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Research article

Panarchy suggests why management mitigates rather than restores ecosystems from anthropogenic impact

David G. Angeler[a,b,c,d,*], Ran Hur[e]

[a] Swedish University of Agricultural Sciences, Department of Aquatic Sciences and Assessment, Box 7050, SE-750 07, Uppsala, Sweden
[b] School of Natural Resources, University of Nebraska—Lincoln, Lincoln, NE, 68583, USA
[c] The PRODEO Institute, San Francisco, CA, USA
[d] IMPACT, The Institute for Mental and Physical Health and Clinical Translation, Deakin University, Geelong, Victoria, Australia
[e] Uppsala University, Department of Earth Sciences, Uppsala, Sweden

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ABSTRACT

Panarchy, a model of dynamic systems change at multiple, interconnected spatiotemporal scales, allows assessing whether management influences ecological processes and resilience. We assessed whether liming, a management action to counteract anthropogenic acidification, influenced scale-specific temporal fluctuation frequencies of benthic invertebrates and phytoplankton assemblages in lakes. We also tested whether these fluctuations correlated with proxies of liming (Ca:Mg ratios) to quantify scale-specific management effects. Using an ecosystem experiment and monitoring data, time series analyses (1998–2019) revealed significant multiscale temporal (and thus panarchy) structure for littoral invertebrates across limed and reference lakes. Such patterns were inconsistent for sublittoral invertebrates and phytoplankton. When significant panarchy structure was found, Ca:Mg ratios correlated with only a few of the identified temporal fluctuation frequencies across limed and reference lakes. This suggests that liming effects become diluted in the managed lakes. The lack of manifestations of liming across the independent temporal fluctuation patterns suggest that this lake management form fails to create and enforce cross-scale interactions, a crucial component of ecological resilience. This interpretation supports liming as a mitigation effort rather than a tool to restore acidified lakes to a self-organizing system equivalent of circumneutral references.

1. Introduction

The increasing demand of food and fiber for a growing human population puts unprecedented pressure on ecosystem management and restoration. The provisioning of ecosystem services can often only be sustained through costly management under system conditions that qualify as “coerced regimes” (Angeler et al., 2020). Coerced regimes are ecosystem regimes that fail to emulate and rather fundamentally alter natural disturbance regimes (Mori, 2011). Coerced regimes therefore only mimic and do not create self-organizing systems with desirable ecosystem services for humans. Coerced regimes are ubiquitous and demonstrate that managed systems can flip or revert to an undesired regime with insufficient ecosystem services once management is ceased. Cases of coerced regimes are limed lakes reverting to acidified conditions (Clair and Hindar, 2005), grasslands succumbing to tree species invasions (Garmestani et al., 2020), the current Holocene climate flipping into a “Hothouse Earth” regime (Steffen et al., 2018), and patients with mental disorders developing full-blown symptoms of mania and depression upon cessation of medication (Angeler et al., 2018).

Ecological resilience (*sensu* Holling, 1973) allows for studying patterns and processes in complex systems of people and nature and may therefore be useful for assessing biophysical mechanisms, which are not well understood, that shape coerced regimes and influence management efficiency. Studying coerced regimes mechanistically is especially important given that complex systems of people and nature can shift between alternative system regimes (Scheffer, 1998; Beisner et al., 2003), which often impact ecosystem service provisioning negatively (Janssen et al., 2021).

Panarchy, a branch of complexity science rooted in ecological resilience, has shown promise for managing ecological challenges such as large-scale terrestrial transitions in the Great Plains of North America (Garmestani et al., 2020), lake acidification (Angeler et al., 2021),

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[*] Corresponding author. Swedish University of Agricultural Sciences, Department of Aquatic Sciences and Assessment, Box 7050, SE-750 07, Uppsala, Sweden.
E-mail address: david.angeler@slu.se (D.G. Angeler).

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ecosystem service provision (Winkler et al., 2022) and invasive species (Mrnak et al., 2022). Panarchy accounts for several features that influence the complexity of ecosystems and other systems of people and nature, such as their multiscale spatiotemporal organization, dynamic system structure at each scale (portrayed as nested adaptive cycles with four inherent phases: conservation, release, reorganization, growth), the interconnectedness of these scales and the ability of ecosystems to exist in alternative regimes, such as lakes in clear-water and turbid regimes (Gunderson and Holling, 2002; Allen et al., 2014). Panarchy theory therefore captures the cross-scale structure posited by hierarchy theory (Allen and Starr, 1982) while acknowledging the flow of matter and energy from higher to lower scales ("top-down") and vice versa ("bottom-up"), as is the case in food webs (e.g., Power, 1992).

Consider the example of a managed lake panarchy related to species invasions (Mrnak et al., 2022): In the conservation phase, inland fisheries invaded by rainbow smelt (*Osmerus mordax*) operate in a specific social-ecological systems regime in which nutrients, biomass and dynamic species interactions from phytoplankton (lowest panarchy level) to fish (highest level) influence ecosystem structure and function. In the reorganization phase ecosystem structure and function can be deliberately changed through management of rainbow smelt (e.g., reducing population stock), which may cause cascading effects to lower trophic levels. In the following post-disturbance reorganization phase, the efficacy of eradication and control efforts can be evaluated, providing learning opportunities about the failures and successes of inland fishery management. Finally, in the growth phase, ecosystem processes are fostered, stabilizing the inland fishery system. Whether fisheries return either to conditions before management action or undergo fundamental reorganization (regime shift) as a result of it can be evaluated in the reorganization phase.

This example demonstrates that assessing panarchy can be useful because the number of scales present in a system as well as ecological patterns and processes operating and manifesting dynamically within and across scales provides insight into resilience (e.g., Allen et al., 2005), and potentially management efficiency.

Since the introduction of panarchy (Gunderson and Holling, 2002), the concept has shown rapid uptake by the scientific community across different fields due to its promise for managing social-ecological challenges on a swiftly changing planet (Gunderson et al., 2022). Despite the promise of panarchy, quantitative analyses are sparse (Rocha et al., 2022), due to data requirements and the need of modeling tools that allow integrative assessment of the theory's tenets. In this study, we aimed to quantify panarchy in lakes that were limed as a management action designed to counteract the effects of anthropogenic acidification in aquatic ecosystems that occurred in the industrial age of the last century (e.g., Wright et al., 1976; Schindler, 1988; Henriksson and Brodin, 1995). Specifically, the application of limestone powder or sand aimed at mitigating low pH and aluminium toxicity and facilitating the protection and recovery of acid-sensitive biota such as fish, crayfish and freshwater mussels, and maintenance of recreational fishing and aquaculture (Appelberg and Svensson, 2001; SEPA, 2007).

