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Research, part of a Special Feature on Panarchy: the Metaphor, the Theory, the Challenges, and the Road Ahead

Panarchy and management of lake ecosystems

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ABSTRACT. A key challenge of the Anthropocene is to confront the dynamic complexity of systems of people and nature to guide robust interventions and adaptations across spatiotemporal scales. Panarchy, a concept rooted in resilience theory, accounts for this complexity, having at its core multiscale organization, interconnectedness of scales, and dynamic system structure at each scale. Despite the increasing use of panarchy in sustainability research, quantitative tests of its premises are scarce, particularly as they pertain to management consequences in ecosystems. In this study we compared the physicochemical environment of managed (limed) and minimally disturbed reference lakes and used time series modeling and correlation analyses to test the premises of panarchy theory: (1) that both lake types show dynamic structure at multiple temporal scales, (2) that this structure differs between lake types due to liming interacting with the natural disturbance regime of lakes, and (3) that liming manifests across temporal scales due to cross-scale connectivity. Hypotheses 1 and 3 were verified whereas support for hypothesis 2 was ambiguous. The literature suggests that liming is a "command-and-control" management form that fails to foster self-organization manifested in lakes returning to pre-liming conditions once management is ceased. In this context, our results suggest that redundance of liming footprints across scales, a feature contributing to resilience, in the physicochemical environment alone may not be enough to create a self-organizing limed lake regime. Further research studying the broader biophysical lake environment, including ecological communities of pelagic and benthic habitats, will contribute to a better understanding of managed lake panarchies. Such insight may further our knowledge of ecosystem management in general and of limed lakes in particular.

Key Words: *cross-scale; lakes; liming; management; panarchy; resilience; time series modeling*

INTRODUCTION

The biophysical environment is hierarchically structured and dynamically changing (Allen et al. 2014). Theories have been developed that have this complexity at their core and that are crucial for understanding the resilience of complex systems of people and nature in times of rapid social-ecological change. For example, panarchy theory, a branch of complexity science incorporating resilience, accounts for the multiscale organization, interconnectedness of scales, and dynamic system structure in social-ecological systems (Gunderson and Holling 2002). Panarchy captures the cross-scale structure envisioned in hierarchy theory (Allen and Starr 1982) and acknowledges the transmission of information (matter, energy) not only from higher to lower scales (top–down processes) but also from lower to higher levels (bottom–up effects) in complex systems (Carpenter 1988). Such organization is ubiquitous and observed, for instance, in lake food webs, regional ecosystem management, and the global climate (Power 1992, Angeler et al. 2016, Garmestani et al. 2020).

Panarchy recognizes extrinsic and intrinsic factors that influence, and are influenced by, interrelated phenomena such as innovation, novelty, and regime shifts in social-ecological systems (Allen et al. 2014). Panarchy therefore is critical for providing a holistic view, and informing, ecosystem management (Garmestani et al. 2020). Ecosystem management is often unsuccessful at emulating natural disturbance regimes constrained by the overwhelming complexity inherent in systems of people and nature (Mori 2011). Such shortcomings of ecosystem management have been recently discussed in the context of coerced regimes (Angeler et al. 2020), which are social-ecosystem states that are not self-organizing but exclusively maintained by management to facilitate the production of selected ecosystem services. Coerced regimes thus only mimic desired system regimes through management but either shift or revert to an undesired regime with limited provision of services once management is ceased.

Lake liming as a management form fits the notion of coerced regimes since, as suggested in the literature, lakes fall back into a pervasive pre-liming regime when liming is discontinued (e.g., Clair and Hindar 2005). Liming is a management intervention for lakes, streams, wetlands and their catchments intended to counteract the effects of anthropogenic acidification, a major environmental problem during the industrial epoch in eastern North America and northern Europe (e.g., Wright et al. 1976, Schindler 1988, Henriksson and Brodin 1995, Bradley and Ormerod 2002). Liming consists of the application of limestone sand or powder to mitigate acidification impact in the abiotic (low pH, aluminum toxicity) and biotic (biodiversity and ecosystem service loss) environment.

Many countries implemented large-scale liming projects (Henriksson and Brodin 1995, Sandøy and Romunstad 1995) to facilitate the recovery of acid-sensitive biota, protect and enhance existing fish populations, and maintain aquaculture and recreational fishing (Appelberg and Svensson 2001). Although some positive outcomes of liming have been reported (Eriksson et al. 1983, Hasselrot and Hultberg 1984, Nyberg et al. 1986, Henriksson and Brodin 1995), reviews show that overall liming effects have been equivocal (Clair and Hindar 2005, Ormerod and Durance 2009, Mant et al. 2013) and often confounded by abiotic, ecological, and historical factors. These factors include episodic fluctuations in water chemistry caused by recurring liming and re-acidification events, limited dispersal of organisms, habitat characteristics, and altered food webs (Yan et al. 2003, Binks et al. 2005, Lau et al. 2017). These results suggest that the effectiveness of liming is riddled with spurious certitude (Bishop et al. 2001, McKie et al. 2006, Angeler and Goedkoop 2010).

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Limed ecosystems provide opportunities to study coerced regimes from a panarchy perspective. There have been diverse and successful applications of panarchy in social and ecological systems, predominately in metaphorical discourse and qualitative analyses (Berkes and Ross 2016, DeWitte et al. 2017, Wilcox et al. 2019) that have informed vulnerability and risk assessments (Angeler et al. 2016) and ecosystem management (Garmestani et al. 2020). However, panarchy offers more than a heuristic for qualitative research (Sundstrom and Allen 2019); it also allows for empirical analyses. We used time series modeling of the physicochemical environment of limed lakes and unmanaged, minimally disturbed reference lakes (sensu Stoddard et al. 2006) to infer scale-specific temporal patterns, indicative of hierarchical structuring over time, in individual lakes (Baho et al. 2015). Specifically, panarchy describes hierarchical and dynamic system change, portrayed as a nested set of adaptive cycles (Gunderson and Holling 2002). Such dynamic system change in lakes can be exemplified with, for instance, fast (e.g., diurnal fluctuation of temperature), slower intra-annual (plankton seasonality), and more gradual, inter-annual patterns (lake browning). Such patterns are expected to be detected by time series modeling because many boreal lakes have experienced a monotonic decrease of total phosphorus and an increase of dissolved organic carbon since the early 1990s due to catchment processes related to changes in climate, catchment soil properties, and recovery from acidification (i.e., slow, gradual dynamic; Huser et al. 2018). Such decadal patterns of monotonic change are uncoupled from, for example, seasonal change, which is manifested in variables such as water temperature and oxygen concentration (e.g., faster intermediate temporal dynamics). Also, more complex patterns of combined inter- and intra-annual variability during specific cycles can be observed (Baho et al. 2015), which shows that biophysical dynamics in lakes are more complex relative to the simplified adaptive cycle dynamics invoked by the panarchy heuristic. That is, in addition to hierarchical temporal structuring (scales), orthogonal (statistically independent) patterns of temporal change within defined cycles can be revealed by our time series models (Legendre and Gauthier 2014). More generally, temporal structure of the abiotic environment in individual lakes can integrate and thus arise from environmental processes, which are themselves structured at, and interacting across, different spatiotemporal scales in catchments (e.g., Strahler 1964, Soranno et al. 2014).

Studying the abiotic environment is deemed especially suitable given the strong and direct physicochemical footprints of liming in freshwater ecosystems. Panarchy theory allows formulating hypotheses for individual premises that can be empirically tested. This is useful for studying liming from a complex systems perspective, which can further our knowledge of the resilience of aquatic ecosystems (Pelletier et al. 2020). Panarchy theory holds the potential to answer lingering questions about the interactions of natural and anthropogenic/management disturbances and provide information about the magnitude and scale-specificity of recurrent liming impacts on the abiotic lake environment. We tested the following hypotheses:

1. In accordance with previous studies (Angeler et al. 2011, Baho et al. 2015), we hypothesized that distinct hierarchical and orthogonal temporal patterns of the physicochemical environment manifest within individual lakes. Verifying this hypothesis is essential to test the premise of panarchy theory that complex systems dynamics are compartmentalized.
2. Following the first hypothesis, and given the alteration of natural disturbance regimes by liming (Bishop et al. 2001, McKie et al. 2006), we postulated that the hierarchical and orthogonal temporal patterns of physicochemical variables differ between limed and reference lakes. Verifying this hypothesis will allow testing the premise of dynamic system change of panarchy theory, and whether management, as opposed to natural dynamics, can alter such patterns.
3. We further hypothesized that, in order to verify the aspect of linked scales of panarchy, the impacts of liming will be manifest across modeled hierarchical and orthogonal temporal dimensions in the lakes. We used Ca:Mg ratios as a surrogate of liming to assess the strength of management footprints across temporal scales and contrasted with reference lakes.

We tested these conjectures relative to the null hypothesis that no liming effects are evident in significant time series models relative to models of reference lakes (liming effects are absorbed and thus undetectable in the complex systems structure of lakes). Verifying either the null hypothesis or alternative conjectures will provide mechanistic insight about limed lakes as coerced regimes. That is, whether limed lakes are robust to management (null hypothesis) or whether cross-scale manifestations of liming footprints alone are not enough for attaining stable, self-perpetuating liming regimes (alternative hypotheses).

