems (e.g., secondary production, leaf litter decomposition, nutrient and matter cycling and energy fluxes; Wallace and Webster 1996).

Multiscale spatial modeling has been used in a wide array of studies for identifying independent spatial patterns in data sets (Andersen and others 2011, Kent and others 2011, Boierio and others 2013, Bertolo and others 2012, Vandam and others 2013). More recently, such approaches have been extended to the evaluation of functional traits within and across spatial patterns to infer resilience of stream invertebrate communities (Göthe and others 2014). Within and across-scale functional distributions are important for understanding resilience (sensu Holling 1973) to environmental perturbations (Peterson and others 1998; Allen and others 2005), and may therefore provide relevant information about resilience in a spatial context (Bengtsson and others 2003; Cumming and others 2010; Cumming 2011). Resilience is theorized to increase with greater functional redundancy and trait differentiation within and across scales (Elmqvist and others 2003; Allen and others 2005). Landscapes are expected to be more resilient to regional environmental change if functional traits are redundant within and across spatial scales. The recognition that resilience increases with overlapping functions within scales relates to the concepts of functional redundancy, or the ‘‘insurance hypothesis’’ (Yachi and Loreau 1999). Furthermore, environmental perturbations may be scale specific; thus, approaches that can identify scales in space and time, and the scale-specific effects of perturbations, are critical (Nash and others 2014).

Multiscale spatial modeling can be used to identify species that exhibit stochastic dynamics (i.e., species that are not correlated with spatial patterns). Stochastic species can play an important role in determining the “adaptive capacity” of ecosystems by increasing their ability to adapt to change without undergoing catastrophic regime shifts (Baho and others 2014). Assessing this adaptive capacity therefore provides complementary information to, and thus a more refined understanding of, resilience (Gallopin 2006).

Understanding temporal trends in patterns of functional trait distributions within and across spatial scales (i.e. those associated with “deterministic species”), as well as the adaptive capacity associated with stochastic species, should increase our mechanistic understanding of community dynamics and their implications for the resilience of lake invertebrate communities (resilience of what; Carpenter and others 2001) to environmental perturbations (resilience to what). Here, we refer to deterministic species as those that show spatial patterns, whilst conversely stochastic species are those that are not correlated with either spatial or environmental gradients. The spatial patterns detected by modeling may result from demographic processes (e.g., dispersal) but also from a correlation with environmental (e.g. water quality) variables (Cottenie 2005; Leibold and others 2004). It is therefore important to account for covariation from environmental effects in spatial modeling, because the lack of both significant unique environmental and spatial variation biases species groupings in favor of stochastic species. Variation partitioning analyses can accomplish the detection of unique environmental and spatial effects, and in turn validate the classification of deterministic and stochastic species revealed by spatial modeling.

Considering alternative plausible scenarios of spatial and temporal patterns of functional trait distribution of lake invertebrates can help accomplish an improved understanding of spatial resilience. We present three hypothetical scenarios of how spatial resilience patterns may change in response to environmental change (Figure 1), in addition to a null expectation of no temporal patterns: (1) functional metrics associated with deterministic and stochastic species fluctuate around a long-term mean (i.e. temporal stability), (2) functional metrics of deterministic and stochastic species increase over time, and (3) functional metrics of these species decrease over time. These scenarios have very different implications for management and conservation. Scenarios 1 and 2 suggest that little management is required because the regional communities seem resilient over the time period studied. Scenario 3 is the least desired because it indicates an erosion of resilience that might eventually lead to a broad-scale regime shift (Hughes and others 2013). If a regime shift is unavoidable, management can be designed to cope with alternative futures (Folke and others 2001).

To date, these scenarios and their relevance for conservation have been difficult to test due to the limited availability of long-term data series with sufficient spatial and temporal sampling resolution. Here, we use 16-year (1996–2011) time series data from 85 lakes in the National Swedish Lake Monitoring Program to study spatial patterns of composition and abundance in littoral invertebrate communities, followed by an assessment of spatial resilience through the evaluation of feeding guilds (here referred to as functional feeding group attributes) of species associated with within and cross scale spatial patterns, and in the stochastic species. Given the local and regional changes documented in water quality and community composition of invertebrates in these lakes during the last twenty years (Angeler and Johnson 2012; Angeler 2013; Angeler and Drakare 2013), we test the hypothesis that regional patterns of functional metrics, and thus regional resilience of invertebrate communities, is changing over time. Using spatial modeling and variation partitioning analyses that distinguishes between deterministic and stochastic species, we provide a refined view of regional community responses to environmental change by evaluating the complementarity of resilience and adaptive capacity when assessing these responses.

Material and Methods

Study area

In the late 1980s, Sweden initiated a long-term monitoring program of its lakes aimed at determining responses of multiple habitats and communities to global change. This monitoring program is overseen by the Swedish Agency for Marine and Water Management (https://www.havochvatten.se/en). Information about the monitoring program is available online: http://www.slu.se/en/faculties/nl/about-the-faculty/departments/department-of-aquatic-sciences-and-assessment/data-host/. For this study, environmental and littoral invertebrate assemblage data from 85 lakes between 1996 and 2011 was used to cover broad spatial and temporal extents (Figure 2; Electronic Appendix 1).

Sampling

Standard sampling and analyses protocols for abiotic variables and invertebrates, certified and quality controlled through the Swedish Board for Accreditation and Conformity Assessment (SWEDAC; http://www.swedac.se/en/), were employed during data collection. Water quality data were obtained from surface water samples, which were obtained at 0.5 m depth four to eight times each year at a mid-lake station in each lake. Samples were collected with a Ruttner sampler and kept cool during transport to the laboratory, where they were analyzed for temperature, acidity (pH, alkalinity, SO_4^{2-} concentration), nutrients (total P, total N, total organic C), and water clarity (Secchi disc depth, water color). All physicochemical analyses were conducted at the Department of Aquatic Sciences and Assessment (Swedish University of Agricultural Sciences) following international (ISO) or European (EN) standards (Wilander and others 2003). Measurement intervals and analytical precision for each variable are available online at: http://www.slu.se/en/faculties/nl/about-the-faculty/departments/department-of-aquatic-sciences-and-assessment/laboratories/geochemical-laboratory/water-chemical-analyses.

Sampling of benthic invertebrates followed Swedish standards (SS-EN 27828) throughout the study period. Invertebrates were usually collected from each lake in one wind-exposed, vegetation-free littoral habitat during late autumn (end of October– early November) each year. Many boreal lakes lack clear macrophyte beds, and habitat-specific sampling is therefore expected to increase the detection of trends within a lake and also among lakes. In the most northern lakes, sampling was conducted at the end of September, so that similar seasonal conditions were covered during surveys. Five replicate samples were taken, using standardized kick sampling with a hand net (0.5 mm mesh size). For each sample, the bottom substratum was disturbed for 20 seconds along a 1 m stretch of the littoral zone at a depth of c. 0.5 m. Invertebrate samples were preserved in 70% ethanol in the field and processed in the laboratory, where they were sorted against a white background with 10x magnification, identified to the finest taxonomic unit possible, and counted using dissecting and light microscopes. All processing was conducted by one individual, a trained taxonomist, in order to reduce bias in sample evaluation.