Assessing panarchy in limed lakes is useful because these lakes comprise coerced regimes (Angeler et al., 2020; Heino et al., 2021). Ecologically, this was manifested in few positive liming outcomes (Eriksson et al., 1983; Hasselrot and Hultberg, 1984; Nyberg et al., 1986) where overall liming effects are equivocal and confounded by historical, abiotic, and ecological factors (Clair and Hindar, 2005; Ormerod and Durance, 2009; Mant et al., 2013). These factors include episodic water chemistry fluctuations due to recurrent re-acidification and liming, limited dispersal of biota, habitat conditions, and altered food webs (Yan et al., 2003; Binks et al., 2005; Lau et al., 2017). That liming fits the notion of a coerced regime is further supported by ecological communities being markedly different between acidified and circumneutral reference lakes (Angeler and Goedkoop, 2010). The limited long-term efficiency of liming is also manifested in lakes reverting to pervasive acidified conditions upon the cessation of liming (Clair and Hindar, 2005). Such a return to acidified conditions has been specifically observed in the abiotic environment (Lydersen et al., 2002; Hindar et al., 2013; Hindar and Skancke, 2015). This finding is supported by geochemical modelling of pH and aluminium concentrations in a large number of Swedish lakes (Sjöstedt et al., 2013). Also, internal phosphorus cycling and the susceptibility of limed lakes to re-acidification events limits their restoration (Dickson et al., 1995; Hu and Huser, 2014).

We used time series modeling of phytoplankton and littoral and sublittoral invertebrates in limed lakes and unmanaged minimally disturbed reference lakes (sensu Stoddard et al., 2006) to test the premises of panarchy theory that communities fluctuated at independent temporal frequencies (or scales) in limed and reference lakes. Our approach allowed us to test our first hypothesis that community dynamics in managed and unmanaged lakes organized according to panarchy theory's tenet of ecological dynamics unfolding at distinct spatiotemporal scales. Because liming is considered a significant ecosystem disturbance (Bishop et al., 2001; McKie et al., 2006), we further hypothesized (second hypothesis) that liming altered the natural patterns of temporal community fluctuation frequencies and thus the biotic panarchy structure of limed lakes relative to reference lakes. Our third hypothesis related to cross-scale manifestations of liming that may provide insight into management efficacy. Given that liming comprises a coerced regime that fails to create self-organization, we posited that liming effects became diluted in the panarchy across scales. This dilution would be evident in liming effects manifesting at a few temporal fluctuation frequencies (scales) revealed by the time series models. This hypothesis was based on cross-scale interactions being considered important for contributing to ecosystem resilience (Allen et al., 2005); that is, resilience is expected to increase when ecological key characteristics are redundant across scales. We used Ca:Mg ratios as a liming management proxy, to test for redundancies across the temporal fluctuation frequencies detected by the time series models. Our results complement a previous assessment of panarchy in the physicochemical environment of limed lakes, which was inconclusive about the cross-scale dilution of liming effects (Angeler et al., 2021).

Our approach allows for advancing panarchy theory by mapping empirical results of complex system dynamics through time (Twidwell et al., 2022). Visualizing panarchy based on empirical analyses makes the management effects of liming on the complex systems structure of lakes more tractable, which facilitates an exploration of the implication of management for resilience and coerced regimes of these systems (Pelletier et al., 2020; Heino et al., 2021).

2. Methods

2.1. Study lakes

We used environmental monitoring data and an ecosystem experiment approach (Carpenter, 1998) for studying lake management panarchies related to liming. Four circumneutral reference lakes and four limed lakes with the most exhaustive time series data were chosen for our study (Fig. 1; Appendix A). All lakes were located in the boreonemoral ecoregion of southern Sweden. Lake selection avoided confounding effects due to ecoregion-specific abiotic and biotic features of other ecoregions. The limed lakes were integrated in the Swedish national liming program started in 1989 by the Swedish Environmental Protection Agency (Appelberg and Svensson, 2001). Liming was carried out between 1974 and 1985, prior to the start of the program, and consisted of applying limestone powder by helicopter or boat at varying intervals and quantities across lakes (Appendix B). The minimally disturbed reference lakes were chosen to assess the footprints of management on temporal patterns of littoral and sublittoral invertebrates and phytoplankton relative to unmanaged conditions. These reference systems were robust against acidification due to high acid buffering capacity (Fölster et al., 2014).

Fig. 1. Map of Sweden showing location of study lakes (limed, circles; reference, squares). 1, Ejgdesjön; 2, Stora Härsjön; 3, Stengårdshjultasjön; 4, Gyslättasjön; 5, Allgjuttern; 6, Fiolen; 7, Stora Skärsjön; 8, Stora Envättern.

2.2. Sampling procedures

The physicochemical environment was analyzed comprehensively in previous research (Angeler and Goedkoop, 2010; Angeler et al., 2017), including a panarchy study (Angeler et al., 2021). We therefore used for this study a selection of physicochemical variables related to acidification status (pH, alkalinity, Ca concentrations), nutrients (total P, total organic carbon (TOC)) and water temperature to support the biological analysis with a description and visual presentation of the abiotic environment (Fig. 2).

Mid-lake water samples were taken for physicochemical variables and phytoplankton in August between 1998 and 2019 (21 years) in the epilimnion (0–2 m) with a Ruttner sampler. Samples for physicochemical analyses were kept cool during transport to the laboratory. In the laboratory, samples were analyzed for alkalinity, concentrations of Ca, total P and total organic carbon (TOC). Water temperature and 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).

Phytoplankton was sampled by taking a water sample from the epilimnion using a 2-m-long plexiglass tube sampler and preserving it with Lugol's iodine-solution. Phytoplankton counts were made using an inverted light microscope and the modified Utermöhl technique commonly used in the Nordic countries (Olrik et al., 1998). Taxa were identified to the finest taxonomic unit possible (usually species), and species-specific biovolume measures were calculated using a geometric formula (Blomqvist and Herlitz, 1998). Littoral macroinvertebrate samples were collected using standardized kick sampling with a hand net (0.5-mm mesh). A composite sample of five standardized kick samples (20-s duration × 1 m long × *c.* 0.5–1 m depth) was taken from stony, vegetation-free sites in each lake. Sublittoral macroinvertebrates were evaluated from five Ekman samples (247 cm^2) taken within a 50 × 100 m rectangular area at 4–6 m depth. The sublittoral was defined as being located above the late-summer thermocline in stratified lakes. Samples were preserved in 70% ethanol in the field. All macroinvertebrate samples were sorted under 10 × magnification and invertebrates were counted using dissecting and light microscopes. Organisms were identified generally to the species level, except some chironomid larvae and immature Oligochaeta.