METHODS

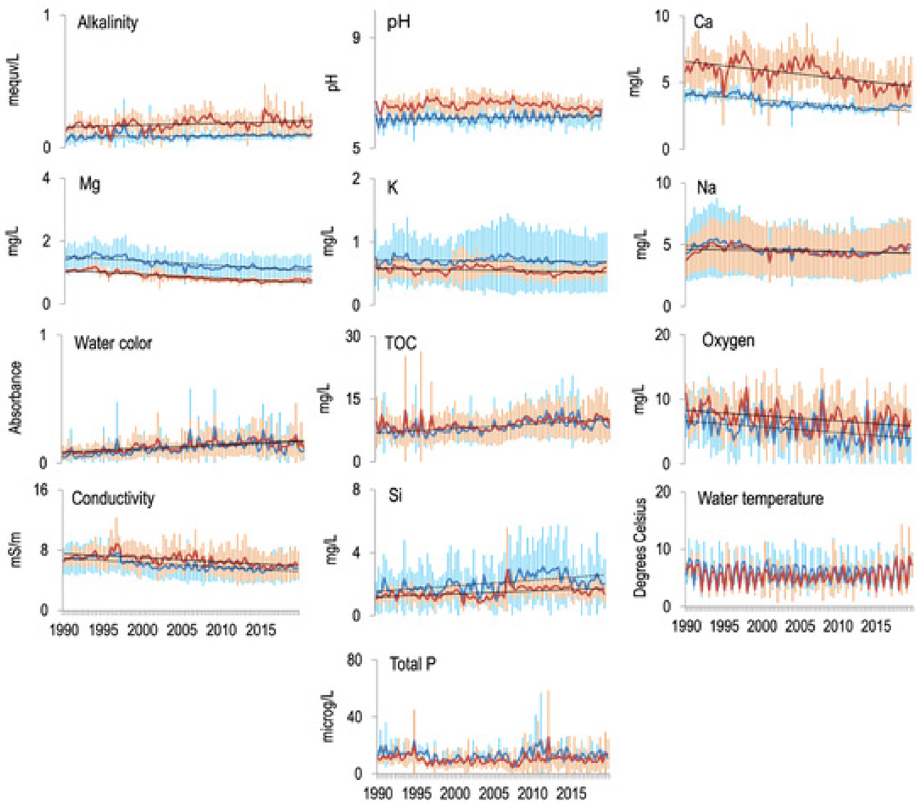
Study lakes

We used an ecosystem experiment approach and environmental monitoring data for assessing lake management panarchies. Four limed lakes and four circumneutral reference lakes with the most exhaustive time series data were selected (Appendix 1). All lakes are situated in the boreonemoral ecoregion of southern Sweden and were chosen to avoid confounding effects due to idiosyncratic biophysical features of other ecoregions. The limed lakes were integrated in the national liming program initiated in 1989 by the Swedish Environmental Protection Agency (Appelberg and Svensson 2001). Liming was carried out prior to the start of the program between 1974 and 1985 and consisted of application of limestone powder by boat or helicopter at different intervals across lakes (Appendix 1). The minimally disturbed reference lakes were chosen to assess the footprints of management on temporal patterns of water quality relative to unmanaged conditions. These reference systems have a high buffering capacity and were thus robust against acidification (Fölster et al. 2014).

Sampling procedures

Mid-lake water samples were taken in near-equidistant sampling intervals (early spring, summer, and late autumn) over a 30-y study period between 1990 and 2019 in the epilimnion (0-2 m) using a Ruttner sampler. Samples were kept cool during transport to the laboratory where they were analyzed for alkalinity, concentrations of calcium (Ca), magnesium (Mg), sodium (Na), potassium (K), total phosphorus (P), silicon (Si), total organic carbon (TOC), and water color. Water temperature, dissolved oxygen concentration, electrical conductivity, and potential of

Fig. 1. Temporal patterns of physicochemical variables in reference lakes (blue lines) and limed lakes (red lines). Trend lines (full, limed lakes; dashed, reference lakes) indicate significant components of monotonic change revealed by Kendall tau correlation analysis. Shown are means ± standard deviations.



hydrogen (pH) were measured in situ. All physicochemical analyses were performed at the Department of Aquatic Sciences and Assessment following international (ISO) or European (EN) standards (Fölster et al. 2014).

Statistical analysis

Kendall tau rank correlation analyses were carried out to assess whether individual physicochemical variables changed monotonically over time. The entire set of physicochemical variables for each lake was subsequently analyzed using redundancy analysis (RDA) where time was modeled using Asymmetric Eigenvector Maps (AEM; Baho et al. 2015). When used in time series modeling, this analysis is useful for extracting independent temporal patterns and scaling relationships necessary for assessing the panarchic organization of lakes from the data. That is, the analysis is capable of discerning, for example, between seasonal, inter-annual, and decadal patterns (and their combinations) inherent in the dynamics of the environment. It also allows for detecting orthogonal patterns that can arise from differentiated temporal variability within defined cycles of periodicity (Legendre and Gauthier 2014). This analysis is therefore useful for testing hypothesis 1, that there is, following the premise of panarchy, hierarchical structure in the physicochemical environment, while accounting for orthogonality as an additional factor capturing ecological complexity.

The time series analysis was conducted by first converting the linear time vector consisting of 90 steps between years 1990 and 2019 in a set of independent temporal AEM variables. These AEMs comprise a set of sine waves ranging from long to short frequencies that allow the modeling of fluctuation patterns together with a linear vector, which simultaneously accounts for monotonic trends in the data (Blanchet et al. 2008, Legendre and Legendre 2012). These AEMs are then used as explanatory variables in the time series models using redundancy analysis (RDA). Time series models were constructed individually for each lake, resulting in eight time series models, four for the limed lakes and four for the reference lakes, using the 13 physicochemical variables (Fig. 1) as response variables. The RDA selects significant temporal variables (AEMs) using forward selection, and these variables are linearly combined to extract temporal structures from the matrices containing physicochemical variables. The modeled temporal patterns that are extracted from the data are collapsed onto significant RDA axes, which are tested through permutation tests. These RDA axes are then used to distinguish independent temporal (hierarchical and orthogonal) patterns in the data, which can be visualized through linear combination (lc) score plots. All physicochemical variables were standardized prior to the analysis.

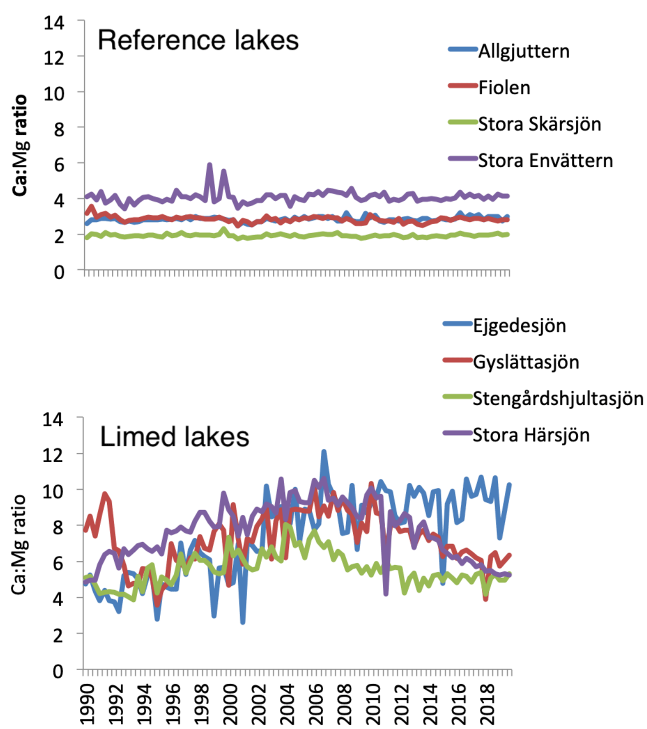
Table 1. Summary statistics of AEM-RDA models. Not applicable (na) because axes were not significant.

	Adjusted R^2 min. model	No. of vectors selected	No. of significant axes	Variance RDA 1	Variance RDA 2	Variance RDA 3	Variance RDA 4	Variance RDA 5
Reference lakes								
Allgjutten	49.60	15	3	15.10	6.36	2.53	na	na
Fiolen	66.07	16	4	23.00	11.96	6.33	2.87	na
Stora Skärsjön	45.84	14	4	9.56	8.09	3.02	1.94	na
Stora Envättern	45.29	15	4	9.27	6.09	4.17	1.83	na
Limed lakes								
Ejgdesön	48.08	15	4	12.77	6.14	2.88	2.08	na
Gyslättasjön	40.67	8	5	7.43	3.51	3.32	1.92	1.19
Stengårdshultasjön	62.86	25	5	21.01	8.49	5.34	4.17	2.05
Stora Härsjön	53.22	15	5	13.92	7.28	3.86	3.34	1.71

To test hypothesis 2, that temporal patterns differ between limed and reference lakes, two ANOVA analyses were conducted. First, one-way ANOVA was used to compare RDA-AEM model structure and performance between limed and reference lakes contrasting the following variables: adjusted R^2 of the minimum models, their numbers of significant axes, numbers of vectors selected, and the variances explained by individual RDA axes. Second, repeated measures analysis of variance (rm-ANOVA) was used to compare the temporal patterns of individual RDA axes, and their interaction, between reference and limed lakes. For this we used a mixed model approach, based on restricted estimation of maximum likelihood (REML), accounting for the temporal autocorrelation structure of order one, AR(1), of the time series. Lakes were treated as random variables in this model to allow for more generalized inference about liming impacts on temporal patterns of water quality beyond the set of lakes used in this study. Significant lake "Type" (reference lakes vs limed lakes) terms and interaction terms between lake "Type" and "Time" (90 time steps between 1990 and 2019) are considered crucial for inferring that liming alters natural patterns of temporal variability of lake physicochemical conditions. Because of unbalanced designs caused by different numbers of significant RDA axes across time series models (Table 1), comparisons were made only for the first three RDA axes.

Finally, to test hypothesis 3, assessing the strength of liming impacts on the modeled hierarchical and orthogonal temporal patterns, Spearman rank correlation analysis was used to relate lc scores of individual RDA axes with Ca:Mg ratios. These ratios serve as surrogates of the management regime imposed by liming on the natural dynamics of lake physicochemistry, which is manifested in substantial inter-annual variation relative to unmanaged lakes (Fig. 2). The strength and nature of the interference of liming with natural fluctuation patterns across temporal scales revealed by the RDA analyses can be assessed through significant correlations across individual axes. Specifically, correlation analysis can reveal whether monotonic or fluctuating patterns of change of water quality are associated with liming within and across lakes. These correlations are also carried out for reference lakes to assess the degree of associations between modeled temporal patterns and Ca:Mg ratios unbiased by liming. All statistical analyses were carried out in R Studio 1.1.383 (https://www.rstudio.com/) using the "cor.test" function and packages vegan, adespatial, tidyverse, reshape, ade4, quickMEM, nlme, data table, and car.

Fig. 2. Temporal patterns of Ca:Mg ratios as a surrogate of management disturbance imposed by liming compared to patterns of reference lakes.



RESULTS

Individual physicochemical variables showed significant monotonic change (Kendall tau rank correlations; $p < 0.05$) in limed and reference lakes over the study period, except water temperature and total P in both lake types and pH and TOC in limed lakes (Fig. 1). Alkalinity and water color in limed and reference lakes and pH and TOC in reference lakes significantly increased while ions, Si, oxygen concentration and conductivity significantly decreased in both lake types over time (Fig. 1).