Statistical analyses

Detecting spatial patterns in invertebrate communities - To reveal spatial structure in the invertebrate communities for each year of the 16-year study period, we used a common spatial modeling technique capable of identifying spatial structure at multiple scales (Borcard and Legendre 2002, Borcard and others 2004). This method is based on Redundancy Analysis (RDA), which uses distance-based Moran Eigenvector Maps (dbMEM) to model space (Dray and others 2006). Essentially, the dbMEM analysis produces a set of orthogonal spatial variables derived from the geographic XY coordinates of each lake, which in turn are used as explanatory variables in models of spatial relationships in community data. This process yielded a total of 26 dbMEM variables for the 85 study lakes, each of which corresponds to a specific spatial structure and pattern ranging from fine- to broad-scale in the community data. Next, a parsimonious spatial model for each year of study (1996-2011) was produced by running a forward selection process on these dbMEM variables.

In the RDA analysis, significant dbMEM variables are retained and then linearly combined, so that spatial patterns may be extracted from Hellinger-transformed species x space matrices (Legendre and Gallagher 2001). That is, species or groups of species with similar spatial patterns are identified and collapsed onto independent RDA axes. The identified spatial patterns associated with each RDA axis are rigorously tested using permutations, so that the patterns identified are independent from each other. The resulting patterns can, but must not necessarily reflect hierarchical structures (i.e. broad-scale vs fine-scale variation) in the landscape. That is, the technique is sensitive enough to identify even subtle differences in community structure at any spatial scale discernable given data resolution and extent, allowing for identification of independent patterns of functional redundancies in the landscape. For simplicity, these independent patterns have been referred to as different scales being present in ecosystems (Borcard and others 2004; Blanchet and others 2011).

Linear combination (lc) score plots are used to visually represent the modeled spatial patterns in species groups associated with each RDA axis (Electronic Appendix 2). The number of modeled spatial patterns of species groups is deduced from the number of significant RDA axes, and the ecological relevance of the spatial patterns is quantified with the adjusted R^2 values of the RDA axes. Finally, the overall spatial structure of a community is inferred from the number of significant axes in the RDA models.

dbMEM analysis is powerful for detecting spatial patterns, but the method is inefficient in handling linear trends; therefore, the detrending of raw data is required prior to analysis (Borcard and others 2004; Dray and others 2006). Although methods exist that account for linear trends (i.e. asymmetric eigenvector maps; Blanchet and others 2008), linearity is modeled according to explicit connectivity patterns among sites (for instance, upstream and downstream sites in a stream network) (Göthe and others 2013). Because the lakes in our study have clear insular metacommunity structure and no specific connectivity patterns (i.e. hydrological connections or dispersal routes of invertebrates) at the scale of our study, we believe the dbMEM approach is suitable for identifying spatial relationships in our data. Notwithstanding, we also conducted dbMEM models without detrending for gaining insight into the potential relevance of a linear trend in our data. All relevant analysis steps were carried out in R 2.15.1 (R Development Core Team 2012) with the packages PCNM (dbMEM variables), AEM (Moran's I spatial autocorrelation), vegan (Hellinger transformations, RDA) and packfor (forward selection).

Variation partitioning — We used variation partitioning analysis (varpart function) in the R package vegan to differentiate between the relative effects of environmental and spatial factors on the structure of invertebrate communities. The analysis uses partial redundancy analysis (pRDA) to calculate how much of the variation in community structure can be explained uniquely by each explanatory matrix (here environmental and spatial), as well as the shared variance explained by the explanatory matrices (Peres-Neto and others 2006). In essence, this approach helped to differentiate between patterns that are more likely due to dispersal-related factors and those due to variability in the abiotic lake environment. Variation partitioning also assisted with the identification of significant unique spatial and environmental fractions, which provided confirmation that the patterns detected in the previously-described spatial modeling analyses were not confounded by environmental gradients. We are therefore confident that the classification of taxa into deterministic and stochastic species based on our spatial models is accurate. Prior to pRDA analyses for each year of study, significant environmental (water quality) predictor variables were selected using the ordistep function and compiled into the environmental matrices used for the variance partitioning analyses. Significant spatial (dbMEM) variables were obtained from the previously-described spatial modeling. The significance of each testable fraction (pRDA) in the variance partitioning analysis was obtained by using function rda (R package vegan).

Correlation of invertebrate taxa with modeled spatial patterns — We used Spearman rank correlations to relate the raw abundances of individual invertebrate taxa with the modeled spatial patterns (i.e., to identify deterministic species). We also separated deterministic from stochastic species (i.e., those not associated with any significant canonical axis) by subtracting the number of species correlated with significant canonical axes from the total number of species used for spatial modeling.

In all analyses, we used taxa that had been identified to species and morphotypes, and that could be classified into functional feeding guilds for additional analysis. Taxa classified with lower taxonomic resolution (i.e., family and above) were omitted to avoid unduly influencing results with ambiguous feeding group assignments. Taxa that correlated with modeled spatial patterns and stochastic species were classified as filterers, gatherers, grazers, shredders or predators, using a 1 to 10 grading scale where 10 indicates highest feeding preference, according to the online data base: www.freshwaterecology.info (Schmidt-Kloiber and Hering 2012).

Generalists were defined as taxa with omnivorous feeding modes, i.e. those taxa that scored identically among at least two feeding groups (e.g., gatherers and grazers).

Definition of functional metrics – Upon our classification of invertebrate taxa into feeding guilds, we calculated the following functional measures for each identified spatial pattern and the group of species that exhibited stochastic dynamics: 1) functional richness (the number of feeding groups present); 2) functional diversity based on the exponentiated Shannon-Wiener index (exp H') (Jost 2007; Tuomisto 2010); 3) functional evenness (calculated as the quotient between functional diversity and functional richness; Tuomisto 2012); 4) functional redundancy (the average number of species within each functional group at each spatial scale and the group of stochastic species; Allen and others 2005); and 5) cross-scale redundancy (the average number of spatial scales at which each function is represented; Allen and others 2005). In addition to these functional measures, we calculated taxonomic richness (a structural community metric) for each spatial scale and the stochastic species identified.

Because our spatial modeling was based on taxonomy, we were able to test how structural diversity components of invertebrate communities partition between deterministic and stochastic species, how these patterns change over time, and how these changes affect patterns of change in functional feeding guilds within the lake landscape. Using functional diversity, functional richness, and functional evenness metrics calculated on the basis of taxonomic information allowed for direct comparisons with functional redundancy metrics, which have been critical in resilience assessment studies (Peterson and others 1998; Allen and others 2005; Angeler et al. 2013a).

Evaluation of temporal trends — We used Kendall´s tau rank correlations (Kendall 1938)—a nonparametric test of concordance—to assess whether water quality variables and the calculated community functional metrics and taxonomic richness change monotonically between the years 1996 and 2011. Given our interest in change in the regional lake landscape rather than in individual lakes, we used regionally averaged data for our analyses. Significant monotonic change in environmental variables and metrics allowed us to test the hypothesis that invertebrate communities display changing spatial resilience patterns under changing environmental conditions.

Results

Temporal patterns and trends in regional environmental variables

The average water temperature, nutrients (total N, total P) and pH from the 85 lakes fluctuated over the study period (Fig. 3a-d). Sulfate concentrations and Secchi depth decreased, while alkalinity, water color, and total organic C increased significantly between 1996 and 2011 (Fig. 3e-i).

