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Linking degradation status with ecosystem vulnerability to environmental change[1]

David G. Angeler[1], Didier L. Baho[1], Craig R. Allen[2], 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.

*author for correspondence:
david.angeler@slu.se
Tel: +46 (0) 18-673049
Fax: +46 (0) 18-673156

Running head: degradation, vulnerability and resilience

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Abstract

Environmental change can cause regime shifts in ecosystems, potentially threatening ecosystem services. It is unclear if the degradation status of ecosystems correlates with their vulnerability to environmental change, and thus the risk of future regime shifts. We assessed resilience in acidified (degraded) and circum-neutral (undegraded) lakes with long-term data (1988-2012), using time series modeling. We identified temporal frequencies in invertebrate assemblages, which identifies groups of species whose population dynamics vary at particular temporal scales. We also assessed species with stochastic dynamics, those whose population dynamics vary irregularly and unpredictably over time. We determined the distribution of functional feeding groups of invertebrates within and across the temporal scales identified, and in those species with stochastic dynamics, and assessed attributes hypothesized to contribute to resilience. Three patterns of temporal dynamics, consistent across study lakes, were identified in the invertebrates. The first pattern was one of monotonic change associated with changing abiotic lake conditions. The second and third patterns appeared unrelated to the environmental changes we monitored. Acidified and the circum-neutral lakes shared similar levels and patterns of functional richness, evenness, diversity, and redundancy for species within and across the observed temporal scales and for stochastic species groups. These similar resilience characteristics suggest that both lake types did not differ in vulnerability to the environmental changes observed here. Although both lake types appeared equally vulnerable in this study, our approach demonstrates how assessing systemic vulnerability by quantifying ecological resilience can help address uncertainty in predicting ecosystem responses to environmental change across ecosystems.

Key words: environmental change, benthic invertebrates, functional redundancy, scales, vulnerability, time series modeling, resilience, functional traits

Introduction

Human activity (e.g. overfishing, eutrophication, acidification, global warming) can cause catastrophic regime shifts of ecosystems (e.g. Hirota et al. 2011; Kosten et al. 2012). Increasing pressures from growing human populations will likely continue to push ecosystems beyond their capacity to cope with stress. Consequently, increasing incidences and magnitudes of regime shifts in the future will likely trigger complex social-ecological responses that can transcend scales from local to regional to global (Barnosky et al. 2012; Hughes et al. 2013).

Environmental degradation impacts biodiversity, contributes to the extinction of sensitive species and potentially jeopardizes the provisioning of ecosystem services (Hooper et al. 2005). The loss of species, combined with other alterations of structural and functional community attributes with increasing degradation, has been linked to a decrease in ecosystem resilience (Peterson et al. 1998; Folke et al. 2004; Fischer et al. 2006). If these community changes increase the vulnerability to environmental change stressors, manifested in decreasing resilience, it can be assumed that degraded ecosystems will become more prone to regime shifts than undegraded ecosystems. Therefore, it is necessary to quantify vulnerability at the ecosystem level to assess the likelihood of regime shifts, and to inform management actions that might serve to prevent regime shifts (Angeler et al. 2014). In this paper we test for ecosystem vulnerability by quantifying patterns of richness and function at discrete temporal scales in lakes that have been affected by differential degrees of anthropogenic acidification.

Acidification of surface waters was a severe environmental problem in Europe and North America during the 1970 - 1980s, causing biodiversity loss and altering ecosystem processes (Schindler 1988). International policy was enacted to reduce the emissions of nitrogen oxide and sulfur dioxide to protect and restore natural resources (Stoddard et al. 1999). However, despite reduced acid deposition contributing to chemical recovery of surface waters, empirical evidence of biological recovery (i.e., a return to ecological conditions prior to acidification) has been equivocal

(Skjelkvåle et al. 2003; Ormerod and Durance 2009). Thus, the failure to meet biological recovery goals means that acidification is still considered a critical problem affecting the biodiversity and ecosystem service provisioning of inland surface waters in northern Europe (Johnson and Angeler 2010) and elsewhere (Burns et al. 2008; Batterbee et al. 2014). Furthermore, the combined effects of alterations in land use, catchment hydrology, acid deposition rates, and climatic change trigger similar patterns of ecological change in lakes independent of their acidification status. These changes occur in the form of regionally decreasing water clarity and ion concentrations, the range expansion of nuisance species and changing biodiversity patterns across boreal lakes (Burgmer et al. 2007; Angeler and Johnson 2012; Angeler et al. 2012; Trigal et al. 2013). Lakes can undergo regime shifts triggered by acidification or eutrophication (Scheffer and Carpenter 2003; Baho et al. 2014). Because it is currently unclear whether the environmental changes observed will erode resilience to eventually cause a regime shift of boreal lakes it is necessary to assess vulnerability, and determine if vulnerability differs between lakes of different degradation status.

In this paper, we compare the vulnerability of acidified lakes with those of near-pristine, undegraded, circum-neutral lakes that comprise targeted management references for acidified lakes (Yan et al. 1996). We assess vulnerability from a systemic perspective in both acidified and circum-neutral lakes; that is, we quantify attributes that have been considered important for mediating the ecological resilience of ecosystems (sensu Holling 1973). Ecological resilience is the amount of disturbance an ecosystem can tolerate before shifting into an alternative state with a different set of processes and structures relative to those present in the state before the shift. Ecological resilience is a broad concept, focused on the dynamics of complex adaptive systems (e.g. ecosystems). The definition therefore integrates other concepts related to ecological stability, such as resistance (Walker et al. 2004), and differs from engineering resilience which focuses on the time needed to recover to predisturbed conditions (Pimm 1991).

Central to ecological resilience theory is that structures, functions and processes are regulated by a few variables that operate at characteristic temporal and spatial scales (Allen et al. 2014; Nash et al. 2014). To account for scale, the cross-scale resilience model was developed to empirically quantify ecological resilience (Peterson et al. 1998). In this model resilience is assessed through quantification of functional traits and their distribution within and across scales of space and time (Fischer et al. 2007; Sundstrom et al. 2012). Resilience is hypothesized to increase 1) with an increased redundancy and diversity of ecological function among species that operate at the same spatial or temporal scale (within-scale redundancy), 2) with a redundancy of function across these scales in a system (cross-scale redundancy) (Allen et al. 2005), and 3) with different responses to disturbance by species within the same functional group and scale (response diversity; Elmqvist et al. 2003). An assessment of within and cross-scale redundancy of function allows a quantitative measure of relative resilience (Peterson et al. 1998).

Tools have been developed that allow quantification and comparison of dominant scales of processes and structures that are present in a system (Stow et al. 2007; Nash et al. 2014). Here we use multivariate time series modeling to identify different temporal frequency patterns in the abundance of littoral invertebrate communities. This tool has been recently used in several studies of resilience (e.g. Angeler et al. 2011; Angeler et al. 2013ab; Baho et al. 2014). Specifically, we test for the presence of temporal patterns in the abundance of littoral invertebrate species and the prevailing frequencies of these patterns. Discrete frequencies are used to infer dominant temporal scales in the community dynamics. Next, we focus on the invertebrate taxa associated with the temporal scales identified and evaluate their functional attributes. Invertebrate taxa have a variety of feeding modes (predators, shredders, grazers, gatherer-collectors, filterers) and are therefore important for different ecosystem functions, including nutrient cycling and matter fluxes, leaf litter processing, and secondary production (e.g. Covich et al. 1999).