These patterns of change were reflected in the AEM-RDA time series models, which explained 41% to 66% of the adjusted variance (Fig. 3; Appendix 2). RDA axis 1, which captured the component of monotonic change over time (i.e., slow dynamics at the highest panarchy level), explained a large part of the variance across the lakes studied relative to the other axes revealed by the models, although the range of variance was variable (7%-23%; Table 1). The time series models also revealed seasonal patterns reflecting the sampling periods in early spring, summer, and late autumn and different degrees of inter-annual variation across RDA axes (i.e., faster cycling at lower panarchy levels; Fig. 3). Some of these RDA axes showed orthogonal patterns (for instance, at roughly 15-year fluctuation cycles at RDA 2 and RDA 3 of reference lakes and broadly 20-year cycles at RDA 3 and RDA 4 of limed lakes) in addition to hierarchical (slow to fast) temporal structure (Fig. 3).

In total, temporal patterns were manifested at three to four RDA axes in reference lakes and four to five RDA axes in limed lakes (Table 1; Appendix 2). Despite limed lakes tending to have an apparent "finer" temporal structure relative to reference lakes, it was too subtle to be significant in the mixed model. ANOVA comparisons also revealed no significant differences ($P > 0.05$) regarding model structure and performance, indicating that the number of AEM vectors selected for modeling temporal patterns and the variance explained by the models and individual RDA axes were similar between limed and reference lakes (not highlighted in Table 1).

Within reference lakes, Ca:Mg ratios correlated significantly with RDA 1 in Allgjuttern and Fiolen and with RDA 4 in Stora Skärsjön and Stora Envättern. In contrast, within limed lakes, significant correlations between Ca:Mg ratios and linear combination scores of RDA axes from the time series models (a management surrogate of liming) were more prevalent. Specifically, significant correlations were found between Ca:Mg ratios and RDA 1 and 2 for lake Ejgdesjön, RDA 1, 2 and 4 for lake Gyslättasjön, RDA 2 and 4 for lake Stengårdshultasjön, and RDA 1 to 4 for lake Stora Härsjön (Table 2). Despite these differences between limed and reference lakes, the mixed models revealed no significant interaction terms or lake type (limed vs reference lakes) effects comparing individual RDA axes (Table 3). Only significant time effects were found for RDA 1 and 2 (Table 3).

DISCUSSION

Panarchy has clear implications for the management of social-ecological systems (Garmestani et al. 2020). As environmental change accelerates, it becomes increasingly important to understand ecosystem dynamics at different spatiotemporal scales, cross-scale interactions, and the consequences of the structures and processes in lake systems. This study quantitatively tested three hypotheses related to core aspects of panarchy theory: hierarchical structuring, dynamic system changes, and cross-scale connectivity (Gunderson and Holling 2002). The panarchy analysis revealed that lakes have structure at multiple temporal (hierarchical and orthogonal) scales and that the effects of liming manifests at different temporal scales.

The results of our study supported our first hypothesis that the physicochemical environment in individual lakes shows dynamics at distinct temporal scales, including seasonal, inter-annual and monotonically changing patterns and their combinations. This fits the premise of panarchy theory that complex system dynamics are bound, both hierarchically (Allen et al. 2014), and, as revealed by our study, orthogonally. These results are in agreement with previous studies showing such compartmentalized temporal variation in lake biogeochemistry (Baho et al. 2015) and biota (phytoplankton [Baho et al. 2014], macroinvertebrates [Angeler et al. 2011]).

Fig. 3. Linear combination (lc) score plots showing distinct temporal patterns modeled by RDA analyses. These temporal patterns correspond to different scaling patterns indicative of hierarchical and orthogonal structuring of lake panarchies. Shown are the averages ± standard deviations of four reference (blue lines) and limed (red lines) lakes; except RDA 4, which is based on the average of three reference lakes and RDA 5, which was significant only in three limed lakes (See Table 1).

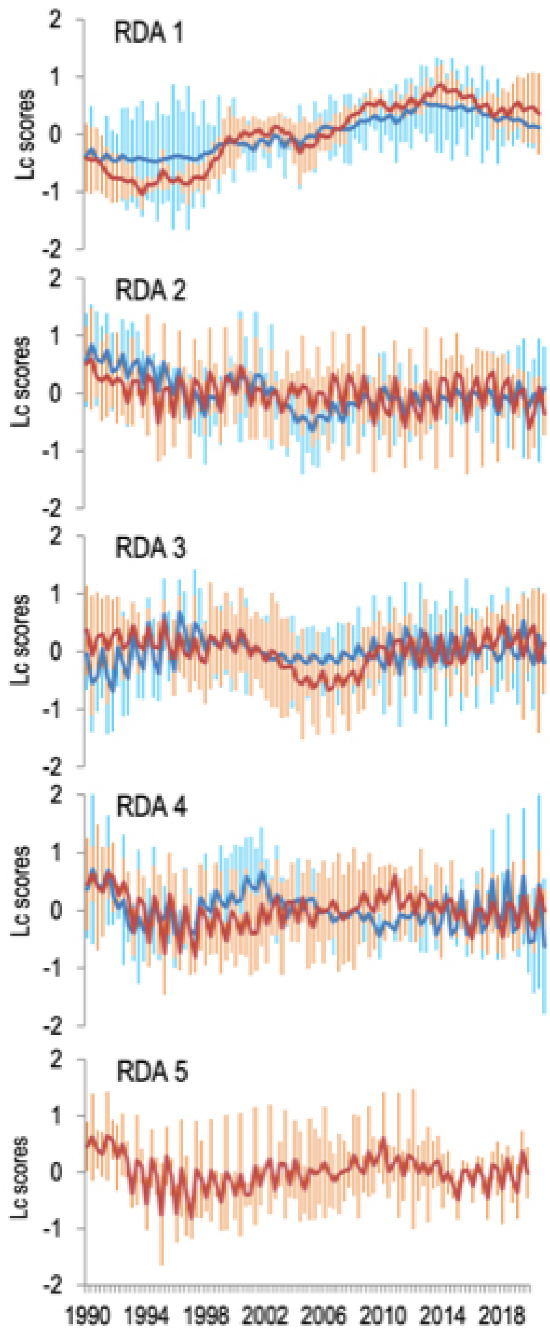


Table 2. Spearman rank correlation analysis associating temporal patterns determined by AEM-RDA and Ca:Mg ratios. Shown are correlation coefficients (rho). Significant correlations (highlighted in bold) where * p < 0.05; ** p < 0.01; *** p < 0.001. Not applicable (na) because axes were not significant.

	RDA 1	RDA 2	RDA 3	RDA 4	RDA 5
Reference lakes					
Allgjuttern	**0.26***	-0.06	0.15	na	na
Fiolen	**-0.37*****	0.16	0.14	0.06	na
Stora Skärsjön	0.18	-0.13	0.09	**0.24***	na
Stora Envättern	0.09	0.08	-0.01	**-0.27****	na
Limed lakes					
Ejgdesjön	**0.75*****	**-0.35*****	0.17	0.11	na
Gyslättasjön	**0.34*****	0.05	**-0.61*****	**0.27***	0.13
Stengårdshultasjön	-0.08	**-0.78*****	-0.04	**-0.31****	-0.02
Stora Härsjön	**-0.29****	**-0.74*****	**-0.30****	**0.32****	0.15

Table 3. Results of linear mixed models showing main effects of lake type (“Type”; Reference lakes vs limed lakes) and period of study (“Time”; 1990–2019) and their interactions for dominant temporal scales (RDA 1–3) in the time series models. Note: no contrasts were made for subordinate scales (RDA 4 and RDA 5), present only in limed lakes, resulting in an unbalanced design (see Table 1). Significant factors are highlighted in bold.

	Factor	Chi square	P
RDA 1	Type	0.008	0.93
	Time	**39.51**	**> 0.001**
	Type x Time	2.27	0.13
RDA 2	Type	0.006	0.98
	Time	**22.25**	**> 0.001**
	Type x Time	2.62	0.11
RDA 3	Type	< 0.001	0.99
	Time	< 0.001	0.94
	Type x Time	1.54	0.21

Although catchment processes related to changes in climate, catchment soil properties, and recovery from acidification have been reported to influence local lake biogeochemistry (Huser et al. 2018) our study is agnostic about mechanisms leading to the hierarchical and orthogonal temporal scaling structures in lakes. That is, our study prevents us from determining the influence of spatially scaled processes in the catchments and the interactions that may arise between such landscape effects and local lake conditions (Soranno et al 2014). It also does not account for social aspects (governance, environmental laws) that influence social-ecological water panarchies (Pope et al. 2014, Cosens and Gunderson 2018). Notwithstanding, all lakes studied here are situated in near-pristine catchments and in the same ecoregion. Assuming that unmeasured environmental processes are similar across limed and reference lakes, we are confident that the hierarchical and orthogonal structures observed are not confounded by potential catchment scale (land use and other anthropogenic disturbances) processes. This suggests that our comparisons between lake types are suitable, especially for assessing liming effects on the lakes’ panarchy structure.

This brings us to our second hypothesis, for which support was ambiguous. We expected liming to substantially alter the temporal patterns and scaling structure in the physicochemical environment given its profound disturbance on biophysical conditions of aquatic ecosystems (Bishop et al. 2001, McKie et al. 2006). It can be particularly expected that liming footprints manifest strongly at scales that are associated with the temporal fluctuations of variables that are directly affected by liming (Ca concentrations, pH, alkalinity). This in turn should be captured by model performance of the RDA, a method sensitive to different patterns in the data (Baho et al. 2015). However, RDA model performance was similar across limed and reference lakes. Also, the lack of significant interaction terms (lake type x time) in the ANOVA suggests that scale-specific temporal patterns were similar between limed and reference lakes. A subtle difference was that limed lakes generally had a more differentiated temporal structure, manifested in additional temporal scales (RDA axes) in comparison with reference lakes. A similar observation contrasting these lake types has been made in previous comparisons using phytoplankton (Baho et al. 2014). However, sample sizes are currently too low for attributing this differentiation unambiguously to liming.