2.3. Statistical analysis

Redundancy analysis (RDA) with Asymmetric Eigenvector Maps (AEM) for modelling time (Baho et al., 2015) was used for testing hypothesis 1, that, following the premise of panarchy, there is, hierarchical and dynamic structure in the ecological assemblages. Hierarchical temporal structure can manifest as seasonal (plankton seasonality), interannual (climate-mediated variability; Johnson and Angeler, 2010) and gradually changing (boreal lake oligotrophication; Huser et al., 2018) patterns and combinations of these (Baho et al., 2015). These hierarchical and dynamic patterns can be compared between limed and reference lakes, allowing to test hypothesis 2 that liming disturbances alter temporal fluctuation patterns relative to those in the latter lakes. In addition to the hierarchy aspect of panarchy, the modelling allows for detecting "orthogonal" patterns that can arise from differentiated temporal variability within defined cycles of periodicity in environmental

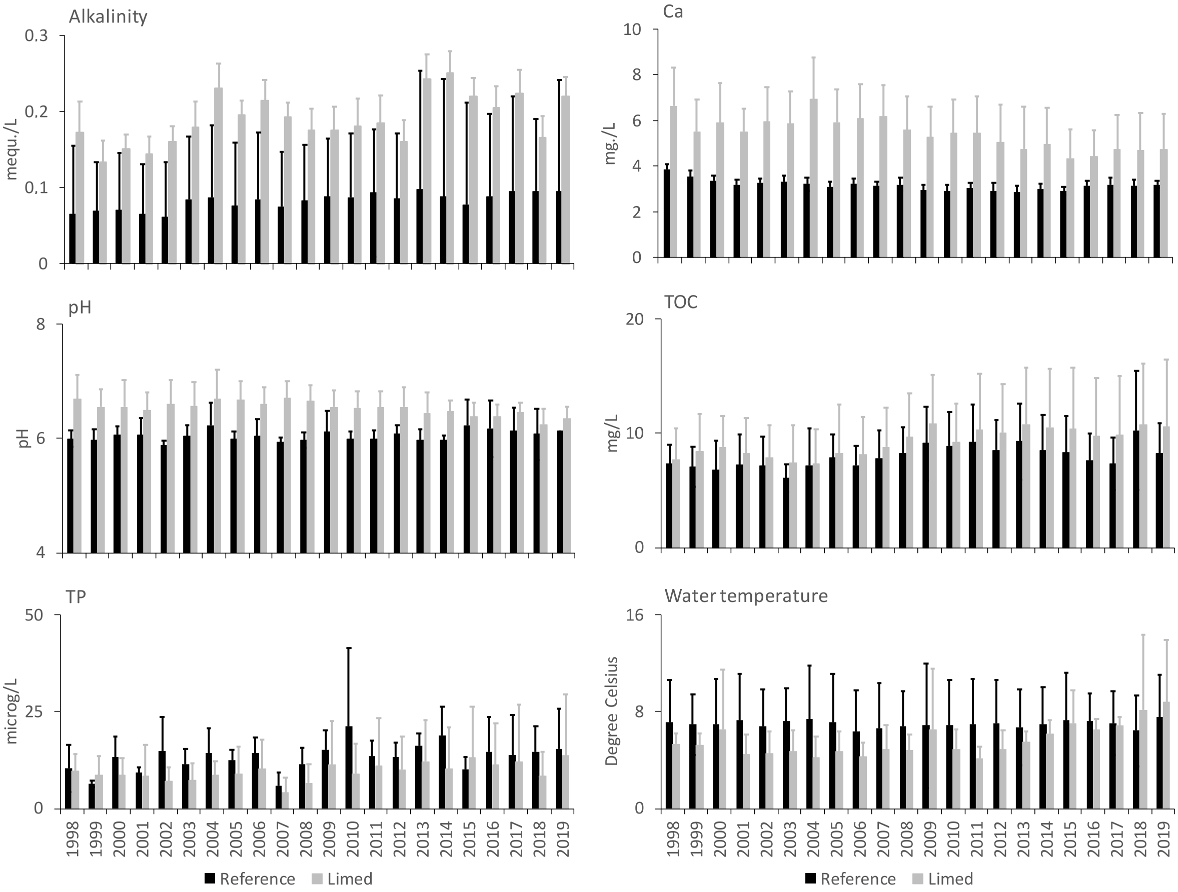

Fig. 2. Temporal patterns of physicochemical variables in reference lakes (black lines) and limed lakes (gray lines). Shown are means ± standard deviations of four lakes per lake category.

dynamics (Legendre and Gauthier, 2014; Angeler et al., 2021). Orthogonality allows for a more nuanced representation of complex ecological dynamics represented by panarchy.

The time series analysis was conducted by first converting the linear time vector consisting of 21 steps between years 1998 and 2019 in a set of independent temporal AEM variables. These AEMs manifest as sine waves ranging from long to short frequencies that allow to model temporal frequency fluctuation patterns. The AEMs also comprise a linear vector, which accounts for monotonic trends in the data (Blanchet et al., 2008; Legendre and Legendre, 2012). These AEMs are subsequently used as explanatory variables in the RDA-AEM time series models. These models were constructed individually for each assemblage (phytoplankton, littoral and sublittoral invertebrates) in each lake, resulting in 24 time series models, using the species x time matrices 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 biota matrices. The modeled temporal patterns that are extracted from the data are collapsed onto significant RDA axes, which are tested through permutation tests. For this study, significance levels were set to obtain significant models at $P \leq 0.05$. These RDA axes are then used to distinguish independent temporal (hierarchical and orthogonal) patterns in the data. The modeled temporal patterns can be visualized using linear combination (Lc) score plots. All biotic matrices were Hellinger-transformed prior to the analysis (Legendre and Gallagher, 2001).

Spearman rank correlation analysis was used to test hypothesis 3, that the strength of liming influences differ between the modeled hierarchical and orthogonal temporal patterns. Specifically, Lc scores of individual RDA axes of each model were tested for correlations with the respective Ca:Mg ratios of each lake. These ratios serve as surrogates of the management regime imposed by liming on the ecological dynamics of the lakes. These ratios show substantial interannual variation in limed lakes and differ from the patterns of unmanaged lakes (Fig. 3). Inference is based on comparing significant correlations ($P \leq 0.05$) between Ca:Mg ratios and monotonic or fluctuating change of the three assemblages within and across lake types (reference, limed). These comparisons therefore allowed assessment of the correlation of Ca:Mg ratios on modeled temporal patterns of each ecological assemblage biased and unbiased by liming. Unbiased ratios refer to Ca:Mg ratios which naturally occur in lakes, and which can originate, for example, from leaching from soils and weathering of rocks in catchments. All statistical analyses were carried out in R Studio March 1, 1093 (RStudio Team, 2020) using the 'cor.test' function and packages 'vegan', 'adespatial, 'tidyverse', 'reshape', 'ade4', 'quickMEM', 'nlme', 'data table, and 'car'.

3. Results

3.1. Physicochemical variables

Acidification-related variables (pH, alkalinity and Ca concentrations) were substantially higher in limed lakes relative to reference lakes (Fig. 2). Ca and pH tended to decrease in limed lakes over the study period while they fluctuated around a long-term mean in reference lakes. Alkalinity slightly increased and fluctuated widely in the limed lakes, while the slight increase of this variable in reference lakes showed less variability along the long-term mean (Fig. 2). In contrast, physicochemical variables unrelated to acidification (TP, TOC, water temperature) overlapped, indicated by standard deviations. TOC slightly increased in limed lakes over the study period, while the remaining variables showed long-term variability without a discernible increase in

Fig. 3. Temporal patterns of Ca:Mg ratios (surrogate of management) in reference (black lines) and limed (gray lines) lakes.

both lake types (Fig. 2).