In addition to quantifying temporal patterns, time series modeling allows for the detection of species with stochastic dynamics; that is, those species (that are often uncommon) whose population dynamics vary irregularly and unpredictably over time. Although stochastic species do not contribute to within and cross-scale patterns in a system, they comprise an important component for resilience (Baho et al. 2014). For instance, when environmental conditions change, stochastic species may become abundant, potentially substituting for species that went extinct, and therefore contribute to the maintenance of ecosystem processes and stability (Walker et al. 1999; Carpenter et al. 2001). The ability to maintain processes while ecosystems undergo change can be defined as adaptive capacity (Carpenter et al. 2001). Thus, both the distribution of functions within and across scales identified and the adaptive capacity that rests in the stochastic group of species are critical for the maintenance of resilient ecosystems.

Assessing the vulnerability of ecosystems based on resilience concepts has clear relevance both for management and conservation, as well as for refining ecological theory. If species that are sensitive to stress such as acidification are lost from the system, reduced biodiversity may result in lower within and cross-scale redundancy under degraded ecosystem conditions, relative to higher diversity states of near-pristine ecosystems. Stress could be further manifested in lower functional richness, diversity and redundancy in groups of species with stochastic dynamics, thereby reducing adaptive capacity to respond to further environmental stress. Lower diversity of functional attributes and lower abundance of species with certain functional attributes, could increase vulnerability to regime shifts. Here we test this conjecture using acidified lakes as models of degraded ecosystems. We identify temporal scales in invertebrate communities with time series modeling, and compare the patterns of functional attributes in invertebrate species within and across the identified scales. We compare the patterns identified in acidified lakes with those in circum-neutral reference lakes to assess if the acidified lakes appear more vulnerable to environmental change.

Material and Methods

Study area

Sweden began a long-term lake monitoring program in multiple habitats and across trophic levels to follow the effects of anthropogenic acidification of regionally representative lakes in relation to lakes with a higher acid neutralizing capacity (Johnson 1999). Twelve lakes with monitoring data for water quality and littoral invertebrate communities were chosen for this study, and provided data for the period 1988 to 2012. Six lakes were culturally acidified and six lakes were circum-neutral, based on biogeochemical modeling criteria (Fölster et al. 2007). Biogeochemical modeling estimates the changes in buffering capacity between preindustrial periods and the present, and calculates changes in pH between these periods. A lake is considered acidified if 0.4 pH units between periods are exceeded. Information regarding the monitoring program can be found in Fölster et al. (2014) and at: http://www.slu.se/en/faculties/nl/about-the140faculty/departments/department-of-aquatic-sciences-and-assessment/data-host/. Selected environmental variables and the geographical coordinates of these lakes are provided in Electronic Supplementary Material.

Sampling

Sampling and analyses of abiotic and biological variables was based on standard protocols throughout the study. These protocols are quality controlled and certified by the Swedish Board for Accreditation and Conformity Assessment (SWEDAC; http://www.swedac.se/en/). Surface samples for physicochemical analyses (taken at 0.5 m depth) were collected with a Plexiglas sampler four to eight times each year at a mid-lake station in each lake and kept cool during transport to the laboratory. Samples were analyzed for acidity (pH, alkalinity, SO_4^{2-} concentration), nutrients (total P, phosphate, total N, Ca), water clarity (Secchi disc depth, water color, total organic carbon), and ionic strength (electrical conductivity). The analyses were conducted at the Department of Aquatic Sciences and Assessment complying with international (ISO) or European (EN) standards (Fölster et al. 2014). Measurement intervals and uncertainties for each variable can be found at: http://www.slu.se/en/faculties/nl/about-the-faculty/departments/department-of-aquaticsciences-and-assessment/laboratories/geochemical-laboratory/water-chemical-analyses/.

Invertebrate sampling adhered to Swedish standards (SS-EN 27828). Briefly, five replicate samples were taken using standardized kick sampling with a hand net (0.5 mm mesh size) from one wind-exposed, vegetation-free littoral habitat in late autumn (end of October to early November each year) in each lake. Sampling consisted of disturbing the substratum along a 1 m long stretch for 20 seconds in the littoral region at a depth of c. 0.5 m. Samples were immediately preserved in 70% ethanol and later processed in the laboratory by sorting against a white background with 10x magnification. Invertebrates were sorted, identified to the lowest feasible taxonomic unit and counted using light and dissecting microscopes. The same person, a trained taxonomist, has evaluated all samples throughout our study.

Statistical analyses

Time series modeling – Time series of multispecies assemblages can show a wide range of temporal patterns in species occurrence and abundance, including monotonic, stochastic and cyclic patterns, the latter occurring at distinct frequencies. Here we use a method that objectively identifies temporal patterns that are inherent in time series of ecological communities. Because it is able to identify fluctuation frequencies at different temporal scales (e.g. decadal, annual, seasonal), the method has been useful for assessing resilience (Angeler et al. 2014; Baho et al. 2014). The method is based on redundancy analysis (RDA) (Angeler et al. 2009), and uses temporal variables extracted by AEM analysis (Asymmetric Eigenvector Maps, Blanchet et al. 2008). Details of all steps in the analyses are in Electronic Supplementary Material. The approach can be summarized as follows:

1) The AEM analysis creates the temporal variables necessary for extracting distinct temporal patterns from the data set. This is accomplished by converting the linear time vector that comprises

the sampling frequency and length of the study period into a set of orthogonal temporal variables. In our study, these variables correspond to a specific temporal structure and scale in the invertebrate community. That is, the first AEM variable models linear trends and the subsequent variables capture temporal variability from slow to increasingly shorter fluctuation frequencies in the community data over the study period. The scales of pattern and structure that can be discerned have upper bounds set by the limit of the temporal extent of the data series, and lower bounds set by the frequency of sample collection. Accordingly, in our study the shortest fluctuation frequency captures yearly variation because invertebrates have been sampled once per year and the temporal extent consisted of 25 equidistant time steps (in years) between 1988-2012. The AEM analysis thus yielded 8 variables with positive eigenvalues from the conversion of the linear time vector.

2) For each lake, we constructed a parsimonious RDA model for invertebrate community dynamics by running a forward selection on these 8 AEM variables. Because AEM analysis is efficient in covering linear trends no detrending of models was necessary. The RDA retains significant AEM variables and these are linearly combined to extract temporal patterns from the Hellinger-transformed species matrices; that is, the RDA identifies species with similar temporal patterns in the species x time matrix and uses their temporal patterns to calculate a modeled species group trend for these species based on linearly combined AEMs. The significance of the temporal patterns of all modeled species groups revealed by the RDA is tested by means of permutation tests. The RDA relates each modeled temporal fluctuation pattern with a significant canonical axis. The R software generates linear combination (lc) score plots, which visually present the modeled fit of temporal patterns of species groups that are associated with each canonical axis.

3) The modeling results provide insight into resilience. Canonical axes are orthogonal (independent from each other) and thus can be used to assess the number of temporal patterns/scales representing

community dynamics. In the context of resilience cross-scale community dynamics were quantified by counting the number of significant canonical axes in the RDA models, while within-scale of resilience was determined by quantifying species correlations with the temporal pattern of each significant canonical axis in the model (see below).