We speculate that the similar temporal patterns of dominant scales (RDA 1-RDA 3) between limed and reference lakes may partly be due to liming frequencies not being aligned with lake sampling. This may lead to the wrong impression that liming effects dissipate quickly after application indicative of fast re-establishment of temporal dynamics in limed lakes similar to reference conditions. Liming partly correlated to different degrees with subordinate scales in the time series models (RDA 4-RDA 5; see below). However, the unequal number of such subordinate scales prevented statistical comparisons with the temporal structure of reference lakes and therefore the unambiguous detection of potential liming effects given our sampling design. Although methods for such comparisons exist (PERMANOVA, ANOSIM), ambiguity remains an issue because they perform unreliably with unbalanced designs (Anderson and Walsh 2013).

More generally, the weak evidence of liming in our time series models and ANOVA comparisons suggests that the natural disturbance regimes mitigate anthropogenic impacts, as has been shown in systems exposed to high natural variation (intermittent streams [Soria et al. 2020], Mediterranean coastal lagoons [Franzo et al. 2019]). However, this interpretation is at odds with pervasive impacts on physicochemical variables, especially Ca, alkalinity, and pH, as long as lakes are limed (Fig. 1). It also contradicts many lake studies reporting anthropogenic stress (e.g., acidification or eutrophication) and management forms to “override” natural disturbance regimes, as is the case with command-and-control management (Holling and Meffe 1996). Such profound anthropogenic effects in the environment, of which liming is an example, fit interpretations of acidification mitigation as an anthropogenic perturbation (e.g., McKie et al. 2006). We speculate that the relatively high standard deviations of lc-scores describing AEM-RDA temporal patterns resulted in high within-group variability of limed and reference lakes. This variability may have obscured the statistical detection of liming effects, providing unambiguous support for hypothesis 2. Further research, using more lakes with greater resolution of temporal structure than three sampling events per year and potentially longer time series with periods before and after liming, might help to more clearly detect and accurately describe liming effects on the temporal dynamics in managed lakes.

Although liming effects were ambiguous in the time series and ANOVA analyses, there is stronger evidence of liming footprints in the physicochemical lake environment in our correlation analyses. This is manifested in the significant correlations of Ca: Mg ratios, which are substantially altered by and thus serve as a surrogate of liming, and the temporal patterns identified by the RDA. Ca:Mg ratios correlated across different modeled hierarchical and orthogonal scales in the limed lakes, which supports our third hypothesis that "(management) information" manifests across different scales, more specifically across the independent significant temporal patterns revealed by time series modeling. Interconnectedness is a fundamental aspect of panarchy theory, and its ubiquity is evident in the flow of matter and energy in nature, ranging bottom-up and top-down effects in lake food webs (Gruner et al. 2008) to the global climate (Angeler et al. 2016) to biochemical cycling (Friedl and Wüest 2002). Interconnectedness of scales and cross-scale interactions in a panarchy invoke dynamic processes (Gunderson and Holling 2002). Our results, rather than describing dynamic processes, show static pattern manifestations of liming footprints at individual temporal dimensions in the time series models. However, the detection of patterns in this study is not at odds with the premise of dynamic information flow in a panarchy. These patterns suggest that liming, because of its significant impact on the biophysical environment of lakes, can have parallel and independent effects on multiple time scales.

We acknowledge that Ca:Mg ratios are not only a surrogate of liming effects but also inherent in the natural variability of lakes. Both elements originate from weathering of rocks and leaching from soils in catchments. It is therefore not surprising that these ratios also correlated with temporal patterns in reference lakes. Contrary to limed lakes, lake- significant correlations only occurred at a single scale in the unmanaged lakes (Table 2). This finding provides support for a classical notion of ecological complexity: that a few key variables, such as, Ca and Mg concentrations, manifest at specific scales in ecosystems (Holling 1992). This scale-specificity in reference lakes versus the cross-scale manifestation of Ca:Mg ratios in limed lakes provide insight into management footprints on lake panarchies.

There is increasing evidence that limed lakes comprise coerced regimes that fail to restore baseline conditions of self-organization and ecosystem services (i.e., lake restoration), and are maintained exclusively through management (Angeler et al. 2020). That limed lakes comprise coerced, rather than self-organizing regimes is supported by a body of research that documents that limed lakes revert to acidified conditions once liming is discontinued (Clair and Hindar 2005). Such patterns have been specifically observed in the abiotic environment (Lydersen et al. 2002, Hindar et al. 2013, Hindar and Skancke 2014) and are supported by geochemical modeling of pH and aluminum concentrations in a large number of Swedish lakes (Sjöstedt et al. 2013). Also, evidence of coerced regimes has been revealed by research showing that lake internal phosphorus cycling in limed lakes and their susceptibility to re-acidification events limit their restoration (Dickson et al. 1995, Hu and Huser 2014).

Taken together our results suggest that management footprints are evident but become diluted in limed lake panarchies. From a coerced regime perspective, our results suggest that redundance of liming footprints across scales—a feature considered to contribute to resilience (Allen et al. 2005)—in the physicochemical environment alone may not be enough to create self-organizing limed lake regimes. Our results reject the null hypothesis that liming effects are absorbed and therefore undetectable in the abiotic environment. However, potential verification of our null hypothesis cannot be completely discarded at this preliminary stage as liming footprints in the biotic lake environment may differ. Further research studying the broader biophysical lake environment, including ecological communities of pelagic and benthic habitats, shall contribute to a better understanding of managed lake panarchies.

We conclude with highlighting that the abiotic environment of managed and unmanaged lakes strikingly fit the premises of panarchy theory. This theory has so far only been used to describe "living" (ecological, social, combined social-ecological, including economic) systems (Holling 2001, Garmestani et al. 2009, 2020). This study reveals for the first time that the organization of the abiotic environment of lakes also fits the premises of panarchy theory. Our study suggests that further quantitative evaluations of panarchy across different types of social-ecological systems may be useful to inform ecosystem management and resilience science in general.

Responses to this article can be read online at:
https://www.ecologyandsociety.org/issues/responses.php/12690

Author Contributions:

DGA conceived this study, analyzed the data, and wrote the paper. All co-authors contributed to the writing.

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Data Availability:

All data are freely available at: https://www.slu.se/en/departments/aquatic-sciences-assessment/data-host/. The R script for analysis is available in Appendix 3.

LITERATURE CITED

Allen, C. R., D. G. Angeler, A. S. Garmestani, L. H. Gunderson, and C. S. Holling. 2014. Panarchy: theory and application. Ecosystems 17:578-589. https://doi.org/DOI: 10.1007/s10021-013-9744-2

Allen, C. R., L. Gunderson, and A. R. Johnson. 2005. The use of discontinuities and functional groups to assess relative resilience in complex systems. Ecosystems 8:958-966. https://doi.org/10.1007/s10021-005-0147-x

Allen, T. F. H., and T. B. Starr. 1982. Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago, Illinois, USA.

Anderson, M. J., and D. C. I. Walsh. 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? Ecological Monographs 83(4):557-574. https://doi.org/DOI: 10.1890/12-2010.1

Angeler, D. G., C. R. Allen, A. S. Garmestani, L. H. Gunderson, and I. Linkov. 2016. Panarchy use in environmental science for risk and resilience planning. Environment Systems and Decisions 36:225-228. https://doi.org/10.1007/s10669-016-9605-6

Angeler, D. G., B. C. Chaffin, S. M. Sundstrom, A. Garmestani, K. L. Pope, D. R. Uden, D. Twidwell, and C. R. Allen. 2020. Coerced regimes: management challenges in the Anthropocene. Ecology and Society 25(1):4. https://doi.org/10.5751/ES-11286-250104

Angeler, D. G., S. Drakare, and R. K. Johnson. 2011. Revealing the organization of complex adaptive systems through multivariate time series modeling. Ecology and Society 16(3):5. http://dx.doi.org/10.5751/ES-04175-160305

Angeler, D. G., and W. Goedkoop. 2010. Biological responses to liming in boreal lakes: an assessment using plankton, macroinvertebrate and fish communities. Journal of Applied Ecology 47(2):478-486. https://doi.org/10.1111/j.1365-2664.2010.01794.x

Appelberg, M., and T. Svensson. 2001. Long-term ecological effects of liming-the ISELAW programme. Water, Air, and Soil Pollution 130:1745- 1750. https://doi.org/10.1023/A:1013908003052

Baho, D. L., S. Drakare, R. K. Johnson, C. R. Allen, and D. G. Angeler. 2014. Similar resilience characteristics in lakes with different management practices. PLoS ONE 9(3):e91881. https://doi.org/10.1371/journal.pone.0091881

Baho, D. L., M. N. Futter, R. K. Johnson, and D. G. Angeler. 2015. Assessing temporal scales and patterns in time series: comparing methods based on redundancy analysis. Ecological Complexity 22:162-168. https://doi.org/10.1016/j.ecocom.2015.04.001

Berkes, F. and H. Ross. 2016. Panarchy and community resilience: sustainability science and policy implications. Environmental Science & Policy 61:185-193. https://doi.org/10.1016/j.envsci.2016.04.004

Binks, J. A., S. E. Arnott, and W. G. Sprules. 2005. Local factors and colonist dispersal influence crustacean zooplankton recovery from cultural acidification. Ecological Applications 15 (6):2025-2036. https://doi.org/10.1890/04-1726

Bishop. K., H. Laudon, J. Hruska, P. Kram, S. Köhler, and S. Löfgren. 2001. Does acidification policy follow research in northern Sweden? The case of natural acidity during the 1990's. Water, Air, and Soil Pollution 130:1415-1420. https://doi.org/10.1023/A:1013936224549

Blanchet, F. G., P. Legendre, and D. Borcard. 2008. Modelling directional spatial processes in ecological data. Ecological Modelling 215(4):325-336. https://doi.org/10.1016/j.ecolmodel.2008.04.001

Bradley, D. C., and S. J. Ormerod. 2002. Long-term effects of catchment liming on invertebrates in upland streams. Freshwater Biology 47(1):161-171. https://doi.org/10.1046/j.1365-2427.2002.00770.x

Carpenter, S. R. 1988. Transmission of variance through lake food webs. Pages 119-135 in S.R. Carpenter S.R., editor. Complex interactions in lake communities. Springer, New York, New York, USA.