3.2. *Littoral invertebrates*

Significant AEM-RDA time series models were found for all limed lakes with the adjusted variance explained, based on selected AEMs, ranging *ca* 43–77% (Table 1, Fig. 4). All limed lakes showed panarchy structure in terms of hierarchical organization with more than one significant RDA axes indicating that temporal scales were compartmentalized into discrete levels. The Stengårdshjultasjön model had 2 significant RDA axes, 3 RDA axes were detected in Ejgdesjön, and 5 RDA axes in Gyslättasjön and Stora Härsjön. RDA 1 usually comprised a component of monotonic change over time combined with fluctuation cycles at roughly 8-year intervals. The remaining RDA axes showed different fluctuation cycles without directional change. Some of these fluctuation cycles were orthogonal, for instance in Gyslättasjön for which the model shows similar periodicity at RDA axes 2 and 3.

Significant time series models for circumneutral reference lakes were only found for Allgjuttern (31.2% adj. R^2) and Stora Skärsjön (26.4% adj. R^2), with significant temporal patterns associated with 3 and 2 RDA axes, respectively (Fig. 4). Allgjuttern showed fluctuation patterns with longer periodicity, and a relatively smooth monotonic change at RDA 1, which deviated from the patterns in limed lakes. Stora Skärsjön showed more marked short-term fluctuation cycles relative to Allgjuttern, and displayed monotonic change at RDA 2.

In all significant littoral invertebrate models RDA 1 comprised the stronger pattern, in term of variance explained, ranging 3.5–18.1%. Ca:Mg ratios in all lakes generally correlated with this axis and with RDA 2. In Stengårdshjultasjön and Allgjuttern correlations were only found between Ca:Mg ratios and RDA 2 (Fig. 4, Table 2).

3.3. *Sublittoral invertebrates*

Significant RDA-AEM models were found for one limed lake (Ejgdesjön; 17.2% adj. R^2; 2 significant RDA axes) and 2 reference lakes, Stora Skärsjön (8.0% adj. R^2, 1 significant axis) and Fiolen (16.2% adj. R^2, 2 significant axes) (Fig. 5). However, Stora Skärsjön did not qualify as a panarchy due to only a single significant fluctuation frequency and thus no hierarchical temporal structure being detected. The RDA axes showed distinct patterns across lakes: Fiolen showed a “smooth” long-periodicity fluctuation pattern and Stora Skärsjön relatively short-term variability. In Ejgdesjön, the fluctuation structure of RDA 1 was similar to the littoral invertebrates, and RDA 2 showed fluctuation periodicities at roughly 6-year intervals. RDA 1 explained most of the variance of all significant axes (Table 1). These values were lower compared to the littoral invertebrates, ranging 3.6–6.6%.

In the limed Ejgdesjön, Ca:Mg ratios correlated with RDA 1 but not RDA 2. In the circumneutral lakes no correlations between Ca:Mg ratios were found (Fig. 5, Table 2).

3.4. *Phytoplankton*

Significant RDA-AEM models were found for two limed lakes (Stengårdshjultasjön: 26.3% adj. R^2, 3 significant RDA axes; Stora Härsjön: 18.9% adj. R^2, 2 significant axis) and one reference lake (Fiolen: 17.8% adj. R^2, 1 significant axis) (Fig. 6). Fiolen did not qualify as a panarchy due to the lack of multiple independent fluctuation frequencies. Stengårdshjultasjön showed relatively homogenous fluctuation cycles, with a component of linear change associated with RDA 1 that explained 8.7% of the constrained variation (Table 1). In Stora Härsjön fluctuations operated at shorter cycles compared to Stengårdshjultasjön but RDA 1 (11.2% variance) also showed patterns of monotonic change.

Ca:Mg ratios correlated with the fluctuation frequency patterns of RDA 1 in limed Stengårdshjultasjön. In Stora Härsjön (limed) correlations of Ca:Mg ratios with the two axes of the model were not significant (Fig. 6, Table 2). The Ca:Mg ratio also correlated with the only significant RDA axes in reference lake Fiolen (Fig. 6, Table 2).

4. Discussion

Using lake phytoplankton and benthic invertebrate communities, our study tested three hypotheses related to the tenets of panarchy theory that community dynamics are 1) hierarchically (and orthogonally) structured; 2) show scale-specific fluctuation patterns, and 3) exhibit cross-scale connectivity in limed and circumneutral reference lakes. Cross-scale connectivity was studied using the correlation of Ca:Mg ratios, a surrogate of liming, across the independent temporal fluctuation frequencies resolved by the RDA-AEM models.

The analysis showed taxon-specific differences with the results being most consistent with expectations for littoral invertebrates but inconclusive for sublittoral invertebrates and phytoplankton. Our results differed from those previously reported for the abiotic environment in the same set of lakes (Angeler et al., 2021). The three hypotheses tested in our study were therefore supported/not supported in context-specific manners, suggesting that multiple lines of evidence are needed for making sound inference (e.g., Hering et al., 2006; Rodrigues and Brooks, 2007; Heino, 2014).

Regarding our first hypothesis (hierarchical [and orthogonal] structuring), it was prerequisite to reveal more than one significant fluctuation frequency pattern in the time series models to support the multiscale aspect of panarchy. We found support for panarchy structure

Table 1

Summary of time series models statistics. Ns, axis not significant; *, model not significant.

	Adjusted R^2 min. Model (%)	Number of vectors selected	Number of significant axes	Variance (%) Constrained/ unconstrained	Variance (%) RDA 1	Variance (%) RDA 2	Variance (%) RDA 3	Variance (%) RDA 4	Variance (%) RDA 5
Littoral invertebrates									
Reference lakes									
Allgjuttern	31.2	3	3	13.3/20.0	9.6	2.6	1.8	Na	na
Fiolen	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns
Stora Skärsjön	26.4	6	2	11.5/12.8	3.5	2.6	Ns	Ns	Ns
* Stora Envättern	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns
Limed lakes									
Ejgdesjön	54.9	7	3	20.8/9.0	12.0	3.0	2.3	ns	ns
Gyslättasjön	70.9	7	5	28.5/6.9	18.1	4.5	1.9	1.8	1.2
Stengårdshultasjön	42.7	5	2	14.8/11.5	9.6	2.6	ns	ns	ns
Stora Härsjön	77.2	14	5	20.8/9.0	12.1	3.0	2.3	1.5	1.0
Sublittoral invertebrates									
Reference lakes									
*Allgjuttern	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns
Fiolen	16.2	2	2	9.2/29.0	6.6	2.7	Ns	Ns	Ns
Stora Skärsjön	8.0	1	1	36.6/25.9	3.6	Ns	Ns	Ns	Ns
*Stora Envättern	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns
Limed lakes								Ns	Ns
Ejgdesjön	17.2	3	2	9.2/22.3	4.9	2.7	Ns	Ns	Ns
*Gyslättasjön	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns
*Stengårdshultasjön	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns
*Stora Härsjön	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns
Phytoplankton									
Reference lakes									
*Allgjuttern	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns
Fiolen	17.8	4	1	20.5/40.8	11.0	Ns	Ns	Ns	Ns
*Stora Skärsjön	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns
*Stora Envättern	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns
Limed lakes									
*Ejgdesjön	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns
*Gyslättasjön	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns	Ns
Stengårdshultasjön	26.3	5	3	23.8/24.4	8.7	5.6	4.3	Ns	Ns
Stora Härsjön	18.9	3	2	21.7/31.1	11.2	5.8	Ns	Ns	Ns