All relevant steps in the analyses were carried out with two functions implemented in R 2.15.1 statistical software package (R Development Core Team 2012). First, the conversion of the linear time vector to AEM variables was done using the “aem.time” function (AEM package). This function accounts for the connectivity of linear time steps. Thus, a connectivity matrix required in spatial analysis with hierarchical or dendritic designs is not necessary in time series analysis. The remaining modeling steps (calculation of modeled species group trends, visual presentation of the results in form of lc score plots) were carried out with the “quickPCNM” function (PCNM package).

Abiotic and biotic correlates of modeled temporal patterns — We aimed to identify the environmental correlates of the temporal pattern of invertebrates found for each significant canonical axis of the RDA models. We used Spearman rank correlation analyses to correlate modeled lc scores with yearly-averaged water quality data. We also used Spearman rank correlation analyses to relate the raw abundance data of individual invertebrate taxa with the modeled lc scores from the RDA models. This helped evaluate the within-scale aspect of resilience. We also evaluated the number of species with presumably stochastic dynamics (that is, species that were not associated with any significant canonical axis). We subtracted the sum of species that correlated with canonical axes from the total number of species present in each lake (Baho et al. 2014).

In our resilience assessment, we used taxa that were identified to species and morphotypes that could be classified into functional feeding groups for further analysis. Taxa with only higher taxonomic level resolution (family and above) were not included to avoid influencing the analyses through ambiguous feeding group assignments. Taxa that correlated with modeled temporal patterns and stochastic dynamics were classified into filterers, gatherers, grazers, omnivores, shredders and predators, based on scores between 1 and 10, with 10 indicating highest feeding preference. The online data base www.freshwaterecology.info (Schmidt-Kloiber and Hering 2012) was used for scoring feeding group traits. Omnivores were comprised of taxa that scored identically among different feeding groups, here mostly gatherers and grazers. We also assessed acid-sensitivity of species following Angeler and Johnson (2012) and the Red List status of the identified taxa for Sweden using the same online database.

Functional community attributes and resilience assessment – We calculated two measures that have been used to infer resilience following the cross-scale resilience model: 1) Within-scale redundancy (the average number of species within each functional group at each temporal pattern; Allen et al. 2005), and 2) Cross-scale redundancy (the average number of temporal frequency scales at which each function is represented; Allen et al. 2005). To allow for a broader characterization of resilience we calculated additional measures: 3) Functional richness (the number of feeding groups present). 4) Functional diversity based on the exponentiated Shannon-Wiener index (exp H’) that accounts for both the presence of feeding groups and the number of species that belong to a feeding group. Exponentiation of H’ makes richness and diversity data directly comparable (Jost 2007; Tuomisto 2010). 5) Functional evenness calculated as the quotient between functional diversity and functional richness. This calculation makes evenness independent from richness (Tuomisto 2012). In addition to these functional measures, we calculated two structural community metrics (total taxon richness and the richness of acid-sensitive taxa). All measures were calculated for each temporal frequency scale (significant canonical axes in RDA models) and the stochastic pattern of each lake. Note that these measures are calculated from the modeling results (species and their functional feeding guild attributes associated with canonical axes and the stochastic group of species). This enabled the characterization of structural and functional characteristics for the distinct temporal patterns identified, although the approach does not identify temporal trends in these measures per se.

Statistical comparisons— Kendall´s tau rank correlations, a nonparametric test of concordance, was used to explore patterns of monotonic change of water chemistry variables over the study period. We used two-way ANOVAs to test for significant differences in the distribution of metrics (taxon richness, richness of acid-sensitive taxa, functional richness, functional diversity, functional evenness, average within-scale redundancy) between acidified and circum-neutral lakes. These metrics comprised the dependent variables and lake type (circum-neutral, acidified; fixed factor) and temporal pattern (temporal frequencies associated with RDA 1 - RDA 3 and stochastic patterns; fixed factor) comprised the independent variables. Note that no comparisons were made for a fourth pattern (RDA 4) because such a pattern was found only in a few lakes. In a second ANOVA, we also examined whether within-scale redundancy at each temporal scale and the cross-scale redundancy between these scales varies as a function of lake type and functional feeding group. In this analysis within-scale redundancy associated with all temporal patterns and the cross-scale redundancy comprised the dependent variables and functional feeding groups the independent variables. When a significant main effect was detected, a posteriori comparisons were made using the Tukey HSD test.

Univariate comparisons were complemented with multivariate analyses using non-metric multidimensional scaling (NMDS) in Primer 6 (Primer-E Ltd, Plymouth, UK) of Bray-Curtis transformed similarity matrices on square-root transformed data (999 re-runs). NMDS was followed by permutational multivariate ANOVA (PERMANOVA) to contrast multivariate invertebrate functional attributes between lake types (circum-neutral vs acidified lakes, fixed factor) and temporal patterns (RDA 1 vs RDA 2 vs RDA 3 vs stochastic, fixed factor). PERMANOVAs were calculated on Bray-Curtis and Sorensen similarity matrices of square-root transformed species data (9999 unrestricted permutations of raw data) using PERMANOVA v1.6 (Anderson 2005).

For both univariate and multivariate comparisons, we consider interaction terms crucial for inference. If the interactions are significant, we conclude that the relative resilience of one lake type, based on the structure and distribution of functions within and across temporal patterns, differs significantly from the other lake type. In turn, this indicates that one lake type is potentially more vulnerable to environmental change relative to the other lake type.

Results

Temporal patterns and trends of environmental variables

The patterns of temporal change in water quality variables were generally congruent between circum-neutral and acidified lakes (Fig. 1). pH increased significantly over time in both lake types (acidified lakes: Kendall's tau = 0.61, $P < 0.001$; circum-neutral: Kendall's tau = 0.47, $P = 0.001$), but remained < 6 in acidified lakes throughout the study, indicating that chemical recovery was weak (Fig. 1A). Alkalinity increased in circum-neutral (Kendall's tau = 0.65, $P < 0.001$) but not in acidified lakes ($P >0.05$) (Fig. 1B). Sulfate concentrations decreased monotonically in both lake types (acidified lakes: Kendall's tau = -0.82, $P < 0.001$; circum-neutral: Kendall's tau = -0.97, $P < 0.001$) (Fig. 1C). Concomitant with changes in acidity, we observed a gradual change in water clarity over the study period, manifested as a significant decrease in Secchi transparency (acidified and circum-neutral: Kendall's tau = -0.81, $P < 0.001$), and increase in water color (acidified: Kendall's tau = 0.70, $P < 0.001$; circum-neutral: Kendall's tau = 0.67, $P < 0.001$) and total organic carbon (acidified: Kendall's tau = 0.67, $P < 0.001$; circum-neutral: Kendall's tau = 0.59, $P < 0.001$) in both lake types (Fig. 1D-F). Water temperature and nutrients (TP, PO_4, TN) fluctuated around a long-term mean ($P > 0.05$; Fig. 1G, J-L), while electrical conductivity (acidified: Kendall's tau = -0.66, $P < 0.001$; circum-neutral: Kendall's tau = -0.74, $P < 0.001$) and Ca concentrations (acidified: Kendall's tau = -0.73, $P < 0.001$; circum-neutral: Kendall's tau = -0.83, $P < 0.001$) decreased significantly through time in both lake types (Fig. 1H, I).