Spatial patterns in invertebrate communities

Spatial modeling of invertebrate communities in Swedish lakes revealed significant spatial structure for all years except 1999 and 2009. These spatial structures explained between 3.1% and 6.7% of the adjusted variance in the constrained RDA models (Fig. 4a; Electronic Appendix 2). The spatial signal remained significant after accounting for environmental effects in the variance partitioning analysis; that is, the fraction of variation explained uniquely by space (space|env) was highly significant ($p < 0.005$) for most study years, and close to significant at $p = 0.05$ for the years 1998 ($p = 0.065$), 2002 ($p = 0.055$), and 2006 ($p = 0.075$) (Electronic

Appendix 3). Also the variation uniquely explained by environmental factors (env|space) was significant ($p = 0.005$) throughout the study (Electronic Appendix 3). Models that were not detrended generally explained a higher amount of adjusted variance (8.8 -15.3%), suggesting that a linear trend was present in the data (Electronic Appendix 2). The number of significant spatial patterns associated with the canonical axes of the detrended models varied during the study; that is, we found between 1 and 3 significant spatial patterns that were associated with the canonical axes 1-3 in the RDA models (Fig. 4b). The relatively low number of spatial patterns identified indicates the influence of invertebrate species at a limited number of spatial scales. Despite the low amount of variance explained, all of the identified spatial patterns reflected community structure at broad spatial scales (Electronic Appendix 2).

Taxonomic and functional structure and redundancy patterns in invertebrates

Because of the low number of spatial patterns identified, only about one third of the invertebrate species exhibited within- and cross-scale patterns (i.e., were classified as deterministic species); the rest (*c.* two thirds) comprised stochastic species (Fig. 4c). Consistent with the patterns of taxonomic richness, functional richness, functional diversity and functional redundancy (Figs. 4d, e, f), but not functional evenness (Fig. 4f), tended to be higher for stochastic than deterministic species. Functional richness and diversity decreased in the deterministic species group (Fig. 4d, e), while taxon richness and redundancy increased monotonically in the stochastic group (Fig. 4c, g).

Predators and gatherers were the dominant feeding types, with high functional redundancies in both the deterministic and stochastic species groups (Figs. 5a, b). By contrast, shredders and filterers were the least dominant groups with the lowest redundancies (Figs. 5e, f). Grazers and omnivores occupied intermediate positions (Figs. 5c, d). All feeding groups, except filterers, increased significantly over time in the stochastic, but not in the deterministic, species group (Fig. 5). Cross-scale redundancy results were similar to those of functional redundancy within spatial patterns for deterministic species and within the stochastic species group, with the highest levels for grazers and the lowest for shredders (Fig. 6). Finally, when multiple patterns were detected, all functions were present at more than the half of all spatial patterns identified, on average (Fig. 6).

Discussion

There is evidence that changes in the abiotic environment of Scandinavian lakes is a result of complex interactions of climate, land use, hydrological change, and recovery from acidification (Evans and others 2005). Even in our relatively short study of 16 years, quantitative changes in monotonically changing water quality variables (i.e., variables related to water clarity and acidity) were apparent. These findings are similar to those of a previous, longer-term study conducted on a smaller number of lakes (Angeler and Johnson 2012), and more generally, support the conjecture that abiotic, long-term shifts occur in the aquatic environments of Sweden and elsewhere (Evans and others 2005, Van Kleef and others 2010).

Several studies have documented changes in biotic communities in response to changing abiotic conditions, including altered patterns of community structure and biodiversity (Stendera and Johnson 2008; Burgmer and others 2007; Angeler 2013), and species invasions (Angeler and others 2012). However, the magnitude of community change in individual lakes was often dependent on observational scale. That is, time series analysis found that only subsets of species composing phytoplankton and invertebrate communities tracked the slow (i.e., decadal) changes in water clarity and recovery from acidification, whilst other subsets of species showed faster fluctuation dynamics at interannual scales that were unrelated to measured environmental variables (Angeler and others 2011; Angeler and Johnson 2012). These results support the notion that ecosystems are hierarchically structured, with dynamics unfolding across distinct spatial and temporal scales (Allen and others 2014), and they also show the footprints of environmental change to be scale-specific (Nash and others 2014).

It has long been recognized that patterns and processes resulting from the distribution of functional community attributes within and across scales have important implications for resilience of ecosystems (Peterson and others 1998; Allen and others 2005) and landscapes (Cumming and others 2010; Cumming 2011). Understanding and quantifying resilience is important for scientists and managers facing unprecedented rates of environmental change that can decrease the capacity of ecosystems to withstand disturbances and eventually lead to catastrophic regime shifts, with negative consequences for biodiversity and ecosystem service provisioning (Hughes and others 2013). Recent research has quantified resilience attributes in Scandinavian lakes and found that communities are surprisingly resilient to environmental change (Angeler and others 2013a); however, it is unclear how the resilience patterns of individual lakes affect the resilience of the entire lake landscape. This study is the first to employ a spatially explicit approach—with a relatively high spatial resolution and the representation of various lake types—to the evaluation of patterns in the spatial redundancies in functional traits of invertebrate communities across boreal lakes, and to assess how these resilience patterns change over time as a function of environmental change patterns.

The spatial modeling tool used has been applied to assessments of multiscale spatial patterns in various studies (Borcard and Legendre 2002; Vandam and others 2013; Göthe and others 2014). Here we used it to identify scaling patterns and stochastic species in a landscape of boreal lakes, and extended its utility to the quantification of spatial functional redundancy and diversity by determining how functional feeding group attributes of invertebrates are distributed within and across spatial scales and in stochastic species. This allowed for an assessment of spatial resilience based on the cross-scale resilience model of Peterson and others (1998), which considers the distribution of functional traits within and across scales, and also allowed for inference regarding the role of stochastic species—which often have been ignored in resilience assessments—in conferring groups of lakes with spatial resilience. The spatial modeling was complemented with a variation partitioning analysis to assess the contribution of unique fractions of environment and space to invertebrate community structure. This analysis revealed that the invertebrate communities were structured by both environmental and spatial factors, which allowed differentiation between patterns that are due to dispersal-related factors from those due to variability in the abiotic lake environment. Assessing the relative contribution of these factors structuring communities is necessary for understanding spatial resilience (Cumming 2011; Göthe and others 2014). The analysis approaches used in this study provide a quantitative framework for assessing these factors.

Although our models explained a low amount of variance, we acknowledge that weak patterns and high variability are a common problem in studies based on survey data. These can often have a high residual variation due to the accumulation of noise related to sampling, ecosystem history and intrinsic variability (e.g., Leibold and others 2010). Specifically, the detection of smaller scale spatial patterns in our approach depends on the spatial resolution of sampling. Our analysis was based on a coarser sample resolution in the north, which potentially limited the detection of some of the small-scale spatial structure present in the southern area that cannot be extracted with the sampling design. Furthermore, recent research has shown that spatial signals can be weak when the effects of dispersal limitation in communities are weak (Fernandes and others 2014). However, dispersal limitation has been shown to persistently influence invertebrate communities over time at the broad spatial extent of our study (Angeler and others

2013b), leading to community structures that reflect different ecozones in the Swedish landscape (Johnson and others 2004). This interpretation is also supported by the results from our variation partitioning analysis, showing that invertebrates were structured by unique effects of space. The low amount of variance explained can also be explained by taking an appropriate approach based on the correction of R^2-values by the number of explanatory variables (Peres-Neto and others 2006). We also used the results of detrended spatial models because the dbMEM approach is inefficient in handling linear trends in data (Borcard and others 2004).

The hypothesis that invertebrate communities across lakes change in response to environmental change was supported, but it is unclear how the observed changes affect the resilience of invertebrate communities in landscapes to changing environmental conditions. This is partly due to the lack of similar studies conducted at the same scale which did not allow any comparison with other studies. Our results also suggest that an evaluation of resilience according to our scenarios is too simplistic because deterministic and stochastic species can show opposite trends and temporal patterns of individual functional metrics can be idiosyncratic. That is, complex patterns of change of functional and structural metrics were observed. Functional evenness fluctuated around its long-term mean. Functional richness and diversity decreased in the deterministic species group which implies a loss of resilience. However, taxon richness and redundancy increased monotonically in the stochastic group, indicating the capacity of regional invertebrate communities to adapt to change. Our results suggest that a refined picture of spatial resilience emerges if patterns of both deterministic and stochastic species are accounted for.