Clair, T. A., and A. Hindar. 2005. Liming for the mitigation of acid rain effects in freshwaters: a review of recent results. Environmental Reviews 13(3):91-128. https://doi.org/10.1139/a05-009

Cosens, B., and L. Gunderson, editors. 2018. Practical panarchy for adaptive water governance: linking law to social-ecological resilience. Springer, New York, New York, USA. DeWitte, S. N., M. H. Kurth, C. R. Allen, and I. Linkov. 2017. Disease epidemics: lessons for resilience in an increasingly connected world. Journal of Public Health 39(2):254-257. https://doi.org/10.1093/pubmed/fdw044

Dickson, W., H. Borg, C. Ekström, E. Hörnström, and T. Grönlund. 1995. Reliming and reacidification effects on lakewater: chemistry, plankton and macrophytes. Water, Air, and Soil Pollution. 85:919-924. https://doi.org/10.1007/BF00476947

Eriksson, F., E. Hörnström, P. Mossberg, and P. Nyberg. 1983. Ecological effects of lime treatment of acidified lakes and rivers in Sweden. Hydrobiologia 101:145-163. https://doi.org/10.1007/BF00008667

Fölster, J., R. K. Johnson, M. N. Futter, and A. Wilander. 2014. The Swedish monitoring of surface waters: 50 years of adaptive monitoring. AMBIO: A Journal of the Human Environment 43:3-18. https://doi.org/10.1007/s13280-014-0558-z

Franzo, A., A. Asioli, C. Roscioli, L. Patrolecco, M. Bazzaro, P. Del Negro, and T. Cibic. 2019. Influence of natural and anthropogenic disturbances on foraminifera and free-living nematodes in four lagoons of the Po delta system. Estuarine, Coastal and Shelf Science 220:99-110. https://doi.org/10.1016/j.ecss.2019.02.039

Friedl, G., and A. Wüest. 2002. Disrupting biogeochemical cycles - consequences of damming. Aquatic Sciences 64:55-65. https://doi.org/10.1007/s00027-002-8054-0

Garmestani, A. S., C. R. Allen, and L. Gunderson. 2009. Panarchy: discontinuities reveal similarities in the dynamic system structure of ecological and social systems. Ecology and Society 14(1):15. https://doi.org/10.5751/ES-02744-140115

Garmestani, A. S., D. Twidwell, D. G. Angeler, S. M. Sundstrom, C. Barichievy, B. C. Chaffin, T. Eason, N. Graham, D. Granholm, L. Gunderson, M. Knutson, K. L. Nash, R. J. Nelson, M. Nyström, T. L. Spanbauer, C. A. Stow, and C. R. Allen. 2020. Panarchy: opportunities and challenges for ecosystem management. Frontiers in Ecology and the Environment 18 (10):576-583. https://doi.org/10.1002/fee.2264

Gunderson, L. H., and C. S. Holling. 2002. Panarchy: understanding transformations in human and natural systems. Island Press, Washington, D.C., USA.

Gruner, D. S., J. E. Smith, E. W. Seabloom, S. A. Sandin, J. T. Ngai, H. Hillebrand, W. S. Harpole, J. J. Elser, E. E. Cleland, M. E. S. Bracken, E. T. Borer, and B. M. Bolker. 2008. A cross-system synthesis of consumer and nutrient resource control on producer biomass. Ecology Letters 11(7):740-755. https://doi.org/10.1111/j.1461-0248.2008.01192.x

Hasselrot, B., and H. Hultberg. 1984. Liming of acidified Swedish lakes and streams and its consequences for aquatic ecosystems. Fisheries 9(1):4-9. https://doi.org/10.1577/1548-8446(1984)009%3C0004:LOASLA%3E2.0.CO;2

Henriksson, L., and Y. W. Brodin, editors. 1995. Liming of acidified surface waters: a Swedish synthesis.Springer-Verlag, Berlin, Germany.

Hindar, A., S. Rognerud, and T. E. Eriksen. 2013. Kvantifisering av kalkrester og metaller i sedimentet etter flere års kalking av 17 innsjøer. NIVA RAPPORT L.NR. 6526-2013. Norsk institutt for vannforskning, Oslo, Norway. ISBN 978-82-577-6261-2. [online] URL: https://niva.brage.unit.no/niva-xmlui/bitstream/handle/11250/216359/6526.pdf?sequence=1

Hindar, A., and L. B. Skancke. 2015. Vannkjemisk utvikling i innsjøer i Buskerud, Telemark og Aust-Agder de 9-12 første årene etter avsluttet kalking. NIVA RAPPORT L.NR. 6874-2015. ISBN 978-82-577-6609-2. Norsk institutt for vannforskning, Oslo, Norway. [online] URL: https://niva.brage.unit.no/niva-xmlui/bitstream/handle/11250/285785/6874-2015_72dpi.pdf?sequence=3&isAllowed=y

Holling, C. S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecological Monographs 62(4):447-502. https://doi.org/10.2307/2937313

Holling, C. S. 2001. Understanding the complexity of economic, ecological, and social systems. Ecosystems 4:390-405. https://doi.org/10.1007/s10021-001-0101-5

Holling, C. S., and G. K. Meffe. 1996. Command and control and the pathology of natural resource management. Conservation Biology 10(2):328-337. https://doi.org/10.1046/j.1523-1739.1996.10020328.x

Hu, Q., and Huser, B. J. 2014. Anthropogenic oligotrophication via liming: long-term phosphorus trends in acidified, limed, and neutral reference lakes in Sweden. Ambio 43:104-112. https://doi.org/10.1007/s13280-014-0573-0

Huser, B. J., M. N. Futter, R. Wang, and J. Fölster. 2018. Persistent and widespread long-term phosphorus declines in Boreal lakes in Sweden. Science of the Total Environment 613:240-249. https://doi.org/10.1016/j.scitotenv.2017.09.067

Lau, D. C. P., T. Vrede, and W. Goedkoop. 2017. Lake responses to long-term disturbances and management practices. Freshwater Biology 62(4):792-806. https://doi.org/10.1111/fwb.12902

Legendre, P., and O. Gauthier. 2014. Statistical methods for temporal and space-time analysis of community composition data. Proceedings of the Royal Society B: Biological Sciences 281 (1778):20132728. https://doi.org/10.1098/rspb.2013.2728

Legendre, P., and L. F. Legendre. 2012. Numerical ecology. Third edition. Elsevier, Amsterdam, The Netherlands.

Lydersen, E., S. Löfgren, and R. T. Arnesen. 2002. Metals in Scandinavian surface waters: effects of acidification, liming, and potential reacidification. Critical Reviews in Environmental Science and Technology 32(2-3):73-295. https://doi.org/10.1080/10643380290813453

Mant, R. C., D. L. Jones, B. Reynolds, S. J. Ormerod, and A. S. Pullin. 2013. A systematic review of the effectiveness of liming to mitigate impacts of river acidification on fish and macro-invertebrates. Environmental Pollution 179:285-293. https://doi.org/10.1016/j.envpol.2013.04.019

McKie, B., Z. Petrin, and B. Malmqvist. 2006. Mitigation or disturbance? Effects of liming on macroinvertebrate assemblage structure and leaf-litter decomposition in the humic streams of northern Sweden. Journal of Applied Ecology 43(4):780-791. https://doi.org/10.1111/j.1365-2664.2006.01196.x

Mori, A. S. 2011. Ecosystem management based on natural disturbances: hierarchical context and non-equilibrium paradigm. Journal of Applied Ecology 48(2):280-292. https://doi.org/10.1111/j.1365-2664.2010.01956.x

Nyberg, P., M. Appelberg, and E. Degerman. 1986. Effects of liming on crayfish and fish in Sweden. Pages 1723-1741 in H.C. Martin, editor. Acidic precipitation. Springer, Dordrecht, The Netherlands. https://doi.org/10.1007/978-94-009-3385-9_172

Ormerod, S. J., and I. Durance. 2009. Restoration and recovery from acidification in upland Welsh streams over 25 years. Journal of Applied Ecology 46(1):164-174. https://doi.org/10.1111/j.1365-2664.2008.01587.x

Pelletier, M. C., J. Ebersole, K. Mulvaney, B. Rashleigh, M. N. Gutierrez, M. Chintala, A. Kuhn, M. Molina, M. Bagley, and C. Lane. 2020. Resilience of aquatic systems: review and management implications. Aquatic Sciences 82(2):1-44. https://doi.org/10.1007/s00027-020-00717-z

Pope, K. L., C. R. Allen, and D. G. Angeler. 2014. Fishing for resilience. Transactions of the American Fisheries Society 143 (2):467-478. https://doi.org/10.1080/00028487.2014.880735

Power, M. E. 1992. Top-down and bottom-up forces in food webs: do plants have primacy. Ecology 73(3):733-746. https://doi.org/10.2307/1940153

Sandøy, S., and A. J. Romunstad. 1995. Liming of acidified lakes and rivers in Norway: an attempt to preserve and restore biological diversity in the acidified regions. Water, Air, and Soil Pollution 85(2):997-1002. https://doi.org/10.1007/BF00476960

Schindler, D. W. 1988. Effects of acid rain on freshwater ecosystems. Science 239(4836):149-157. https://doi.org/10.1126/science.239.4836.149

Sjöstedt, C., C. Andrén, J. Fölster, and J. P. Gustafsson. 2013. Modelling of pH and inorganic aluminium after termination of liming in 3000 Swedish lakes. Applied Geochemistry 35:221-229. https://doi.org/10.1016/j.apgeochem.2013.04.014

Soria, M., C. Gutiérrez-Cánovas, N. Bonada, R. Acosta, P. Rodríguez-Lozano, P. Fortuño, G. Burgazzi, D. Vinyoles, F. Gallart, J. Latron, P. Llorens, N. Prat, N. Cid, and R. Arlinghaus. 2020. Natural disturbances can produce misleading bioassessment results: identifying metrics to detect anthropogenic impacts in intermittent rivers. Journal of Applied Ecology 57(2):283-295. https://doi.org/10.1111/1365-2664.13538

Sorrano, P. A., K. S. Cheruvelil, E. G. Bissell, M. T. Bremigan, J. A. Downing, C. E. Fergus, C. T. Filstrup, E. N. Henry, N. R. Lottig, E. H. Stanley, C. A. Stow, P. Tan, T. Wagner, and K. E. Webster. 2014. Cross-scale interactions: quantifying multi-scaled cause-effect relationships in macrosystems. Frontiers in Ecology and the Environment 12(1):65-73. https://doi.org/10.1890/120366

Stoddard, J. L., D. P. Larsen, C. P. Hawkins, R. K. Johnson, and R. H. Norris. 2006. Setting expectations for the ecological condition of streams: the concept of reference condition. Ecological Applications 16(4):1267-1276. https://doi.org/10.1890/1051-0761(2006)016[1267:SEFTEC]2.0.CO;2

Strahler, A. N. 1964. Quantitative geomorphology of drainage basins and channel networks. Section 4-2 in V.T. Chow, editor. Handbook of applied hydrology: a compendium of water-resources technology. McGraw-Hill, New York, New York, USA.