Temporal frequency patterns of invertebrates

Analyzing invertebrate communities with the RDA-AEM approach revealed significant temporal patterns in all of the twelve lakes between 1988 and 2012. Significant temporal patterns were associated with three canonical axes in the RDA models for most lakes, indicating that species groups of invertebrates reflect three distinct temporal frequencies or scales (Fig. 2). In a few lakes (Humsjön, Harasjön, Storasjö), a fourth temporal pattern was identified (Fig. 2D, I, L). The first frequency pattern explained between 17% and 30% of the adjusted variance across all lakes in the constrained models; the second, third and fourth patterns explained between 8% and 16%, 5% and 10%, and 4% and 6% of the adjusted variance in all invertebrate communities across lakes, respectively.

The first temporal frequency of invertebrate species groups generally showed components of monotonic change combined with sine-wave properties in both lake types (blue lines in Fig. 2A-L). These patterns cover temporal dynamics that were associated mainly with slow changes in acidity and water clarity over the 25-year study period (Electronic Supplementary Material). We therefore refer to this first temporal frequency group of invertebrates as “slow groups” that track these slower changes in the environment. The second and third frequency of species groups showed shorter-term periodicity at roughly 10-year and 5-year intervals (red and green lines in Fig. 2A-L), and although these groups did not show any consistent correlations with the studied environmental variables (Electronic Supplementary Material), they presumably track faster ecological processes. These groups are therefore referred to as “intermediate groups” and “faster groups”. When a fourth frequency patterns was detected, it showed species fluctuations at temporal scales that were intermediate to those resolved by the first three patterns. Because only a few lakes showed this pattern, limiting comparison, we did not use these for the ANOVA analyses of metrics, although these patterns were considered for calculating average within and cross-scale redundancy.

Taxonomic and functional structure of species groups

From the 353 invertebrate taxa present in our data set 65 were classified as acid-sensitive and none was red-listed for Sweden. The distribution of both sensitive and tolerant species among the slow, intermediate, and faster groups was highly variable between lakes (see Angeler and Johnson 2012). However, a common pattern for both lake types was that taxon richness decreased from the slow group towards the intermediate and faster group, whilst the group of stochastic species had highest richness in both lake types (Fig. 3A). A similar pattern was found for acid-sensitive taxa, although circum-neutral lakes had a higher richness of these taxa across the different temporal patterns identified relative to the acidified lakes (Fig. 3B). Despite these structural differences between acidified and circum-neutral lakes, functional richness, functional diversity and functional evenness showed similar ranges across species groups and lake types (Fig. 3C-E).

Coincident with patterns of taxon richness, average functional redundancy was also highest in the stochastic species group, followed by the slow frequency group in acidified and circum-neutral lakes (Fig. 3F). Both circum-neutral and acidified lakes showed similar variability in cross-scale redundancy (Fig. 3G). The importance of stochastic species was also reflected in ANOVA analyses. Higher values for many metrics were found for stochastic species relative to the slow, intermediate and fast groups of species (Tukey HSD test: $P < 0.05$) leading to a highly significant "temporal pattern" term in the model (Table 1). A significant "lake type" effect was found for richness of acid sensitive taxa and average functional redundancy; overall species richness was marginally ($p = 0.07$) higher in circum-neutral lakes (Table 1). However, none of the interaction terms between lake type and temporal patterns was significant, highlighting that the distributions of functions necessary for understanding the relative resilience of ecosystems was similar between the acidified and circum-neutral lakes.

Predators and gatherers were the dominant feeding types, with the highest level of functional redundancy in the slow, intermediate, fast and stochastic species groups in both lake types, relative to the other feeding groups (Fig. 4). The average redundancy for predators and gatherers was higher than for other feeding groups in all frequency fluctuation groups identified (Tukey HSD test: Predators = Gatherers > Grazers = Shredders = Filterers = Omnivores) (Table 1). Circum-neutral lakes had a significantly higher within-scale redundancy in the slow and stochastic species group relative to acidified lakes (Table 1); however, interactions between lake type and functional feeding group were non-significant for within-scale redundancy, highlighting similarities between both lake types (Table 1). Also, the patterns of cross-scale redundancy for each functional feeding group were similar for both lake types (Fig. 4), resulting in non-significant effects in the ANOVAs (Table 1).

The complementary multivariate analyses are in agreement with the patterns found for univariate metrics. Stochastic groups of acidified and circum-neutral lakes with highest richness and functional redundancy clustered towards the right side in multivariate (NMDS) ordination space. The slow species groups in both lake types clustered close to the stochastic species, while the intermediate and faster groups moved towards the left in ordination space, reflecting decreasing species richness and functional redundancy (Fig. 5). Similar to the univariate ANOVA, PERMANOVA based on Bray-Curtis similarities (emphasizing both taxa presences-absences and their abundances) and Sorensen similarity (focusing only on presence-absences) revealed a significant “pattern effect”. This highlights the difference of the stochastic species group from the slow, intermediate and fast frequency fluctuation groups. However, the non-significant interaction term in both models highlights similar distribution of functions between lake types and temporal patterns (Table 2).

Discussion

We tested the proposition that acidified lakes are more vulnerable to environmental change, raising concerns about potential regime shifts in the future, relative to circum-neutral lakes. The low pH values throughout our study (< 6) and the lower number of acid-sensitive taxa in acidified lakes suggest weak chemical and biological recovery. Thus, the acidified lakes studied here remain degraded, despite the implementation of acidification mitigation policy decades ago. Poor habitat quality (Kowalik et al. 2007), combined with altered local (biological structure and food webs; e.g. Ledger and Hildrew 2005) and regional factors (limited dispersal and population connectivity; Gray and Arnott 2011) have been considered major factors maintaining acidified systems in degraded conditions.

Although signs of recovery of acidified lakes were weak, we observed broader environmental change responses that were manifest in similar temporal patterns of environmental variables in both lake types. Consistent with observations made in streams, lakes and ponds across Europe (Evans et al. 2005; Van Kleef et al. 2010), acidified and circum-neutral lakes have experienced a gradual change in water clarity (decreased Secchi disk transparency, increasing TOC concentrations and water colour), which has been attributed to decreasing acid deposition, global warming and land-use change (Evans et al. 2005; Monteith et al. 2007). Concomitant with changes in the abiotic environment, other studies have reported biotic changes, including the range expansions of invasive, nuisance species (Angeler et al. 2012; Trigal et al. 2013) or altered local and regional community structure in lakes (Burgmer et al. 2007). Collectively, these changes show that boreal lakes are affected by environmental change that goes beyond the acidification problem, and similar changes have been observed elsewhere (e.g. Batterbee et al. 2014).

It is uncertain whether the complex ecological changes that affect acidified and circum-neutral lakes similarly will eventually increase the risk of regime shifts in the future. One way to cope with this uncertainty is to assess the vulnerability of lakes to further environmental change by quantifying the attributes of ecological resilience. Many studies have assessed community structure and composition in lakes recovering from acidification (e.g. Hogsden and Vinebrooke 2005, Wesolek et al. 2010). Our study, based on a quantitative assessment of resilience, is the first attempt to test whether acidified lakes in a degraded state are potentially more vulnerable to environmental change than circum-neutral lakes in desirable states.