The correlative nature of our study does not allow us to attribute causal factors to the observed changes in deterministic and stochastic species, but recent long-term studies of invertebrates do promote speculation concerning how biodiversity patterns might have influenced study results. Angeler and Drakare (2013) found that alpha (i.e., local) and gamma (i.e., regional) diversity increased monotonically over an 18-year study period. This increase in local and regional diversity was correlated with an increase of total invertebrate abundance over time, which has been attributed to the ‘‘more individuals’’ effect (i.e., greater detection of species with increasing sampling effort; Scheiner and others 2011). Our results also suggest this effect in the increasing richness and redundancy of stochastic species of all functional feeding groups, except filterers, but not in the deterministic species that explained the modeled scaling patterns. Because our modeling identified stochastic species presumably due to regional rarity and/or low local abundances, results suggest that more species are becoming rare and isolated. This supports results of another recent study, which found that lakes contain more unique sets of invertebrate species (i.e. a higher spatial turnover) over time (Angeler 2013). These findings further underscore the importance of evaluating resilience based on multiple lines of evidence; that is, both through an assessment of within- and cross scale patterns, and the adaptive capacity related to stochastic species.

In addition to the different contributions of deterministic and stochastic species to functional structure across lakes, we found different contributions of functional feeding groups to deterministic and stochastic patterns that are important for understanding the overall resilience of the studied system. Johnson and others (2004) found that filterers had the lowest, and predators and gatherers the highest, representation in invertebrate communities. Consistent with these findings, filterers had the lowest within-scale redundancy, followed by shredders, grazers and omnivores in this study. The highest within-scale redundancy was observed for gatherers and predators. While the patterns of within-scale redundancy fluctuated around a long term mean for the deterministic species in most feeding groups, monotonic increases occurred for the stochastic species in these groups, with the exception of filterers. Cross-scale reinforcement was highest for grazers, followed by gatherers and predators, and lowest for shredders.

The loss of functional group representation at one or more scales, and reduced adaptive capacity resulting from species with stochastic dynamics, would have a greater impact on resilience than the loss of species from functional groups with high redundancy. Our results show that filterers and shredders are the functional groups most vulnerable to loss from lakes. While this suggests that these groups should be most carefully monitored, we acknowledge that these groups usually are much more abundant in streams (Johnson et al. 2004) and that their contribution to matter flux in lakes is low (Bohman and Tranvik 2001).

Gatherers and predators had the highest redundancy across lakes; and therefore, the loss of one or a few species from these functional groups would have relatively minor impact on resilience. Most studies inferring the resilience of ecosystems on the basis of the distribution of functions have not studied the contributions of individual functions explicitly. Discriminating between functional groups can help refine the resilience assessment of the overall system and also of contributing individual functions.

The implications of our results relate to the maintenance of biodiversity, species, and key functions in ecosystems, protected areas and landscapes, which often necessitate costly management interventions. Natural disturbance regimes are altered by human activities (Bengtsson and others 2003), changing the niche dimensions and distribution of species in ways that make the persistence of current sets of species in ecosystems or managed species, or the prediction and management of future sets of species, highly uncertain (Polasky and others 2011). Our results make clear that spatially extensive monitoring efforts can help increase our mechanistic understanding of landscape-level changes in communities and their resilience in response to environmental change. This could prove crucial in the development of management and conservation agendas in this present period of rapid environmental and social change.

Acknowledgements

The Swedish Environmental Protection Agency, the Swedish Agency for Water and Marine Management and the many people involved in the monitoring program for making the analyses of these data sets possible are gratefully acknowledged. This work was funded by the August T. Larsson Foundation (NJ Faculty, Swedish University of Agricultural Sciences), and the Swedish Research Councils Vetenskapsrådet (2014-5828) and Formas (2014-1193). The Nebraska Cooperative Fish and Wildlife Research Unit is jointly supported by a cooperative agreement between the U.S. Geological Survey, the Nebraska Game and Parks Commission, the University of Nebraska−Lincoln, the U.S. Fish and Wildlife Service and the Wildlife Management Institute. Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government. We thank Graeme Cumming, Dirac Twidwell and two anonymous reviewers for helpful comments on previous manuscript versions.

References

Allen CR, Gunderson L, Johnson AR. 2005. The use of discontinuities and functional groups to assess relative resilience in complex systems. Ecosystems 8:958–966.

Allen CR, Angeler DG, Garmestani AS, Gunderson LH, Holling CS. 2014. Panarchy: Theory and applications. Ecosystems 17:578-589.

Andersen R, Poulin M, Borcard D, Laiho R, Laine J, Vasander H, Tuittila E-T. 2011. Environmental control and spatial structures in peatland vegetation. J Veg Sci 22:878–890.

Angeler DG, Drakare S, Johnson RK. 2011. Revealing the organization of complex adaptive systems using multivariate time series modeling. Ecol Soc 16(3):5. [online] http://dx.doi.org/10.5751/ES-04175-160305.

Angeler DG, Johnson RK. 2012. Temporal scales and patterns of invertebrate biodiversity dynamics in boreal lakes recovering from acidification. Ecol Appl 22:1172–1186.

Angeler DG, Allen CR, Johnson RK. 2012. Insight on invasions and resilience derived from spatiotemporal discontinuities of biomass at local and regional scales. Ecol Soc 17(2):32. [online] http://dx.doi.org/10.5751/ES-04928-170232

Angeler DG. 2013. Revealing a conservation challenge through partitioned long-term beta diversity: increasing turnover and decreasing nestedness of boreal lake metacommunities. Divers Distrib 19:772–781.

Angeler DG, Allen CR, Johnson RK. 2013a. Measuring the relative resilience of subarctic lakes to global change: redundancies of functions within and across temporal scales. J Appl Ecol 50:572–584.

Angeler DG, Göthe E, Johnson RK. 2013b. Hierarchical dynamics of ecological communities: do scales of space and time match? PLOS ONE 8(7): e69174. doi: 10.1371/journal.pone.0069174

Angeler DG, Drakare S. 2013. Tracing alpha, beta and gamma diversity responses to environmental change in boreal lakes. Oecologia 172:1191-1202.

Baho DL, Drakare S, Johnson RK, Allen CR, Angeler DG. 2014. Similar resilience characteristics in lakes with different management practices. PLoS ONE 9(3): e91881. doi:10.1371/journal.pone.0091881

Bengtsson J, Angelstam P, Elmqvist T, Emanuelsson U, Folke C, Ihse M, Moberg F, Nyström M. 2003. Reserves, resilience and dynamic landscapes. Ambio 32:389-396.

Bertolo A, Blanchet FG, Magnan P, Brodeur P, Mingelbier M and others 2012. Inferring processes from spatial patterns: The role of directional and non–directional forces in shaping fish larvae distribution in a freshwater lake system. PLoS ONE 7(11): e50239. doi:10.1371/journal.pone.0050239

Blanchet FG, Legendre P, Borcard D. 2008. Modelling directional spatial processes in ecological data. Ecol Model 215:325-336.

Blanchet FG, Legendre P, Maranger R, Monti D, Pepin P. 2011. Modelling the effect of directional spatial ecological processes at different scales. Oecologia 166:357-368.

Bohman I, Tranvik L. 2001. The effects of shredding invertebrates on the transfer of organic carbon from littoral leaf litter to water-column bacteria. Aquat Ecol 35:43-50.