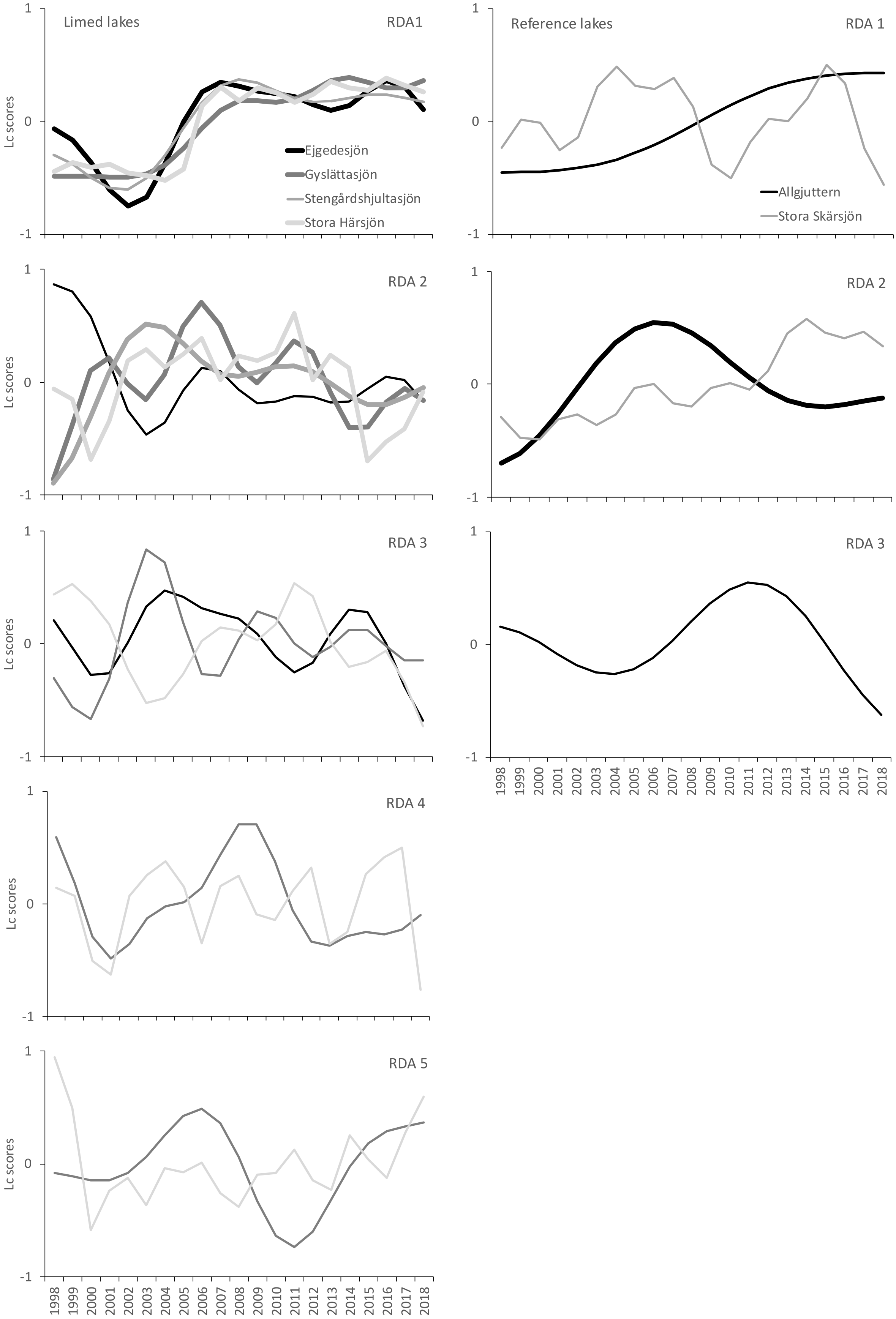

Fig. 4. Linear combination (Lc) score plots showing dominant temporal fluctuation frequencies of littoral invertebrate assemblages in limed and reference lakes identified by RDA-AEM models. These temporal structures (RDA axes) indicate orthogonal patterns in addition to independent hierarchical scaling patterns of a panarchy. Patterns emphasized with thick lines correlate which Ca:Mg ratios, a proxy of liming management (For correlation results see Table 2).

in all four limed lakes but only for two reference lakes (Allgjuttern, Stora Skärsjön) for littoral invertebrates. In contrast, fluctuation patterns at distinct temporal frequencies were only found for one limed (Ejgedejön) and one reference lake (Stora Härsjön) for sublittoral invertebrates and two limed lakes (Stengårdshjuötasjön, Stora Skärjön) for phytoplankton. Although, time series models for phytoplankton and sublittoral invertebrates in reference lake Fiolen were significant, temporal community variability was only detected at a single scale. Therefore, Fiolen does not comprise panarchy structure. Out of 24 potential detectable panarchies in our study (2 lake types (limed, reference) x 4 lakes x 3 communities), only 10 (6 littoral invertebrates, 2 sublittoral invertebrates, 2 phytoplankton) showed panarchy structure.

Panarchy has been used predominantly as a heuristic to describe social-ecological systems change in qualitative analysis (Sundstrom and Allen, 2019; Gunderson et al., 2022; Rocha et al., 2022). However, our results showed that quantitative analyses of panarchy may not always be consistent with expectations and results of qualitative research. This may be due to quantitative approaches, as is the case with our time series modeling, accounting numerically for the complexity inherent in data. This complexity allows for ecologically more realistic representations compared to often subjectively defined models for qualitative research (Angeler et al., 2016). Specifically, our time series modeling was based on extracting independent dynamic fluctuation patterns based on redundant temporal trajectories of individual taxa present in the species x time matrices. That is, RDA synthesizes linear associations between the sets of species that are "redundant" with, or "explained" by the totality of species present in the matrices that are simultaneously linear combinations of the explanatory (AEM) variables (Buttigieg and Ramette, 2014). This manifests in the form of orthogonal (statistically independent) canonical axes (or RDA axes) that are built by the model, and which provides one way to map panarchy (Twidwell et al., 2022). Ecologically this represents modeled species groups wherein individual species show similar temporal dynamics at significant model axes, thereby representing independent fluctuation frequencies. Although the time series models are agnostic regarding system extrinsic (environmental factors) and intrinsic (biological interactions) mechanisms leading to fluctuation frequencies at different temporal scales, they implicitly reflect different key structuring processes leading to multiscalar patterns (Holling, 1992) that can be extracted from the data.