We expected that acidified lakes would exhibit higher vulnerability to environmental change than circum-neutral lakes. We assessed resilience following the cross-scale resilience model (Peterson et al. 1998) and quantified within-scale and cross-scale redundancy. We also quantified additional functional measures (functional richness, functional diversity, functional evenness) for the temporal patterns identified by the time series modeling to allow for a broader characterization of resilience (Angeler et al. 2013a). If acidified lakes are less resilient and thus more vulnerable to environmental change, these measures should be reflected in lower values in acidified relative to circum-neutral lakes. However, comparing the distributions of functional metrics within and across temporal scales and within species groups showing stochastic dynamics, both critical components for quantifying the relative resilience in ecosystems (Peterson et al. 1998; Allen et al. 2005; Baho et al. 2014), failed to discern a relationship between lake type (i.e. acidified *vs* circum-neutral lakes) and temporal pattern in either the univariate or multivariate analyses. Overall, this suggests that invertebrates in acidified and circum-neutral lakes have similar functional attributes that characterize their relative resilience through time. This finding was unexpected because invertebrate communities in the acidified and circum-neutral systems differ both in terms of community composition and trophic associations in their food webs (Ledger and Hildrew 2005; Angeler and Goedkoop 2010; Baho et al. 2014). Our results suggest that despite inherent abiotic and biotic differences between acidified and circum-neutral lakes, the functional attributes in all species groups associated with different temporal patterns were similar. This suggests that resilience in both lakes types is similar, and in turn that acidified and circum-neutral lakes are similarly vulnerable to the environmental change observed in this study. Similar patterns have been found comparing subarctic lakes with a presumed high vulnerability to climate change and hemiboreal lakes at more southern latitudes (Angeler et al. 2013a), and degraded avian communities on continental prairies (Sundstrom et al. 2012). Further studies that quantify attributes of resilience are warranted to test for the generalities of patterns observed in this study and the subarctic lakes and prairies studies.

It is often assumed that impacts of environmental change on biodiversity lead to a decreased resilience in ecosystems (Peterson et al. 1998; Folke et al. 2004; Fischer et al. 2006). Our results suggest that such an assumption is too simplistic, and that accounting for scale-specific drivers of environmental change divers and compensational processes may explain the underlying mechanisms. The impacts of environmental change are scale-specific (Nash et al. 2014). We found variables related to environmental change (acidity, water color) correlating only with specific species groups revealed by the time series modeling. The temporal patterns of other species groups were largely uncorrelated with these variables, and likely associated with other unmeasured abiotic and biotic variables, including dispersal. This resistance at specific scales may help to buffer impacts of environmental change at other scales and confer resilience to ecosystems (Angeler et al. 2013a).

We found that richness of acid-sensitive taxa was lower in the acidified lakes relative to the circum-neutral lakes in this study. Overall taxon richness was only marginally higher in circum-neutral lakes (Table 1). This suggests that other species, tolerant to acidification stress have likely substituted acid-sensitive taxa (Layer et al. 2010). More importantly, these tolerant species seemed to have compensated for the loss of functional attributes of these sensitive taxa. This in turn can explain the similar resilience characteristics observed in acidified and circum-neutral lakes. This finding supports the notion that both degraded and undegraded states of ecosystems can be equally resilient (Standish et al. 2014). Similar functional compensation processes have been observed in some studies (Klug et al. 2000; Fischer et al. 2001). However, other studies have reported week compensatory processes (Huijbers et al. 2015) or that these processes vary depending on context (Yang et al. 2014). This context dependency adds uncertainty to environmental change outcomes, further underscoring the need for more systemic approaches to assess vulnerability to environmental change. Although our study showed similar patterns of vulnerability of acidified and circum-neutral lakes to the environmental change observed in this study, further research comparing different ecosystem types along a range of stress gradients is required to further understand the role of compensatory dynamics in environmental change outcomes.

Despite both lake types sharing similar resilience characteristics, we found scale-inherent patterns and different contributions of functional feeding groups that must be considered for understanding the overall resilience of the studied lakes. Johnson et al. (2004) found that filterers had the lowest and predators and gatherers the highest representation in the invertebrate communities. Consistent with these findings, filterers, shredders, grazers and omnivores had the lowest, and gatherers and predators the highest within-scale redundancy in this study. Similar patterns were found for cross-scale redundancy, and the stochastic group of species considered important for mediating the adaptive capacity of these functional feeding groups. The loss of functional group representation at one or more scales, and reduced adaptive capacity resulting from species with stochastic dynamics, would have a larger 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 recognize 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 the loss of one or a few species from these functional groups would have relatively minor impact on resilience.

We acknowledge that we have characterized resilience based on functional feeding group attributes, which are relatively coarse measures of functional traits. Our analysis is restricted to autumn samples of invertebrates. It is possible that increasing the temporal resolution to also cover seasonal dynamics would have refined our results. Our classification of functional traits is also limited by our current limited knowledge of the ecology and natural history of most species. Resilience assessments might be refined by considering multiple traits within individual species that characterize response diversity (Elmqvist et al. 2003) or through a direct measurement of process rates. We were unable to consider response diversity or processes in our study because of currently insufficient trait information and because our monitoring program does not quantify process rates. Also, a comparison of resilience attributes across multiple taxonomic groups would allow for a more accurate definition of the broader vulnerability of lakes to environmental change. Despite these limitations, our study shows how long-term monitoring efforts, combined with an ecological complexity approach that is often neglected in assessing environmental change problems, can facilitate an evaluation of systemic vulnerability to changing environmental conditions. Measuring ecological resilience attributes, and comparing these attributes across system types with presumed different vulnerabilities has potential to identify ecosystems at risk of undergoing catastrophic regime shifts. This can contribute to reduce uncertainty in the assessment of the potential sensitivity of ecosystems to environmental change, and facilitate the planning of management and conservation action in the long term.

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Electronic Supplementary Material

1. Flow chart outlining steps to time series modeling.
2. Table of water quality characteristics and geographical coordinates of acidified and circum-neutral lakes.
3. Results from Spearman rank correlation analyses.

Table 1: Results from ANOVA analyses contrasting effects of lake type (circum-neutral vs acidified lakes) and temporal pattern (“slow” *vs* “intermediate” *vs* “faster” *vs* “stochastic” species group) (a) and lake type and feeding groups (predators, shredders, gatherers, grazers, filterers, omnivores) (b), and their interactions, on measures used to assess the relative resilience of lakes. Shown are degrees of freedom (df), mean squares, sources of variation (F ratios), significance levels and error terms. Significant effects are highlighted in bold.