Boieiro M, Carvalho JC, Cardoso P, Aguiar CAS, Rego C and others. 2013. Spatial factors play a major role as determinants of endemic ground beetle beta diversity of Madeira Island Laurisilva. PLoS ONE 8(5): e64591. doi:10.1371/journal.pone.0064591

Borcard D, Legendre P. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecol Model 153:51–68.

Borcard D, Legendre P, Avois-Jacquet C, Tuomisto H. 2004. Dissecting the spatial structure of ecological data at multiple scales. Ecology 85:826–1832.

Burgmer T, Hillebrand H, Pfenninger M. 2007. Effects of climate-driven temperature changes on the diversity of freshwater macroinvertebrates. Oecologia 151:93-103.

Carpenter S, Walker B, Anderies JM, Abel N. 2001. From metaphor to measurement: Resilience of what to what? Ecosystems 4:765-781.

Clavel J, Julliard R, Devictor V. 2010. Worldwide decline of specialist species: toward a global functional homogenization? Front Ecol Environ 9:222–228.

Clavero M, Brotons L. 2010. Functional homogenization of bird communities along habitat gradients: accounting for niche multidimensionality. Glob Ecol Biogeogr 19:684–696

Cottenie K. 2005. Integrating environmental and spatial processes in ecological community dynamics. Ecol Lett 8:1175–1182

Cumming GS. 2011. Spatial resilience in social-ecological systems. London: Springer. 243 p.

Cumming GS, Bodin Ö, Ernstson H, Elmqvist T. 2010. Network analysis in conservation biogeography: challenges and opportunities. Divers Distrib 16:414–425.

Dray S, Legendre P, Peres-Neto PR. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbor matrices (PCNM). Ecol Model 196:483–493.

Elmqvist T, Folke C, Nyström M, Peterson G, Bengtson J, Walker B, Norberg J. 2003. Response diversity, ecosystem change and resilience. Front Ecol Environ 1:488–494.

Evans CD, Monteith DT, Cooper DM. 2005. Long-term increases in surface water dissolved organic carbon: observations, possible causes and environmental impacts. Environ Poll 137:55-71.

Fernandes IM, Henriques-Silva R, Penha J, Zuanon J, Peres-Neto P 2014. Spatiotemporal dynamics in a seasonal metacommunity structure is predictable: the case of floodplain-fish communities. Ecography 37:464-475

Folke C, Carpenter S, Elmqvist T, Gunderson L, Holling CS, Walker B. 2001. Resilience and sustainable development: Building adaptive capacity in a world of transformations. Ambio 31:437-440.

Göthe E, Angeler DG, Sandin L. 2013. Metacommunity structure in a small boreal stream network. J Animal Ecol 82:449–458

Göthe E, Sandin L, Allen CR, Angeler DG. 2014. Quantifying spatial scaling patterns and their local and regional correlates in headwater streams: Implications for resilience. Ecol Soc 19(3): 15. http://dx.doi.org/10.5751/ES-06750-190315

Holling CS. 1973. Resilience and stability of ecological systems. Ann Rev Ecol Syst 4: 1-23.

Hooper D, Vitousek PM. 1997. The effects of plant composition and diversity on ecosystem processes. Science 277:1302–1305.

Hooper DU, Chapin III FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecol Monogr 75:3-35.

Hughes TP, Carpenter S, Rockström J, Scheffer M, Walker B. 2013. Multiscale regime shifts and planetary boundaries. Trends Ecol Evol 28:389-395.

Isbell FI, Polley HW, Wilsey BJ. 2009. Biodiversity, productivity and the temporal stability of productivity: patterns and processes. Ecol Lett 12:443–451.

Johnson RK, Goedkoop W, Sandin L. 2004. Spatial scale and ecological relationships between the macroinvertebrate communities of stony habitats of streams and lakes. Freshwat Biol 49:1179-1194.

Jost L. 2007. Partitioning diversity into independent alpha and beta components. Ecology 88:2427–2439.

Kendall M. 1938. A new measure of rank correlation. Biometrika 30:81–89.

Kent R, Bar-Massada A, Carmel Y. 2011. Multiscale analyses of mammal species composition – Environment relationship in the contiguous USA. PLoS ONE 6(9): e25440. doi:10.1371/journal.pone.0025440

Laliberté E, Wells JA, DeClerck F, Metcalfe DJ, Catterall CP, Queiroz C, Aubin I, Bonser SP, Ding Y, Fraterrigo JM, McNamara S, Morgan JW, Merlos DS, Vesk PA, Mayfield MM. 2010. Land-use intensification reduces functional redundancy and response diversity in plant communities. Ecol Lett 13:76–86.

Legendre P, Gallagher ED. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129:271–280

Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, Loreau M, Gonzalez A. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecol Lett 7:601–613

Leibold MA, Economo EP, Peres-Neto P. 2010. Metacommunity phylogenetics: separating the roles of environmental filters and historical biogeography. Ecol Lett 13:1290–1299.

Loureau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, Wardle DA. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294: 804-808.

Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: current state and trends. Island Press, Washington.

Monteith DT, Stoddard JL, Evans CD, De Wit HA, Forsius M, Høgåsen T, Wilander A, Skjelkvåle BL, Jeffries DS, Vuorenmaa J, Keller B, Kopácek J, Vesely J. 2007. Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. Nature 450:537-541.

Mori AS, Furukawa T, Sasaki T. 2013. Response diversity determines the resilience of ecosystems to environmental change. Biol Rev 88:349-364.

Nash KL, Allen CR, Angeler DG, Barichievy C, Eason T, Garmestani AS, Graham NAJ, Granholm D, Knutson M, Nelson RJ, Nyström M, Stow CA, Sundstrom SM. 2014. Discontinuities, cross-scale patterns and the organization of ecosystems. Ecology 95:654-667.

Peterson GD, Allen CR, Holling CS. 1998. Ecological resilience, biodiversity, and scale. Ecosystems 1:6–18.

Peres-Neto PR, Legendre P, Dray S, Borcard D. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. Ecology 87: 2614–2625.

Polasky S, Carpenter SR, Folke C, Keller N. 2011. Decision-making under great uncertainty: environmental management in an era of global change. Trends Ecol Evol 26:398-404.

Pool TK, Olden JD. 2012. Taxonomic and functional homogenization of an endemic desert fish fauna. Divers Distrib 18: 366–376.

R Development Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, http://cran.r-project.org.

Scheiner SM, Chiarucci A, Fox GF, Helmus MR, McGlinn DJ, Willig MR. 2011. The underpinnings of the relationship of species richness with space and time. Ecol Monogr 81:195–213.

Schmidt-Kloiber A, Hering D. 2012. www.freshwaterecology.info - the taxa and autecology database for freshwater organisms, version 5.0.

Steiner CF, Long ZT, Krumins JA, Morin PJ. 2005. Temporal stability of aquatic food webs: partitioning the effects of species diversity, species composition and enrichment. Ecol Lett 8:819–828.

Stendera S, Johnson RK. 2008. Tracking recovery trends of boreal lakes: use of multiple indicators and habitats. J N Am Benthol Soc 27:529-540.

Tilman D, Reich PB, Knops JMH. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature 441:629-632

Tuomisto H. 2010. A diversity of beta diversities: straightening up a concept gone awry. Part 1.

Defining beta diversity as a function of alpha and gamma diversity. Ecography 33:2-22.

Tuomisto H. 2012. An updated consumer´s guide to evenness and related indices. Oikos 121:1203-1218.