Table 2

Results from Spearman rank correlation analyses between temporal frequency patterns (RDA axes) and Ca:Mg ratios. Shown are correlation coefficients (rho). Significant correlations: *, $p \leq 0.05$; **, $p \leq 0.01$, ***, $p \leq 0.001$ (in bold font). Ns, correlation not significant; -, axis not significant; *, no significant time series model.

	RDA 1	RDA 2	RDA 3	RDA 4	RDA 5
Littoral invertebrates					
Reference lakes					
Allgjuttern	Ns	**0.43***	Ns	–	–
*Fiolen	–	–	–	–	–
Stora Skärsjön	Ns	Ns	–	–	–
*Stora Envättern	–	–	–	–	–
Limed lakes					
Ejgdesjön	**0.49***	Ns	Ns	–	–
Gyslättasjön	**0.44***	**0.61****	Ns	Ns	Ns
Stengårdshultasjön	Ns	**0.46***	–	–	–
Stora Härsjön	**0.62****	**0.54***	Ns	Ns	Ns
Sublittoral invertebrates					
Reference lakes					
*Allgjuttern	–	–	–	–	–
Fiolen	Ns	Ns	–	–	–
Stora Skärsjön	Ns	–	–	–	–
*Stora Envättern	–	–	–	–	–
Limed lakes					
Ejgdesjön	**0.72*****	Ns	–	–	–
*Gyslättasjön	–	–	–	–	–
*Stengårdshultasjön	–	–	–	–	–
*Stora Härsjön	–	–	–	–	–
Phytoplankton					
Reference lakes					
*Allgjuttern	–	–	–	–	–
Fiolen	**0.84*****	–	–	–	–
*Stora Skärsjön	–	–	–	–	–
*Stora Envättern	–	–	–	–	–
Limed lakes					
*Ejgdesjön	–	–	–	–	–
*Gyslättasjön	–	–	–	–	–
Stengårdshultasjön	**−0.73*****	Ns	Ns	–	–
Stora Härsjön	Ns	Ns	–	–	–

It was unclear why significant timeseries models were largely lacking for sublittoral invertebrates and phytoplankton. The RDA-AEM approach is sensitive to species incidences and abundances. It is likely that the majority of species in these communities show a relatively strong component of stochastic fluctuations; that is, temporal variability patterns of individual species that are largely unmatched with those of other species. Disparate temporal patterns of individual species would explain why RDA failed to extract redundant patterns across species with similar presence-absence and abundance patterns; however, more research is needed to attribute time series modeling performance with temporal community dynamics and environmental factors shaping ecological assemblages. We acknowledge, however that, although panarchy was not detectable and supported for many lakes with our timeseries modeling, other methods, such as a multiscalar extension of the current QtAC framework (Schrenk et al., 2022), may offer complementary opportunities for analyses. Using different methodologies, in addition to analyzing multiple taxonomic groups, can strengthen inference in resilience assessments (Stow et al., 2007) and facilitate ecosystem and management (Pelletier et al., 2020).

Regarding our second hypothesis, littoral invertebrates again showed the most conclusive results compared with sublittoral invertebrates and phytoplankton. Quantitative comparisons of the dynamic system structure of limed and reference lakes were not possible because of the imbalance between significant timeseries models. However, the patterns for littoral invertebrates allowed for descriptive, explorative interpretations. This taxonomic group revealed that limed lakes had more consistent and nuanced temporal structure compared to the reference lakes. This provides implicit, visual support for our second hypothesis. However, this hypothesis needs further scrutiny in the light of model statistics.

Given that liming is a significant recurring ecosystem disturbance (Bishop et al., 2001; McKie et al., 2006), it could be expected that liming disrupts the temporal structure, leading to more stochastic temporal community variability (Lepori and Malmqvist., 2009). Stochasticity is associated with a larger number of species not correlating with any of the significant modeled temporal fluctuation frequencies detected by RDA-AEM (Baho et al., 2014). Stronger stochasticity in limed lake models should manifest, at least with this modeling, in less variance explained relative to reference lakes models. However, our results differed from this expectation. The inconsistency of results between taxonomic groups and few lakes being available for study currently prevent us from further explaining our findings. Analyzing a larger number of lakes and longer time series may provide more consistent results and interpretations. This supports and emphasizes the need for long-term monitoring of ecosystem-level experiments for better understanding management (Carpenter, 1998; Fölster et al., 2014), especially concerning coerced regimes.

Regarding our third hypothesis, we found that Ca:Mg ratios were only manifested at, and associated with, few temporal fluctuation frequencies in limed and natural lakes. Ca:Mg ratios not only serve as a management surrogate but also are part of the natural abiotic environment in lakes resulting from catchment processes related to soil leaching and geological weathering. In the case of liming Ca:Mg ratios, the surrogacy of management resides in the external Ca subsidy to lakes, wherein the quantity of input can be considered a degree of regime coercion (Angeler et al., 2020). We acknowledge the high variability of liming regimes across our study lakes, which, given the nature of our