a)	Lake type (LT) df (1, 40)			Pattern (P) df (3, 40)			L x P df (3, 40)			Error
	MS	F	P	MS	F	P	MS	F	P	
Taxon richness	0.14	3.35	0.07	**2.71**	**67.03**	**<0.001**	0.01	0.12	0.95	0.04
Richness acid-sensitive taxa	**1.11**	**17.52**	**<0.001**	**1.60**	**25.32**	**<0.001**	0.02	0.32	0.81	0.06
Functional richness	0.01	1.12	0.30	**0.04**	**3.44**	**0.03**	0.01	0.94	0.43	0.01
Functional diversity	0.02	1.92	0.17	**0.02**	**3.08**	**0.03**	<0.001	0.02	0.89	0.01
Functional evenness	<0.001	0.76	0.38	**1.65**	**104.79**	**<0.001**	**0.001**	**3.19**	**0.034**	<0.001
Average within-scale redundancy	**0.09**	**5.53**	**0.02**	**0.22**	**8.95**	**<0.001**	0.01	0.56	0.64	0.02

b)	Lake type (LT) (df 1, 60)			Feeding group (F) (df 5, 60)			LT x F (df 5, 60)			Error
	MS	F	P	MS	F	P	MS	F	P	
Within-scale redundancy (Temporal scale 1)	**0.45**	**10.68**	**0.002**	**1.22**	**28.85**	**<0.001**	0.03	0.66	0.66	0.042
Within-scale redundancy (Temporal scale 2)	<0.001	0.001	0.978	**0.51**	**10.58**	**<0.001**	0.10	1.97	0.10	0.048
Within-scale redundancy (Temporal scale 3)	0.02	0.59	0.336	**0.44**	**11.32**	**<0.001**	0.03	0.83	0.53	0.039
Within-scale redundancy (Stochastic)	**0.67**	**18.86**	**<0.001**	**1.95**	**55.01**	**<0.001**	0.07	1.85	0.12	0.036
Cross-scale redundancy	0.03	1.49	0.23	**0.17**	**9.57**	**<0.001**	0.01	0.50	0.78	0.018

Table 2: Results of PERMANOVA analysis contrasting multivariate community structure based on Bray-Curtis and Sørensen similarity between lake type (circum-neutral *vs* acidified lakes), temporal pattern ("slow" *vs* "intermediate" *vs* "fast" *vs* "stochastic" species groups) and their interactions. Shown are degrees of freedom (df), sums of squares (SS), mean squares (MS), F-ratios (F), and the Monte Carlo asymptotic P values (P(MC)). Significant effects are highlighted in bold.

Source	df	SS	MS	F	P (MC)
Bray-Curtis					
Lake type	1	838.59	838.59	1.50	0.202
Pattern	**3**	**25028.33**	**8342.78**	**14.92**	**<0.001**
Lake type x pattern	3	2137.51	712.50	1.27	0.261
Residual	40	22370.63	559.27		
Total	47	50375.06			
Sørensen					
Lake type	1	523.48	523.48	1.35	0.294
Pattern	**3**	**4398.76**	**1466.25**	**3.78**	**0.004**
Lake type x pattern	3	1528.99	509.66	1.31	0.286
Residual	40	15532.28	388.31		
Total	47	21983.51			

Figure legends

Fig. 1 Temporal patterns of environmental variables in circum-neutral (N=6) and acidified (N=6) lakes. Shown are the means ± standard deviations of circum-neutral (black lines) and acidified (grey lines) lakes. The trend lines indicate significant monotonic change over time revealed by Kendall tau correlation analyses

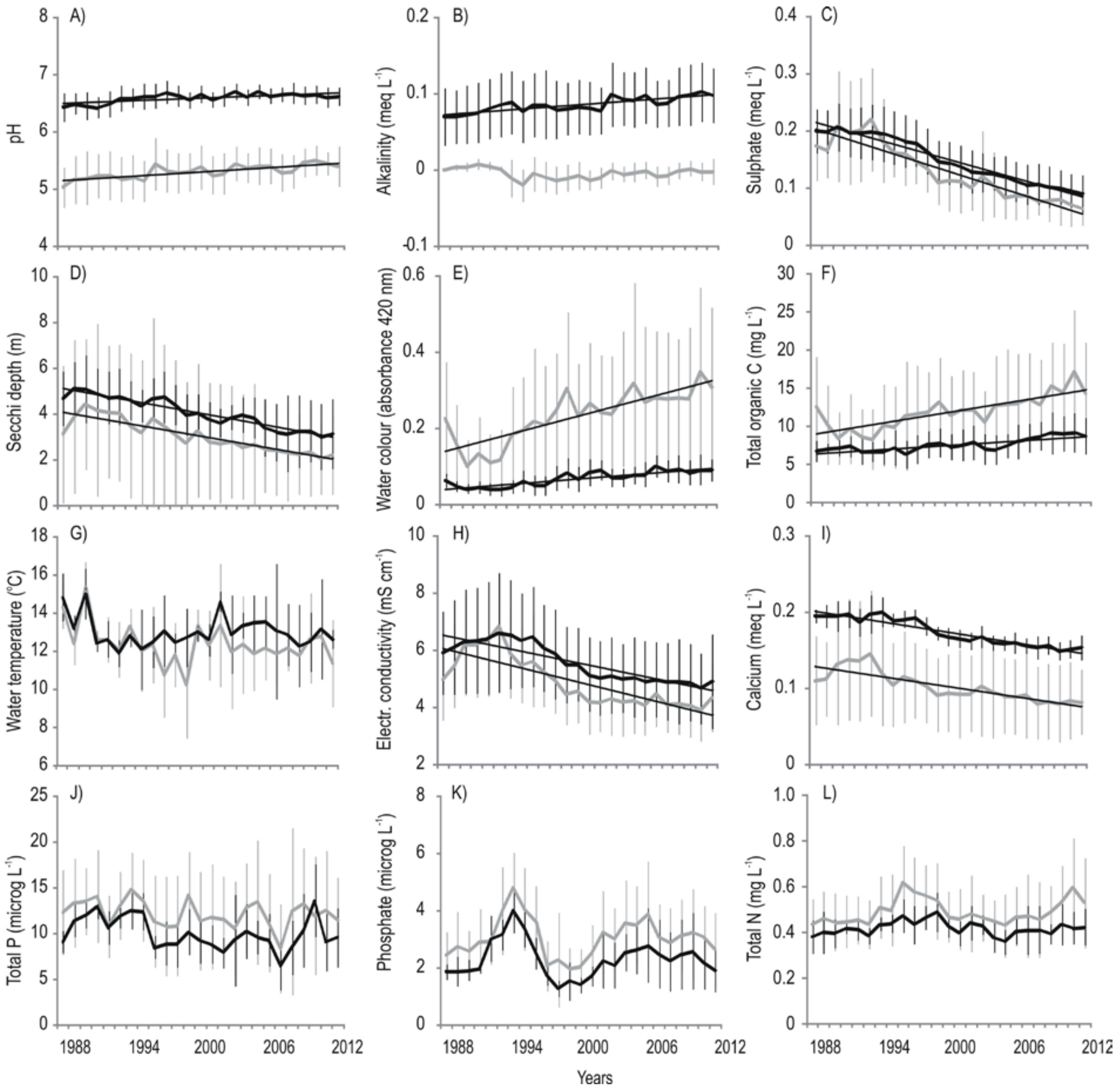
Fig. 2 Temporal patterns of species groups associated with canonical axes obtained from multivariate time series modeling of invertebrate communities in circum-neutral (2A-F) and acidified (2G-L) lakes. Shown are linear combination scores of significant AEM variables (see methods for details)

Fig. 3 Comparison of structural (total taxon richness, 3A; richness acid-sensitive taxa, 3B), functional (3C-E) community metrics, and average within-scale redundancy (3F) associated with the temporal patterns identified by time series modeling for acidified (grey bars) and circum-neutral (black bars) lakes. Shown is also the average cross-scale redundancy for acidified and circum-neutral lakes (3G). Shown are means ± standard deviations of acidified (N=6) and circum-neutral (N=6) lakes

Fig. 4 Patterns of within-scale redundancy associated with temporal patterns identified by time series modeling for predators (4A), gatherers (4B), grazers (4C), omnivores (4D), shredders (4E) and filterers (4F) for acidified (grey bars) and circum-neutral lakes (black bars). Shown are also the cross-scale redundancies for each feeding group in both lake types (4G-L)