Vandam R, Kaptijn E, Vanschoenwinkel B. 2013. Disentangling the spatio-environmental drivers of human settlement: An eigenvector based variation decomposition. PLoS ONE 8(7): e67726. doi:10.1371/journal.pone.0067726

Van Kleef HH, Brouwer E, Leuven RSEW, van Dam H, de Vires-Brock A, van der Velde G, Esselink H. 2010. Effects of reduced nitrogen and sulphur deposition on the water chemistry of moorland pools. Environ Poll 158:2679-2685.

Yachi S, Loreau M. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. Proc Nat Acad Sci USA 96:1463–1468.

Wallace JB, Webster JR. 1996. The role of macroinvertebrates in stream ecosystem function. Ann Rev Entomol 41:115–139.

Wilander A, Johnson RK, Goedkoop W. 2003. Riksinventering 2000. En synoptisk studie av vattenkemi och bottenfauna i svenska sjöar och vattendrag. Institutionen för Miljöanalys, Uppsala, Sweden.

Electronic Appendices

Appendix 1: Names and geographical position of lakes.

Appendix 2: Spatial patterns detected by RDA between 1996 and 2011.

Appendix 3: Results from variation partitioning analyses between 1996 and 2011.

Figure legends

Figure 1: Three possible responses of spatial resilience components (within- and cross scale redundancies of functional traits associated with “deterministic” species [dotted lines]) and adaptive capacity associated with “stochastic” species (full lines). Also shown is a null expectation of no temporal patterns. Scenario1: functional metrics fluctuate around a long-term mean for both deterministic and stochastic species. Scenario 2: functional metrics of deterministic and stochastic species both increase over time. Scenario 3: functional metrics of deterministic and stochastic species both decrease over time. Note: differences in intercepts between deterministic and stochastic species are for demonstration purposes of these scenarios only and therefore not ecologically relevant.

Figure 2: Map of Sweden showing locations of the 85 lakes studied. For lake names and their geographical coordinates see Electronic Appendix 1.

Figure 3: Temporal patterns of environmental variables across Swedish lakes. Shown are the means ± 1 standard deviations of the 85 lakes studied, as well as trend lines, Kendall tau correlation coefficients, and P values for variables that exhibited significant monotonic change over time.

Figure 4: Temporal patterns in the number of spatial scales (a), adjusted variance explained of spatial models (b), structural (taxonomic richness; c) and functional (d-f) metrics, and average redundancy across feeding guilds (g) for littoral invertebrate communities in Swedish lakes. Shown are means ± standard deviations of 85 lakes and trend lines, Kendall tau correlation coefficients and P values for variables with significant monotonic change over time. Note that no spatial structure was detected for the years 1999 and 2009; therefore, no data points are displayed for deterministic species in these years.

Figure 5: Temporal patterns of redundancy for predators (a), gatherers (b), grazers (c), omnivores (d), shredders (e), and filterers (f) for Swedish lakes (full lines, stochastic species; dotted lines, deterministic species). Shown are trend lines, Kendall tau correlation coefficients and P values for feeding groups with significant monotonic change over time. Note that no spatial structure was detected in the years 1999 and 2009; therefore, no data points are displayed for deterministic species in these years.

Figure 6: Time-averaged cross-scale redundancies for averaged functions and individual feeding groups. Shown are means from all study years +/- 1 standard deviations. Label abbreviation: # scales pres. funct., number of scales where a function was present.