Sundstrom, S. M., and C. R. Allen. 2019. The adaptive cycle: more than a metaphor. Ecological Complexity 39:100767. https://doi.org/10.1016/j.ecocom.2019.100767

Wilcox, B. A., A. A. Aguirre, N. De Paula, B. Siriaroonrat, and P. Echaubard. 2019. Operationalizing one health employing social-ecological systems theory: lessons from the Greater Mekong Sub-region. Frontiers in Public Health 7:85. https://doi.org/10.3389/fpubh.2019.00085

Wright, R. F., T. Dale, E. T. Gjessing, G. R. Hendrey, A. Henriksen, M. Johannessen, and I. P. Muniz. 1976. Impact of acid precipitation on freshwater ecosystems in Norway. Water, Air, and Soil Pollution 6:483-499. https://doi.org/10.1007/BF00182887

Yan, N. D., B. Leung, B. Keller, S. E. Arnott, J. M. Gunn, and G. G. Raddum. 2003. Developing conceptual frameworks for the recovery of aquatic biota from acidification. AMBIO: A Journal of the Human Environment 32(3):165-169. https://doi.org/10.1579/0044-7447-32.3.165

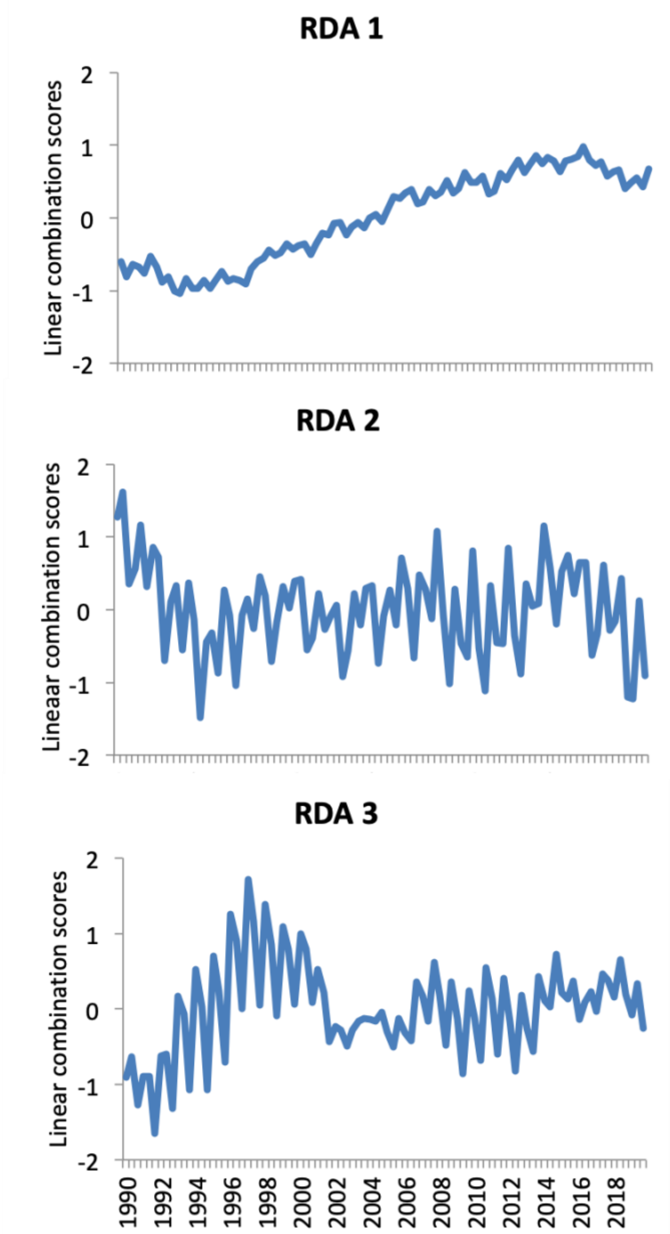
Appendix 1 Water quality of lakes and their location in Sweden. Shown are geographical positions and morphological characteristics of study lakes. Shown are also features of liming management in individual lakes. Abbreviations: na, not applicable

	SMHI X SMHIY	Lake area (km^2)	Max. Depth (m)	Liming period	Liming events	Delivery	Liming quantity (metric tons; means/SD
Reference lakes							
Allgjuttern	642489 151724	0.19	40.70	na	na	na	na
Fiolen	633025 142267	1.65	10.50	na	na	na	na
Stora Envättern	655587 158869	0.38	11.20	na	na	na	na
St Skärsjön	628606 133205	0.31	11.50	na	na	na	na
Limed lakes							
Ejgdesjön	653737 125017	0.83	28.60	1982-2018	16	Boat	60/32
Gyslättasjön	633209 141991	0.33	9.80	1985-2019	32	Helicopter	11/7
Stengårdshultasjön	638317 138010	4.98	26.80	1981-2019	23	Boat	235/325
Stora Härsjön	640364 129240	2.57	42.00	1977-2011	13	Boat	294/145

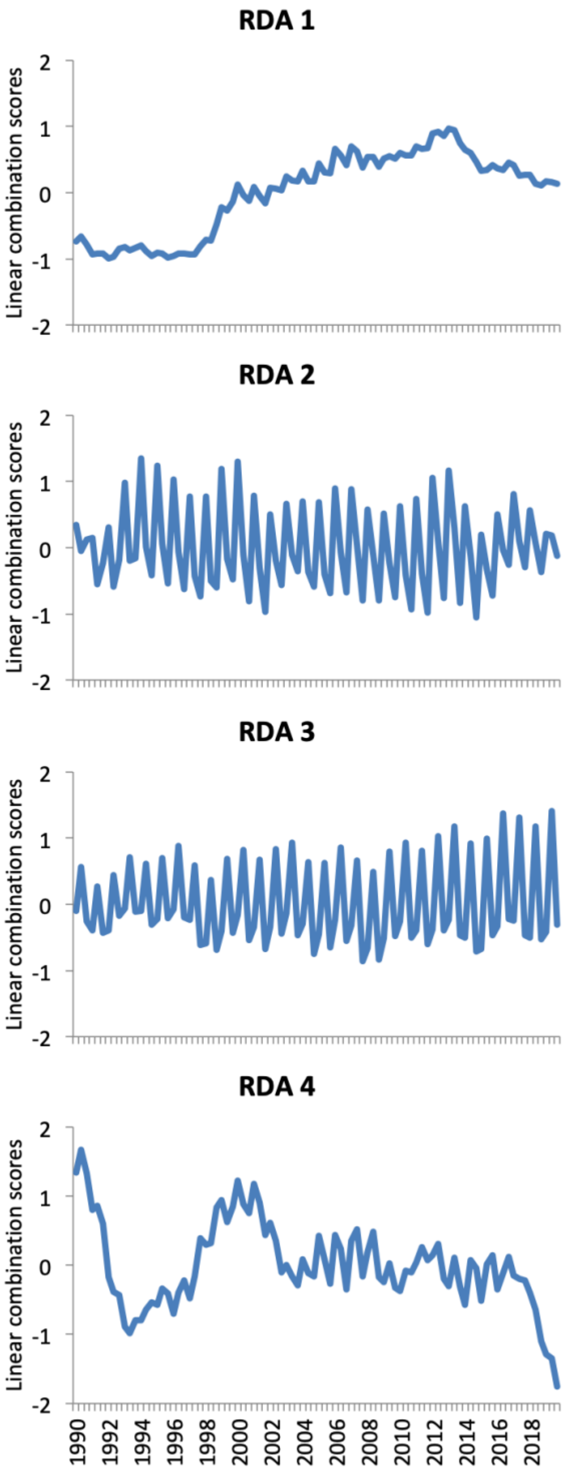
Appendix 2 Linear combination score plots of individual lakes