Fig. 5 Nonmetric multidimensional scaling ordination (Bray-Curtis based) showing similarities of functional attributes across species groups with slow (squares), intermediate (circles), faster (diamonds) species groups in acidified (white symbols) and circum-neutral (black symbols) lakes. For lakes Humsjön and Harasjön functional attributes associated with a fourth temporal pattern (triangles) are shown. Also shown are, similarities of functional characteristics of groups of species with stochastic dynamics (grey symbols)

Fig. 1



A)
pH
8
7
6
5
4
B)
Alkalinity (meq L⁻¹)
0.2
0.1
0
-0.1
C)
Sulphate (meq L⁻¹)
0.4
0.3
0.2
0.1
0
D)
Secchi depth (m)
10
8
6
4
2
0
E)
Water colour (absorbance 420 nm)
0.6
0.4
0.2
0
F)
Total organic C (mg L⁻¹)
30
25
20
15
10
5
0
G)
Water temperature (°C)
18
16
14
12
10
8
6
H)
Electr. conductivity (mS cm⁻¹)
10
8
6
4
2
I)
Calcium (meq L⁻¹)
0.3
0.2
0.1
0
J)
Total P (microg L⁻¹)
25
20
15
10
5
0
K)
Phosphate (microg L⁻¹)
8
6
4
2
0
L)
Total N (mg L⁻¹)
1.0
0.8
0.6
0.4
0.2
0
1988
1994
2000
2006
2012
Years

Fig. 2

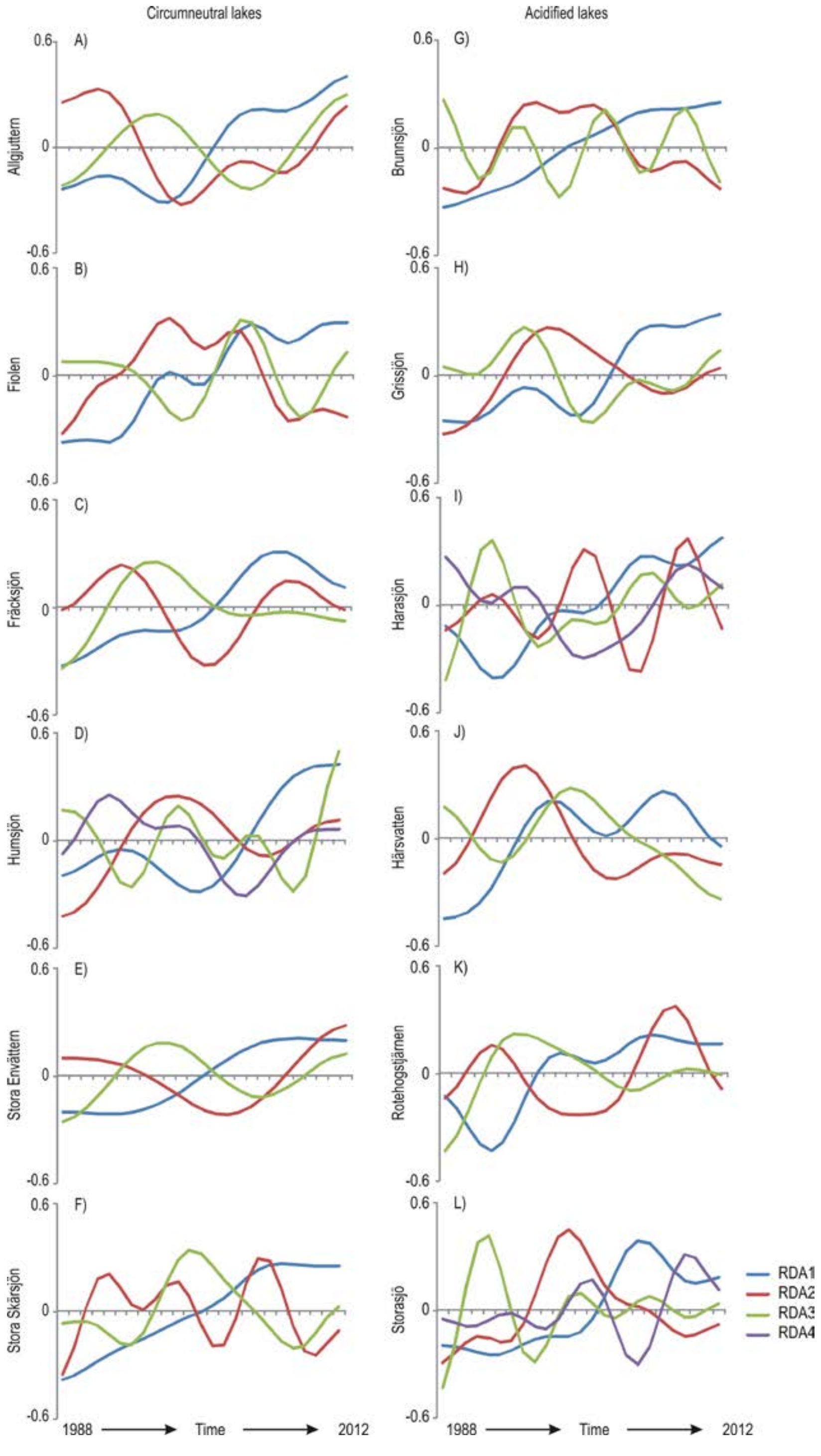

Circumneutral lakes
Acidified lakes
0.6
0
-0.6
A)
Allgjuttern
B)
Fiolen
C)
Fräcksjön
D)
Humsjön
E)
Stora Envättern
F)
Stora Skärsjön
G)
Brunnsjön
H)
Grissjön
I)
Harasjön
J)
Härsvatten
K)
Rotehogstjärnen
L)
Storasjö
RDA1
RDA2
RDA3
RDA4
1988
Time
2012