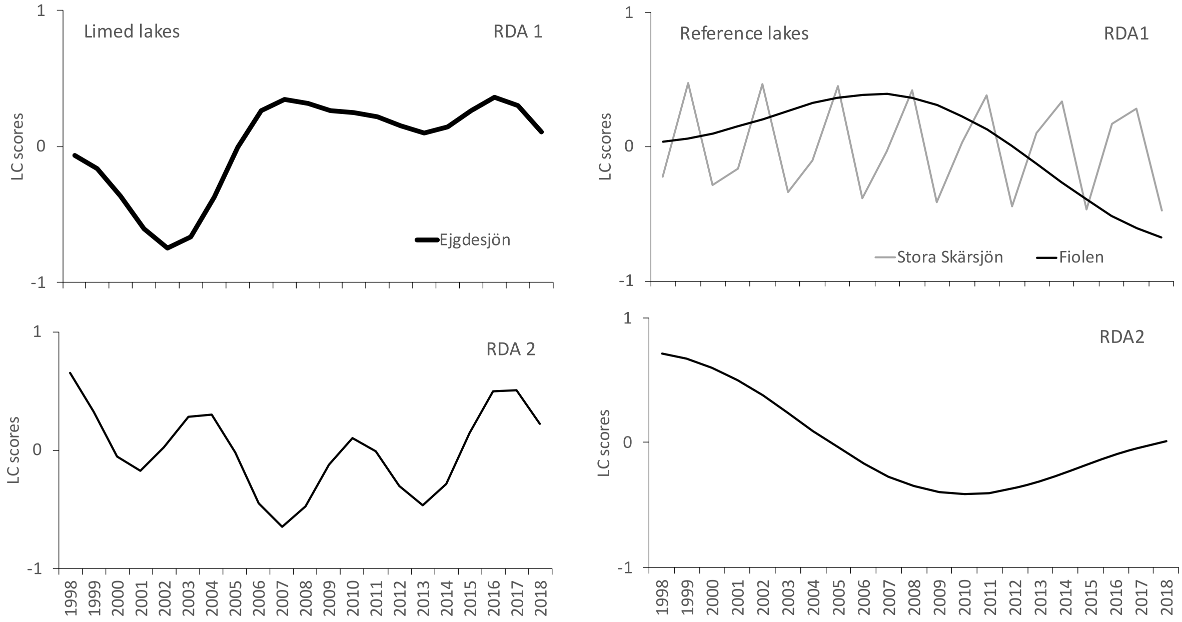

Fig. 5. Linear combination (Lc) score plots showing dominant temporal fluctuation frequencies of sublittoral invertebrate assemblages in limed and reference lakes identified by RDA-AEM models. These temporal structures (RDA axes) indicate orthogonal patterns in addition to independent hierarchical scaling patterns of a panarchy. Patterns emphasized with thick lines correlate which Ca:Mg ratios, a proxy of liming management (For correlation results see Table 2).

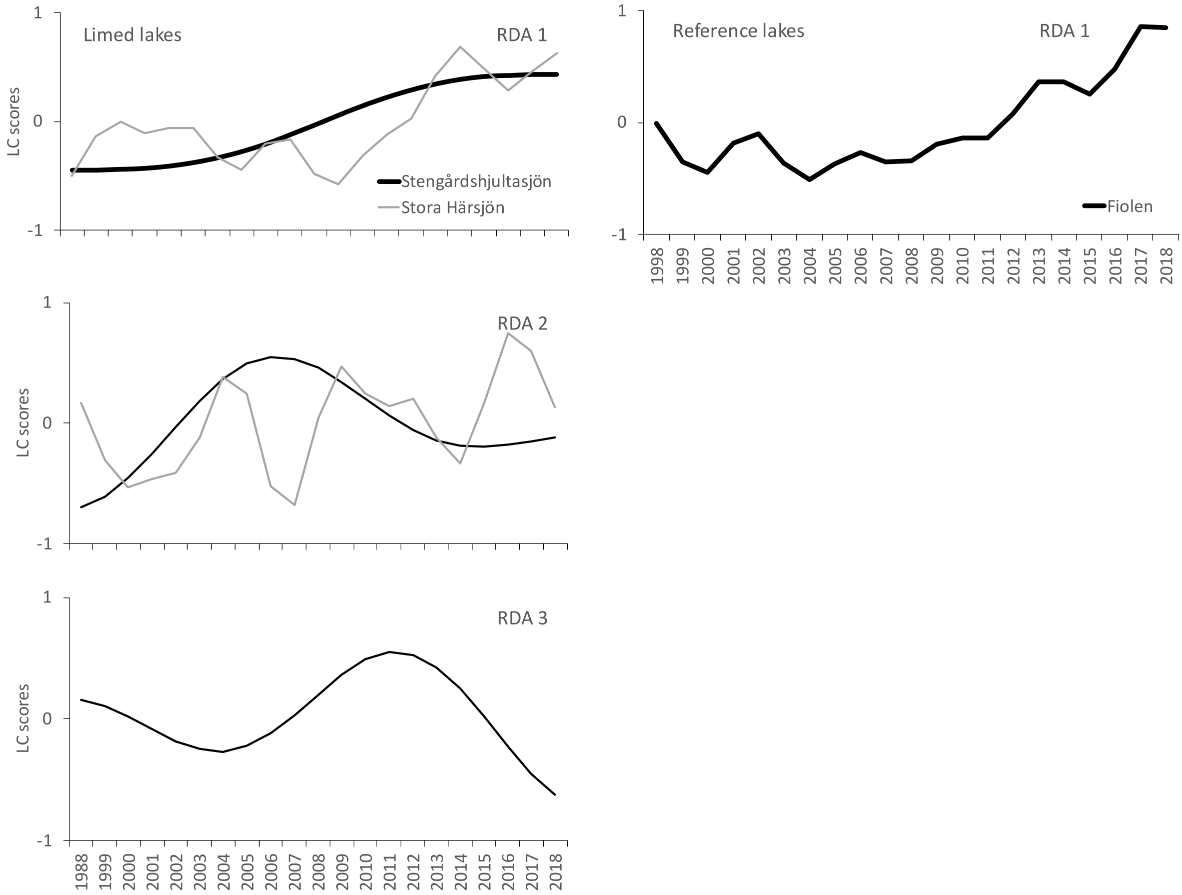

Fig. 6. Linear combination (Lc) score plots showing dominant temporal fluctuation frequencies of phytoplankton assemblages in limed and reference lakes identified by RDA-AEM models. These temporal structures (RDA axes) indicate orthogonal patterns in addition to independent hierarchical scaling patterns of a panarchy. Patterns emphasized with thick lines correlate which Ca:Mg ratios, a proxy of liming management (For correlation results see Table 2).

monitoring-based ecosystem-experiment, was due to the need to adapt management to the lakes' biophysical environments. It was therefore not possible to study an experimental setting in which liming comprised a standardized treatment across lakes. However, we regard our results about the weak cross-scale manifestations of Ca:Mg ratios across the limed lakes with confidence because inference was based on ecologically realistic conditions.

That the limited cross-scale manifestation or redundancy of Ca:Mg ratios in limed lakes matches the patterns in reference lakes supports the conjecture that liming effects become diluted across scales in limed lakes. Cross-scale redundancy of ecological key attributes, such as functional aspects mediating ecological processes, has been suggested to mediate resilience (e.g., Allen et al., 2005). For instance, the cross-scale resilience model (Peterson et al., 1998) posits that the resilience of a system increases with increasing redundancy of ecological key attributes across scales. Regarding management from a coerced regime perspective, Angeler and Allen (2022) suggested the cross-scale coercion model as an analogue of the cross-scale resilience model. This model is specifically rooted in panarchy and has been discussed theoretically. It suggests that management effectiveness increases with an increasing redundancy of interventions within and across scales.

The results of this study empirically support this model by showing evidence of weak cross-scale manifestations of liming in the lake panarchies. These weak manifestations potentially serve an explanation for coerced (liming) regimes (and potentially other forms of management) being limited to mitigation. Further testing of our model is needed, however, because it can currently not be generalized; specifically, to which degree within-and cross-scale manifestations of management contribute to management efficiency and thus cost effectiveness needs further assessment. A large body of biomanipulation (a lake restoration tool, Hansson et al., 1998) and Earth Stewardship for climate mitigation (Steffen et al., 2018) research provide opportunities for further testing this model. Similar to "coerced" global climate regimes (Angeler and Allen, 2022), biomanipulation research may provide a solid basis for assessing whether redundancies of technological and biological solutions manifest at and across scales in lakes.