Reference lakes

Allgjuttern

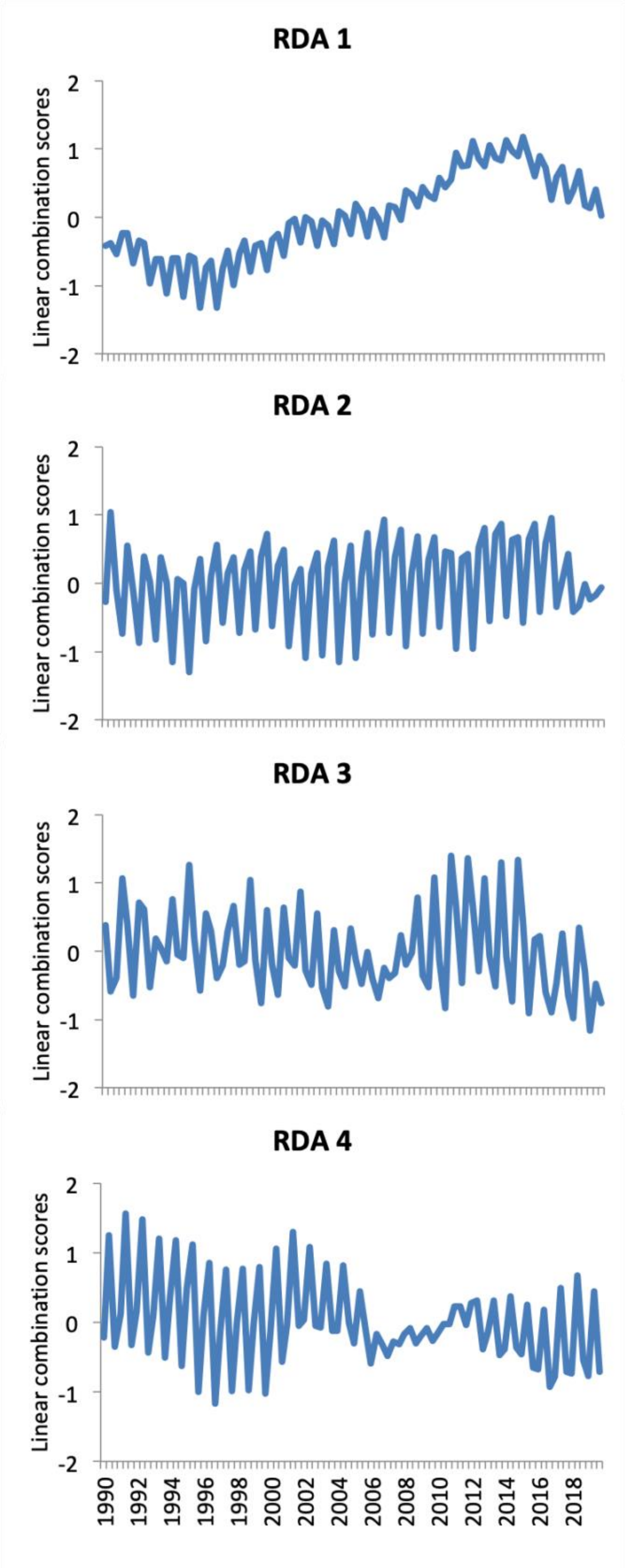


Fiolen

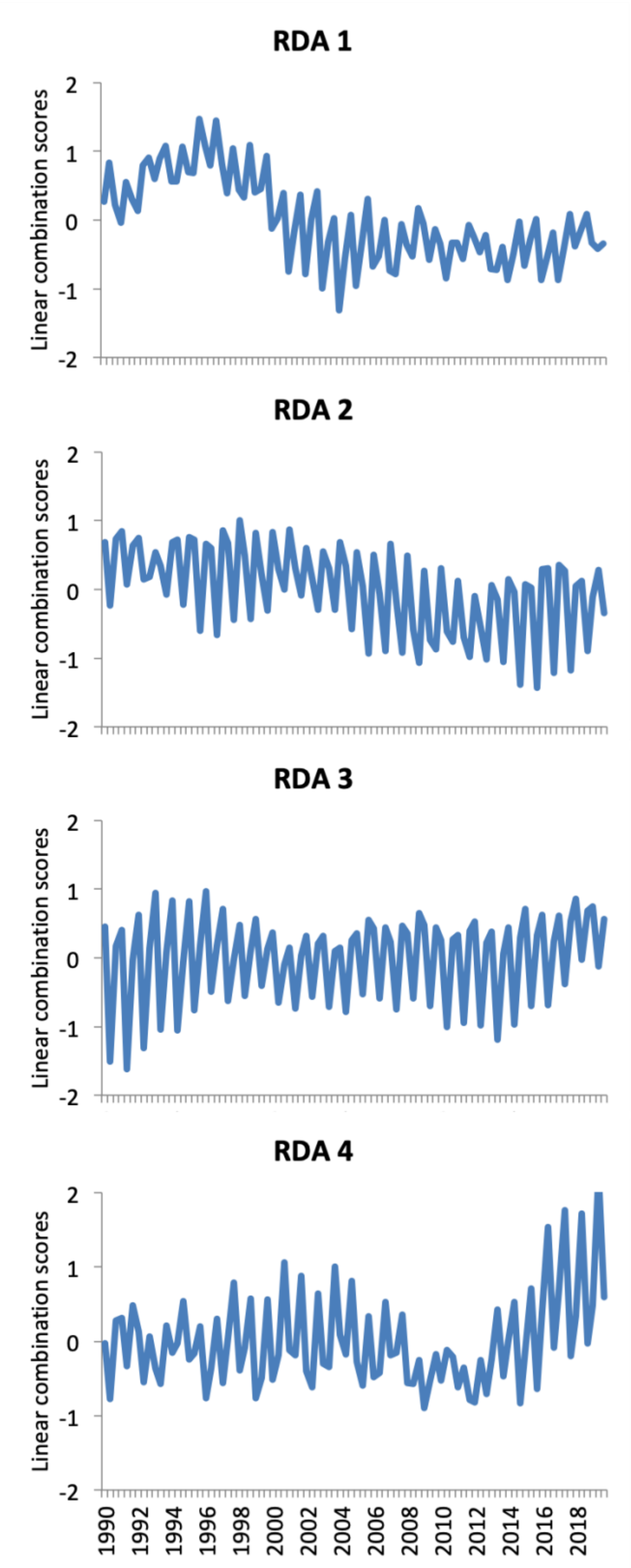


RDA 1
RDA 2
RDA 3
RDA 4
Linear combination scores
2
1
0
-1
-2
1990
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
2016
2018