Fig. 3

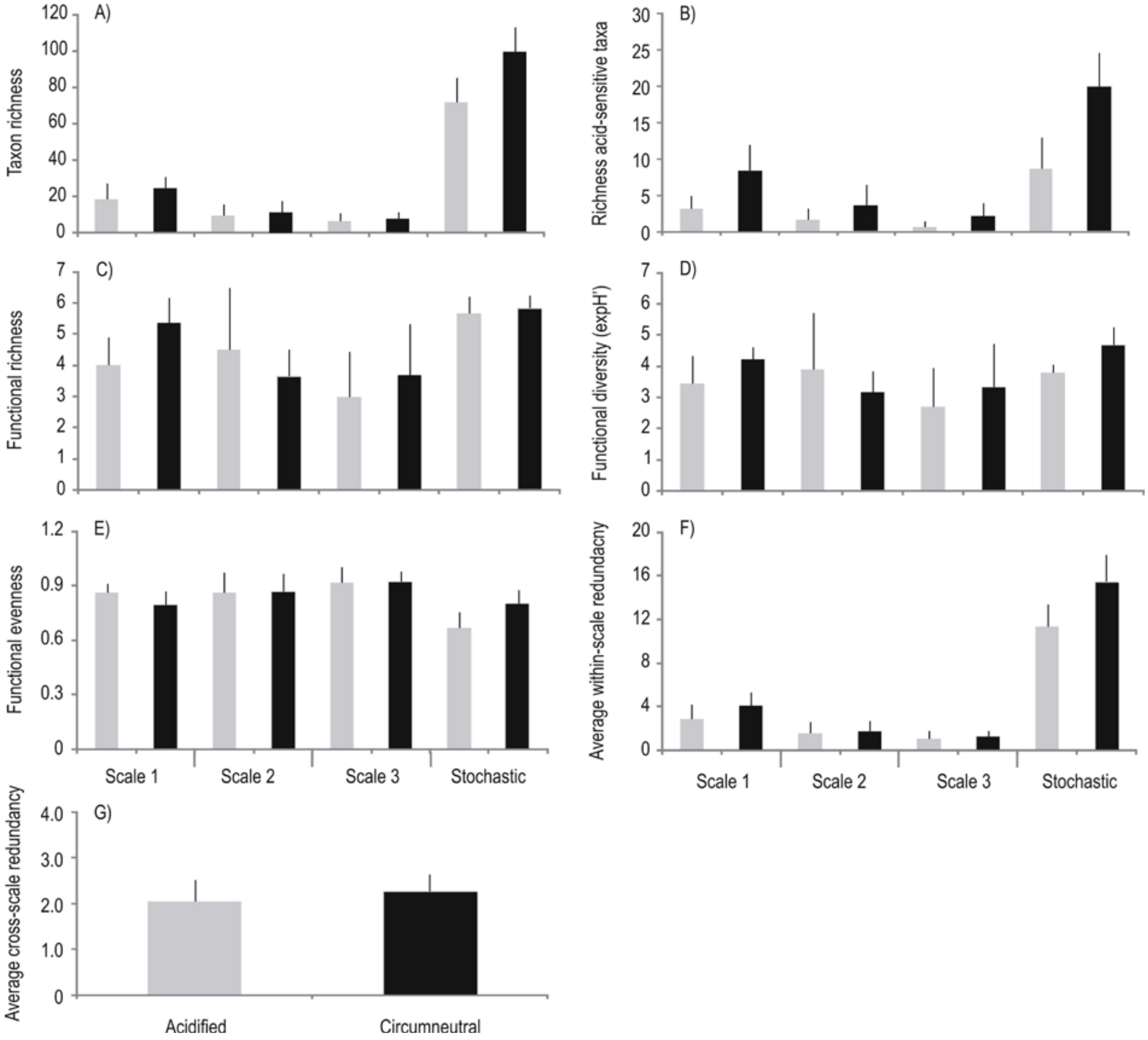
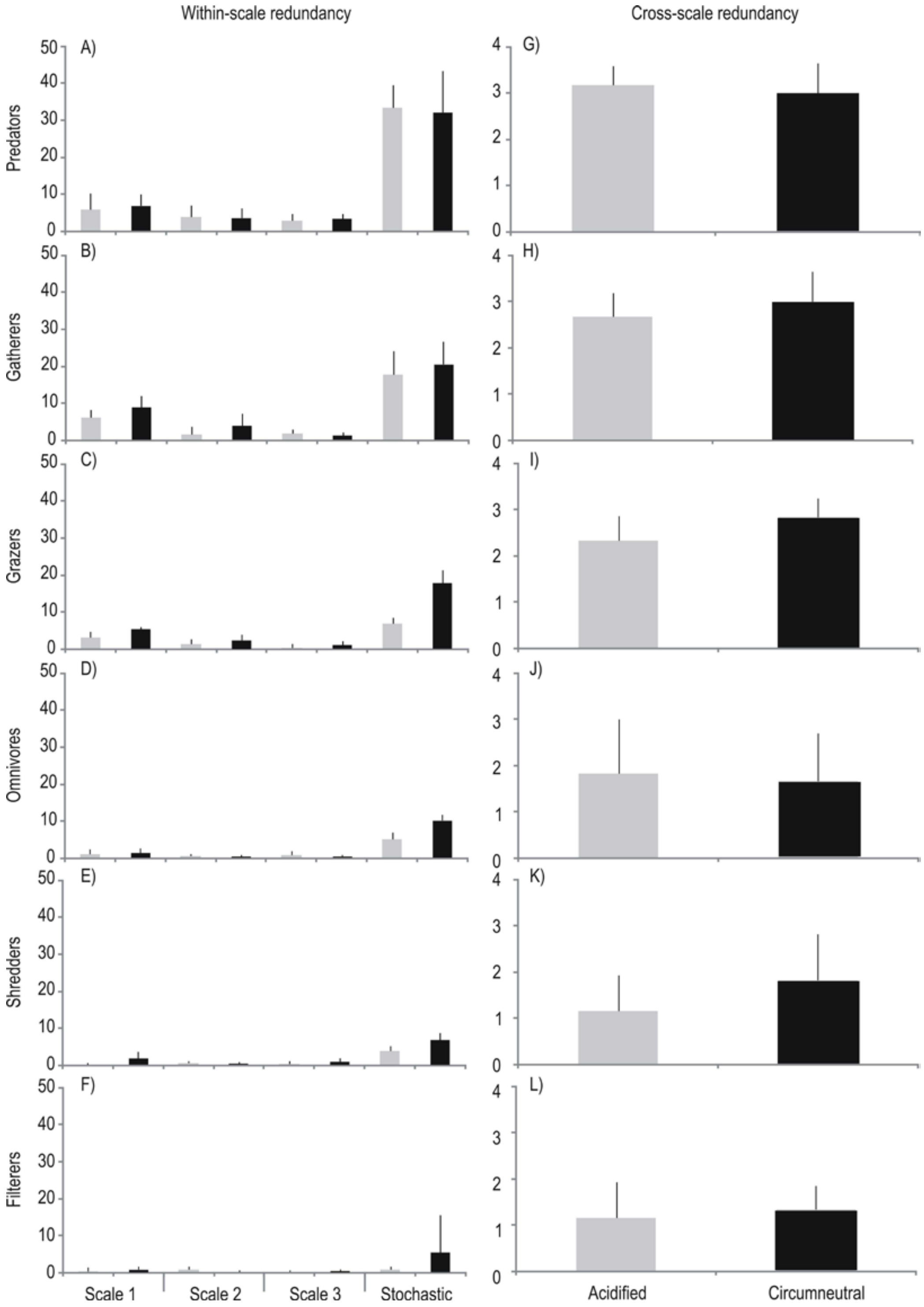

A)
Taxon richness
0
20
40
60
80
100
120
B)
Richness acid-sensitive taxa
0
5
10
15
20
25
30
C)
Functional richness
0
1
2
3
4
5
6
7
D)
Functional diversity (expH')
0
1
2
3
4
5
6
7
E)
Functional evenness
0
0.3
0.6
0.9
1.2
F)
Average within-scale redundacny
0
4
8
12
16
20
Scale 1
Scale 2
Scale 3
Stochastic
Scale 1
Scale 2
Scale 3
Stochastic
G)
Average cross-scale redundancy
0
1.0
2.0
3.0
4.0
Acidified
Circumneutral

Fig. 4



Within-scale redundancy
Cross-scale redundancy
A)
B)
C)
D)
E)
F)
G)
H)
I)
J)
K)
L)
Predators
Gatherers
Grazers
Omnivores
Shredders
Filterers
0
10
20
30
40
50
0
1
2
3
4
Scale 1
Scale 2
Scale 3
Stochastic
Acidified
Circumneutral

Fig. 5