Biomanipulation and Earth Stewardship offer potential to assess management efficiency in terms of mitigation (coerced regime) or restoration (self-organized systems) potential. Specifically, both examples account for ecological complexity. That is, biomanipulation considers, for instance, cascading effects of planktivorous fish removal and/or piscivorous fish addition to control phytoplankton structure and biomass and improve water-quality (Carpenter and Kitchell, 1996), an example of top-down information flow in panarchy. Similarly, Earth Stewardship exemplifies how transformation of people's life-styles, energy and transportation systems, and economic and policy models may "percolate up" from the individual and society level to global mitigation of climate warming. Both examples suggest how management failures may be reduced by fostering regime coercion, i.e. nutrient precipitation in and oxygenation of the water column in lakes in addition to food web control (Cowell et al., 1987; Zamparas and Zacharias, 2014) or transnational agreements for climate mitigation in addition to national policies (Österblom et al., 2022). Importantly, these cases highlight the need to account for social-ecological factors mediating mitigation and restoration potential and associated costs. Specifically, deeply entrenched system structure of an undesirable regime (turbid lake, Hothouse Earth) can mediate hysteresis and limit restoration, despite significant within-scale and cross-scale coercion through management. Also, increasing magnitudes and severity of climate change impacts that outweigh management benefits need to be considered (Zhan et al., 2022).

5. Conclusions

Our planet is undergoing significant social-ecological change as a result of human activities. Ecosystems will likely need intensified management with increasing costs to sustain human needs for ecosystem services in the future. 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. This can be done by specifically accounting for social aspects such as environmental laws governance that influence social-ecological water panarchies (Pope et al., 2014; Cosens and Gunderson, 2018), and that might inform liming as a social-ecological system.

Credit author statement

David Angeler conceived this study, analyzed the data and wrote the paper. Ran Hur analyzed the data contributed to idea development and the writing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data are freely available at: https://www.slu.se/en/departments/aquatic-sciences-assessment/data-host/

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Appendix A

Summary of geographical position, morphological characteristics and features of liming management of study lakes. Shown are also features of liming management in individual lakes.

	SMHI X SMHIY	Lake area (km^2)	Max. Depth (m)	Liming period	Liming events	Delivery	Liming quantity (metric tons; means/SD
Reference lakes							
Allgjuttern	642,489 151,724	0.19	40.70	Na	na	na	na
Fiolen	633,025 142,267	1.65	10.50	Na	na	na	na
Stora Envättern	655,587 158,869	0.38	11.20	Na	na	na	na
Stora Skärsjön	628,606 133,205	0.31	11.50	Na	na	na	na

(continued on next page)

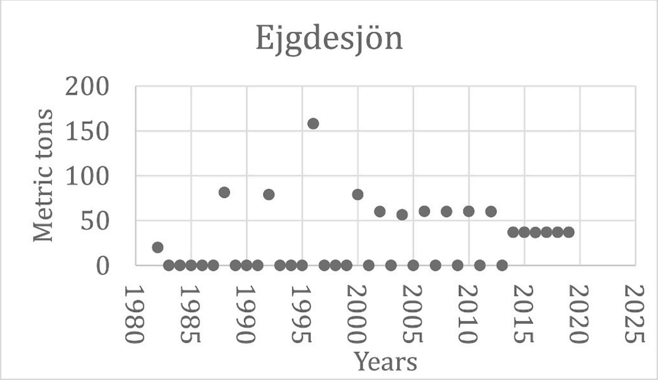
(*continued*)

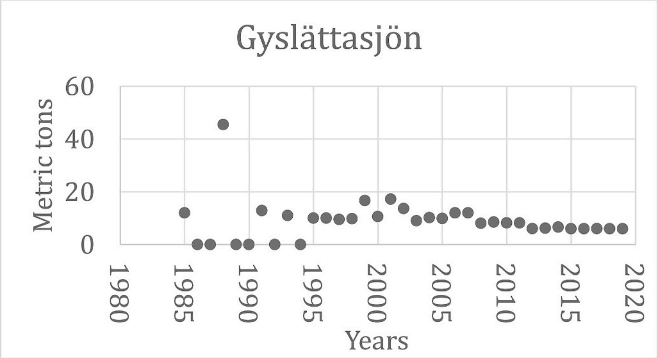
	SMHI X SMHIY	Lake area (km^2)	Max. Depth (m)	Liming period	Liming events	Delivery	Liming quantity (metric tons; means/SD
Limed lakes							
Ejgdesjön	653,737 125,017	0.83	28.60	1982–2018	16	Boat	60/32
Gyslättasjön	633,209 141,991	0.33	9.80	1985–2019	32	Helicopter	11/7
Stengårdshultasjön	638,317 138,010	4.98	26.80	1981–2019	23	Boat	235/325
Stora Härsjön	640,364 129,240	2.57	42.00	1977–2011	13	Boat	294/145

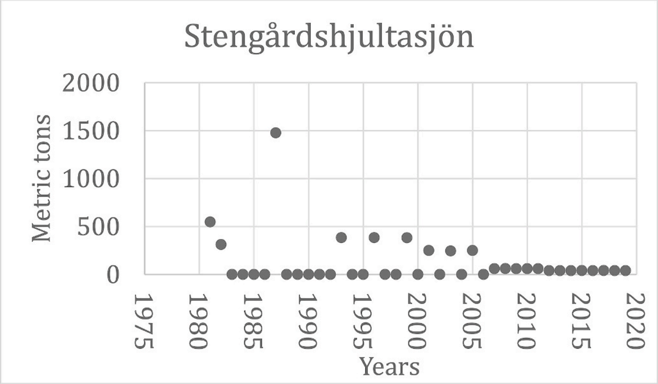
Abbreviation: na, not applicable.

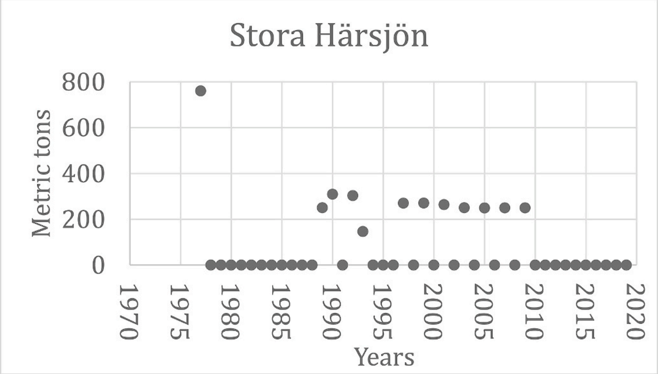
Appendix B

Liming frequencies/quantities of managed lakes









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