Figure 1

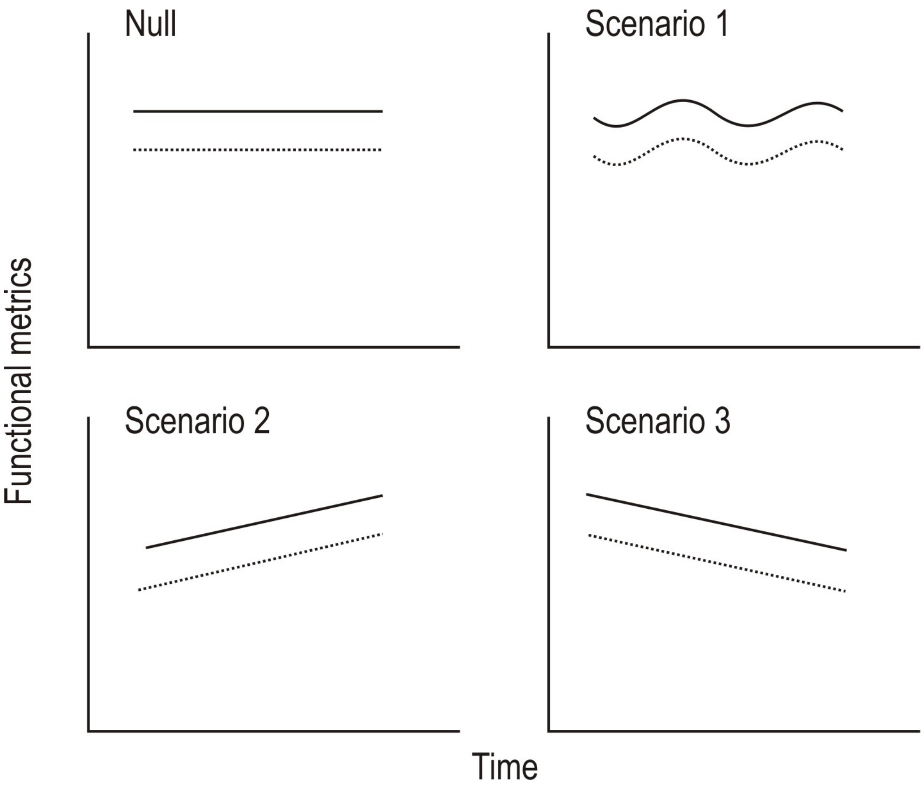

Null
Scenario 1
Functional metrics
Scenario 2
Scenario 3
Time

Figure 2

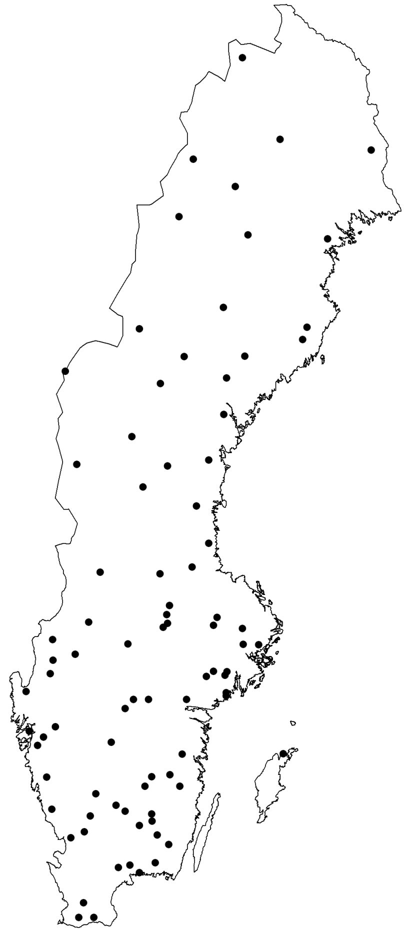


Figure 3

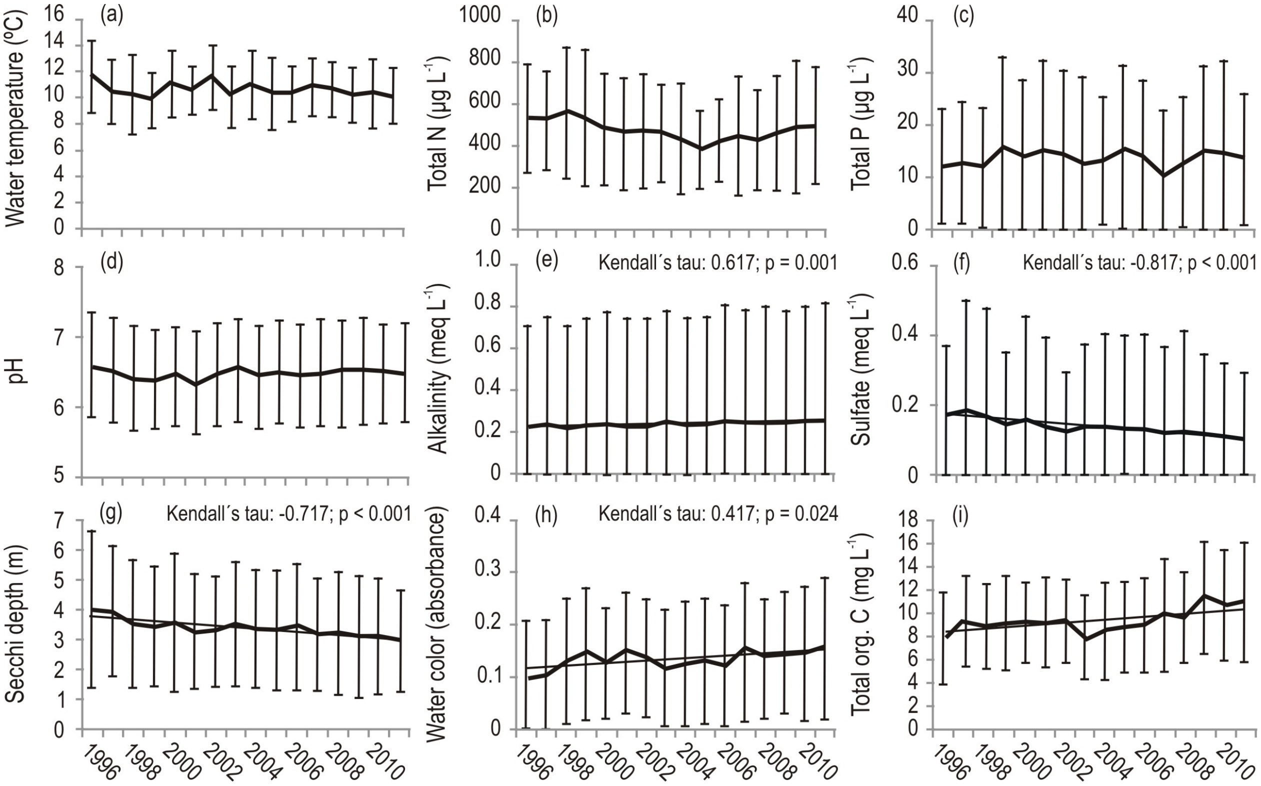
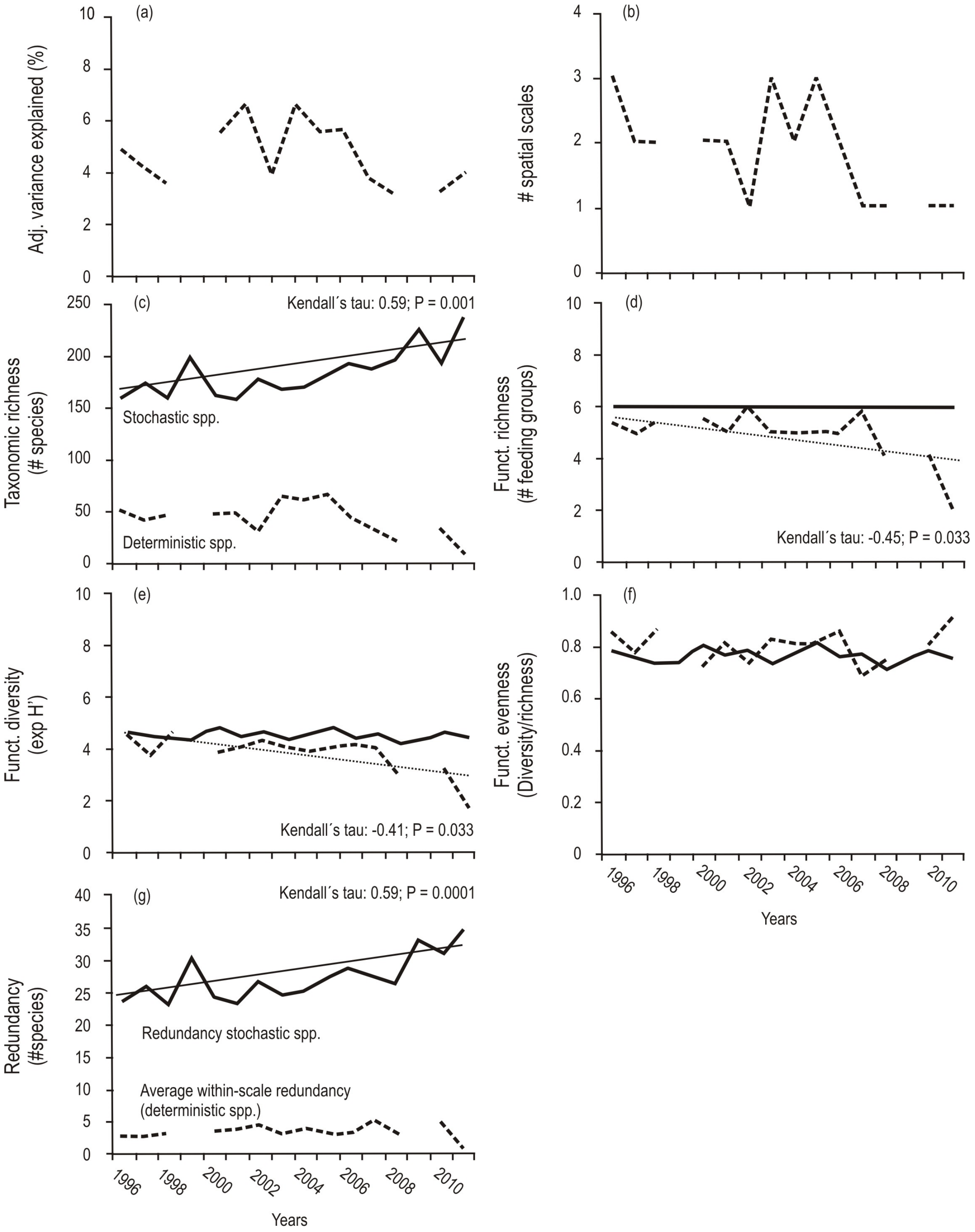

(a)
Water temperature (ºC)
0
2
4
6
8
10
12
14
16
(b)
Total N (μg L-1)
0
200
400
600
800
1000
(c)
Total P (μg L-1)
0
10
20
30
40
(d)
pH
5
6
7
8
(e)
Kendall´s tau: 0.617; p = 0.001
Alkalinity (meq L-1)
0
0.2
0.4
0.6
0.8
1.0
(f)
Kendall´s tau: -0.817; p < 0.001
Sulfate (meq L-1)
0
0.2
0.4
0.6
(g)
Kendall´s tau: -0.717; p < 0.001
Secchi depth (m)
0
1
2
3
4
5
6
7
(h)
Kendall´s tau: 0.417; p = 0.024
Water color (absorbance)
0
0.1
0.2
0.3
0.4
(i)
Total org. C (mg L-1)
0
2
4
6
8
10
12
14
16
18
1996
1998
2000
2002
2004
2006
2008
2010