Stora Envättern

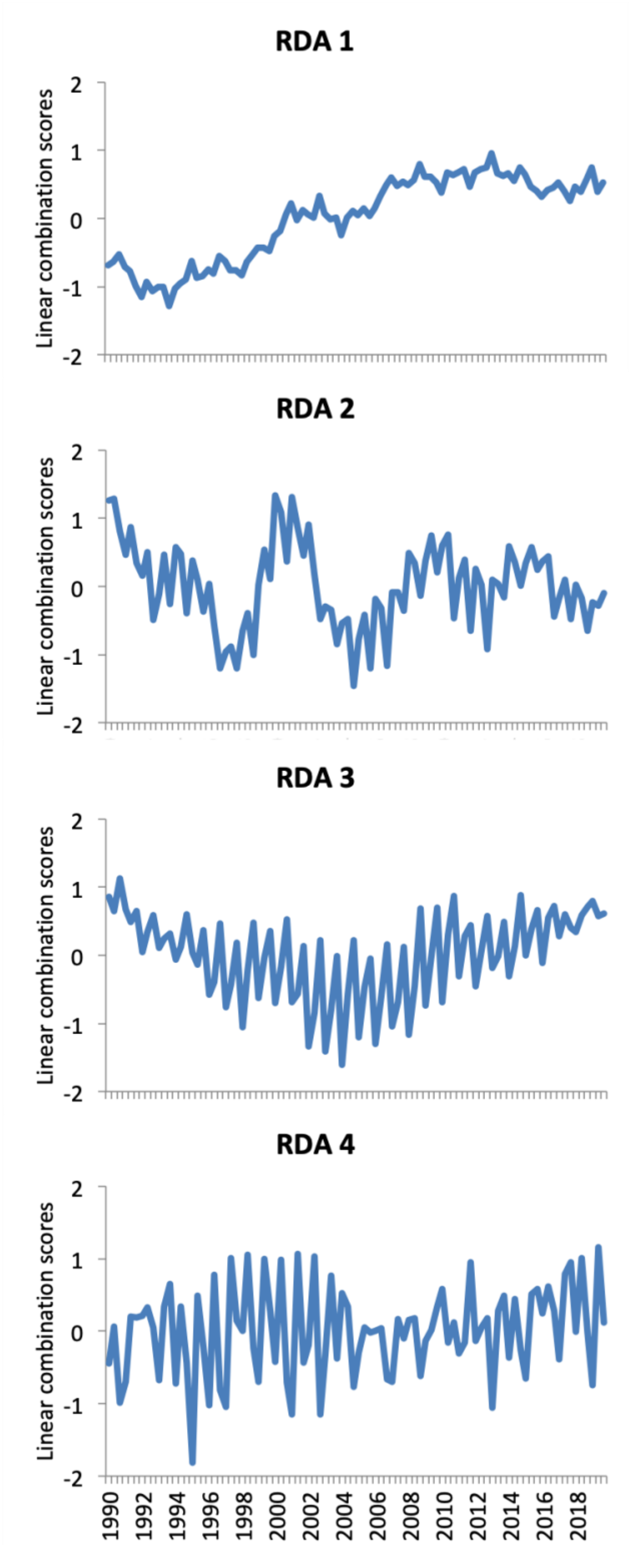


Stora Skärsjön

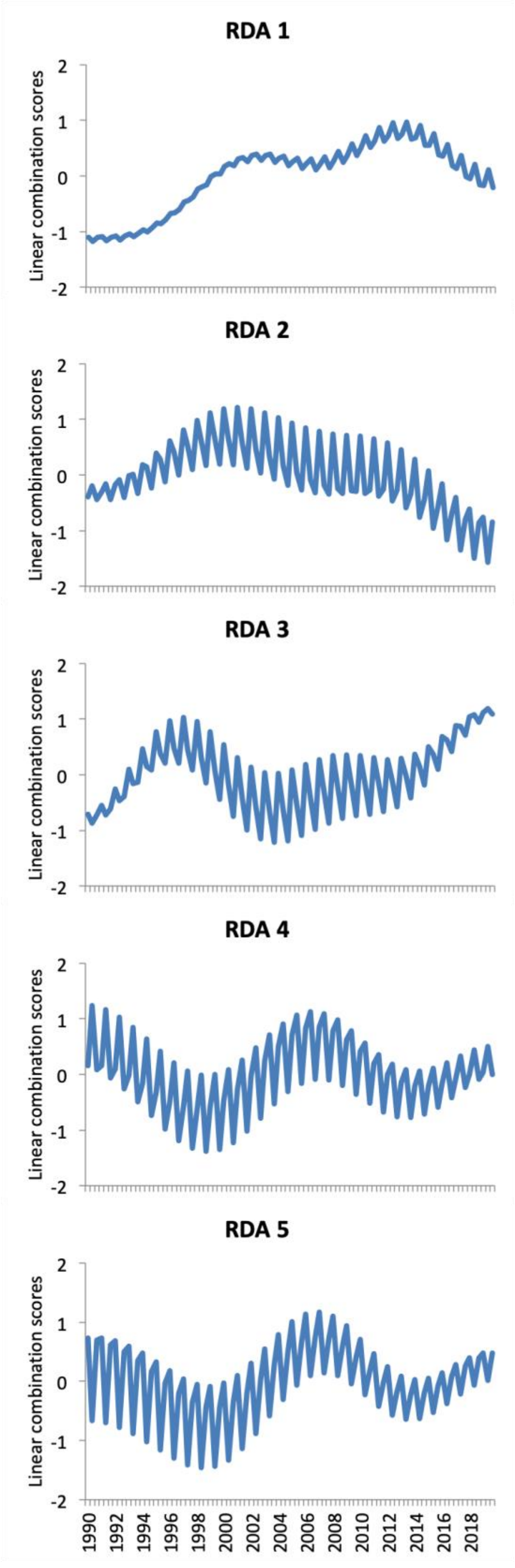


Limed lakes

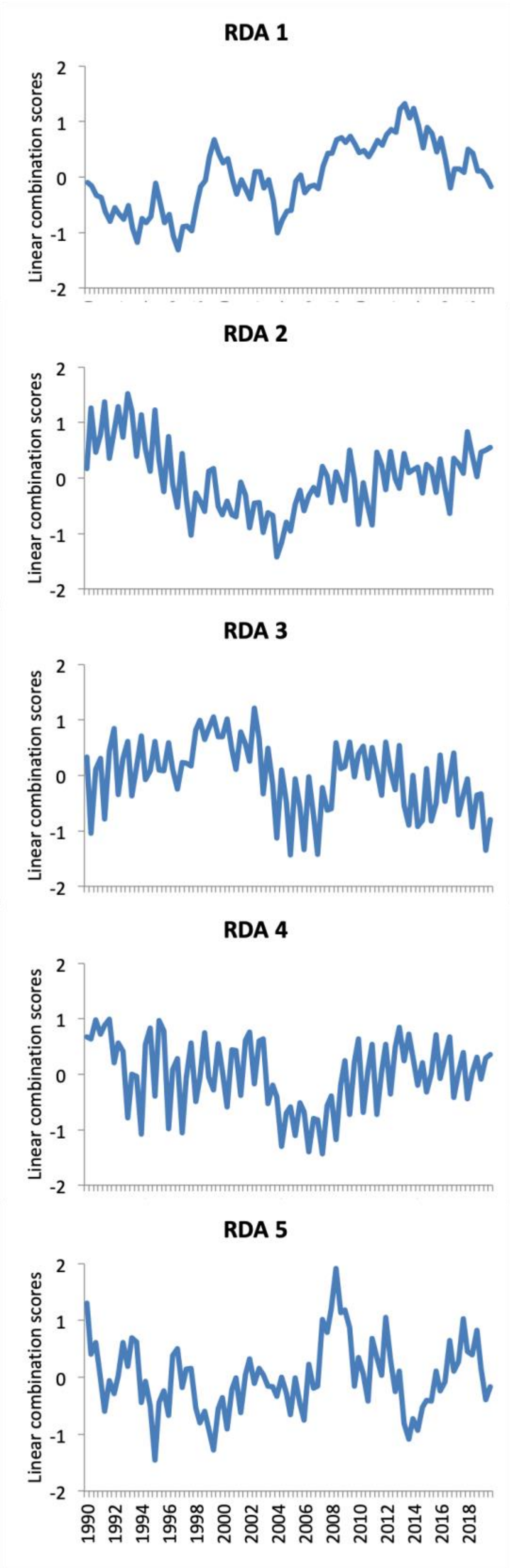
Eigdesjön



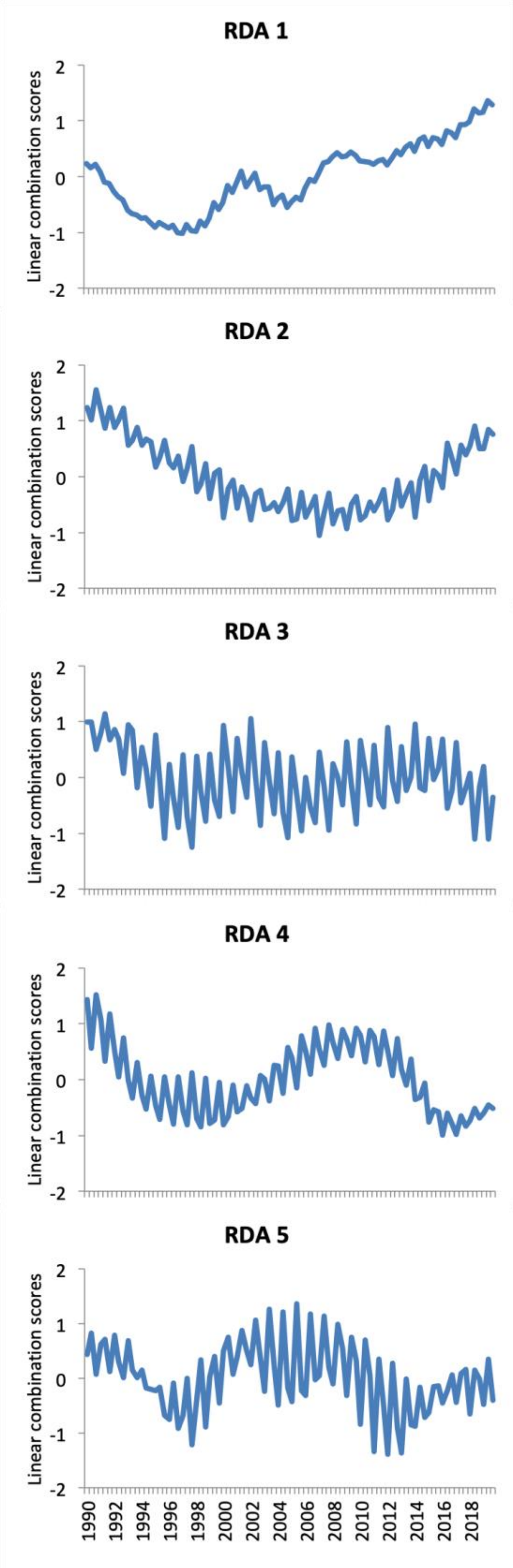
Gyslättasjön



Stengårdshultasjön



Stora Härsjön



Appendix 3 RScript

#load packages
library(vegan)
library(adespatial)
library(tidyverse)
library(reshape)
library(ade4)
library(readxl)

##get quickMEM function (replacement of old quickPCNM function)
source ('http://www.davidzeleny.net/anadat-r/doku.php/en:numecolr:sr.value?do=export_code&codeblock=1')
source ('http://www.davidzeleny.net/anadat-r/doku.php/en:numecolr:sr.value?do=export_code&codeblock=1')
source ('https://raw.githubusercontent.com/zdealveindy/anadat-r/master/scripts/NumEcolR2/quickMEM.R')
source ('https://raw.githubusercontent.com/zdealveindy/anadat-r/master/scripts/NumEcolR2/scalog.R')

#Lakes data
#Time 90 steps, 30 years with 3 steps per year (1990-2019); this time vector is use for the individual time series models of all lakes
Timesteps <- read_excel("file_location_on_disk.xlsx", sheet = "Time vector 90 steps")
#Lakes: Example of data import with explanatroy (water quality) variables
Lake <- read_excel("file_location_on_disk.xlsx.xlsx", sheet = "Lake_name")

#Standardization of water quality variables
Lake_scaled <- scale(Lake, center = TRUE, scale = TRUE)

TIME SERIES MODELING
#creating AEM variables
out <- aem.time(90, moran = TRUE)

#AEM-RDA models using quickMEM function
modelLake <- quickMEM(Lake_scaled, Timesteps, myspat=out$aem[,1:70], alpha=0.05, perm.max=999, detrend = FALSE)

#Extract lc scores for significant RDA axes; note: choices=1:X refers to significant RDA axes in the models, where X stands for the number of significant axes
fitted.scores.Lake <- data.frame(scores(modelLake$RDA,display="lc",choices=1:X))

#LINEAR MODEL
#ANOVA for significant RDA axes, folllowing https://rcompanion.org/handbook/I_09.html
rmANOVA_RDA1 <- read_excel("file_(significant_axes)_import_from_file_location_on_disk.xlsx", sheet = "rm-ANOVA RDA1")
rmANOVA_RDA2 <- read_excel("file_(significant_axes)_import_from_file_location_on_disk.xlsx", sheet = "rm-ANOVA RDA2")
rmANOVA_RDA3 <- read_excel("file_(significant_axes)_import_from_file_location_on_disk.xlsx", sheet = "rm-ANOVA RDA3")
rmANOVA_RDA4 <- read_excel("file_(significant_axes)_import_from_file_location_on_disk.xlsx", sheet = "rm-ANOVA RDA4")

library(nlme)
if(!require(psych)){install.packages("psych")}
if(!require(nlme)){install.packages("nlme")}
if(!require(car)){install.packages("car")}
if(!require(multcompView)){install.packages("multcompView")}
if(!require(lsmeans)){install.packages("lsmeans")}
if(!require(ggplot2)){install.packages("ggplot2")}
if(!require(rcompanion)){install.packages("rcompanion")}

```
#accounting for temporal autocorrelation structure; finds value for corAR1 function
#RDA1
model.RDA1 = gls(RDA1 ~ Type + Time + Type*Time,data=rmANOVA_RDA1)
ACF(model.RDA1, form = ~ Time | Lake)
#RDA2
model.RDA2 = gls(RDA2 ~ Type + Time + Type*Time, data=rmANOVA_RDA2)
ACF(model.RDA2,form = ~ Time | Lake)
#RDA3
model.RDA3 = gls(RDA3 ~ Type + Time + Type*Time, data=rmANOVA_RDA3)
ACF(model.RDA3, form = ~ Time | Lake)
#RDA4
model.RDA4 = gls(RDA4 ~ Type + Time + Type*Time, data=rmANOVA_RDA4)
ACF(model.RDA4,form = ~ Time | Lake)

#Lake (i.e. replicates) treated as random variable, using lme function; without random effects the gls function can be used
model.RDA1 = lme(RDA1 ~ Type + Time + Type*Time, random = ~1|Lake, correlation = corAR1(form = ~ Time | Lake, value = 0.8210608), data=rmANOVA_RDA1, method="REML")
model.RDA2 = lme(RDA2 ~ Type + Time + Type*Time, random = ~1|Lake, correlation = corAR1(form = ~ Time | Lake, value = 0.17883266), data=rmANOVA_RDA2, method="REML")
model.RDA3 = lme(RDA3 ~ Type + Time + Type*Time, random = ~1|Lake, correlation = corAR1(form = ~ Time | Lake, value = 0.059594695), data=rmANOVA_RDA3, method="REML")
model.RDA4 = lme(RDA4 ~ Type + Time + Type*Time, random = ~1|Lake, correlation = corAR1(form = ~ Time | Lake, value = 0.0328), data=rmANOVA_RDA4, method="REML")

#car package not working without loading data.table package
install.packages("data.table")
library(data.table)
install.packages("car")
library(car)

#display ANOVA tables
Anova(model.RDA1)
Anova(model.RDA2)
Anova(model.RDA3)
Anova(model.RDA4)

Anova(model.RDA1.gls)
Anova(model.RDA2.gls)
Anova(model.RDA3.gls)
Anova(model.RDA4.gls)


# adj. R2 of RDA axes
RsquareAdj(modelLake)$r.squared
coef(modelLake)

##CORRELATION ANALYSES
#All analyses carried out at: https://www.socscistatistics.com/tests/spearman/default2.aspx
```