Figure 4



(a)
Adj. variance explained (%)
0
2
4
6
8
10
(b)
spatial scales
0
1
2
3
4
(c)
Kendall´s tau: 0.59; P = 0.001
Taxonomic richness (# species)
0
50
100
150
200
250
Stochastic spp.
Deterministic spp.
(d)
Funct. richness (# feeding groups)
0
2
4
6
8
10
Kendall´s tau: -0.45; P = 0.033
(e)
Funct. diversity (exp H')
0
2
4
6
8
10
Kendall´s tau: -0.41; P = 0.033
(f)
Funct. evenness (Diversity/richness)
0
0.2
0.4
0.6
0.8
1.0
1996
1998
2000
2002
2004
2006
2008
2010
Years
(g)
Kendall´s tau: 0.59; P = 0.0001
Redundancy (#species)
0
5
10
15
20
25
30
35
40
Redundancy stochastic spp.
Average within-scale redundancy (deterministic spp.)
1996
1998
2000
2002
2004
2006
2008
2010
Years

Figure 5

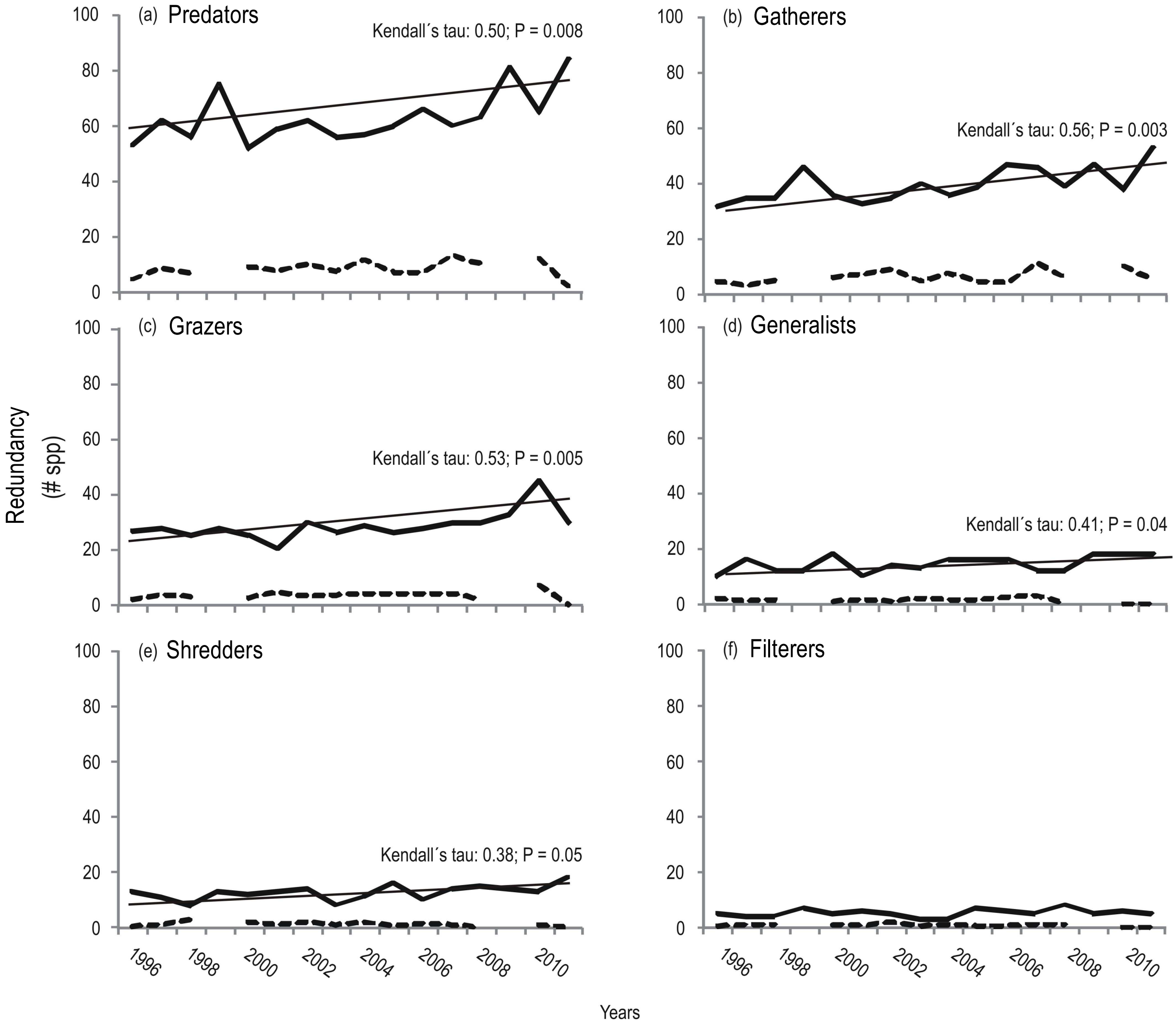
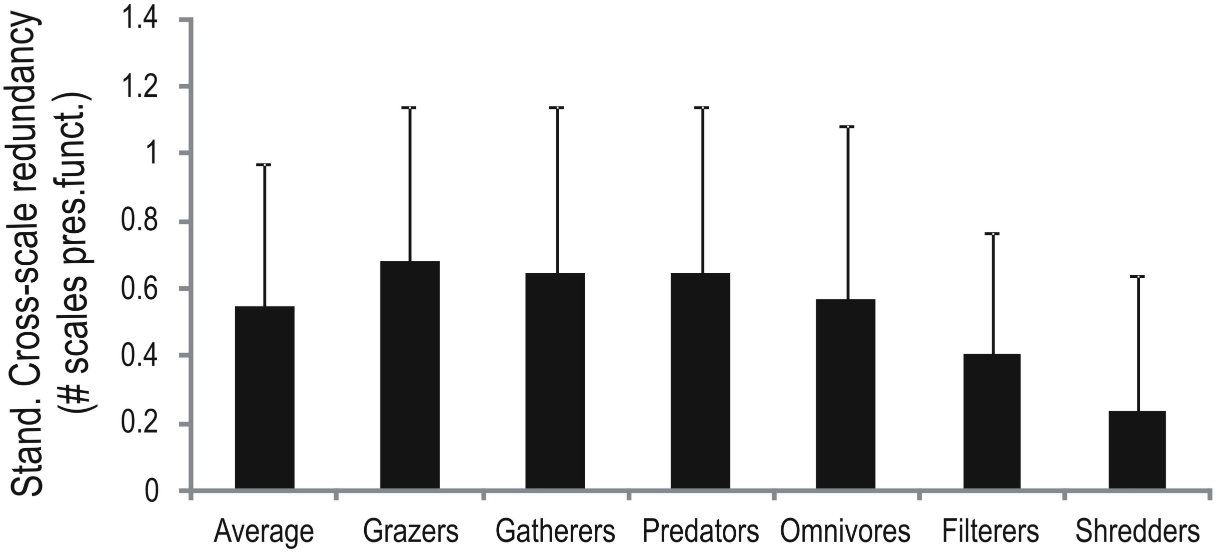

(a) Predators
Kendall´s tau: 0.50; P = 0.008
(b) Gatherers
Kendall´s tau: 0.56; P = 0.003
(c) Grazers
Kendall´s tau: 0.53; P = 0.005
(d) Generalists
Kendall´s tau: 0.41; P = 0.04
(e) Shredders
Kendall´s tau: 0.38; P = 0.05
(f) Filterers
Redundancy (# spp)
0
20
40
60
80
100
1996
1998
2000
2002
2004
2006
2008
2010
Years

Figure 6


Stand. Cross-scale redundancy
(# scales pres.funct.)
1.4
1.2
1
0.8
0.6
0.4
0.2
0
Average
Grazers
Gatherers
Predators
Omnivores
Filterers
Shredders