Quantifying Ecological Resilience in Lakes – Bridging Theory and Management

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Doctoral Thesis
Swedish University of Agricultural Sciences
Uppsala 2015

Acta Universitatis agriculturae Sueciae
2015:60

Cover: Clear water lake in Lapland
(photo: Didier Baho)

ISSN 1652-6880
ISBN (print version) 978-91-576-8318-2
ISBN (electronic version) 978-91-576-8319-9

Print: SLU Service/Repro, Uppsala 2015

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Abstract

Ecological resilience, defined as the capacity of an ecosystem to withstand disturbances without losing original structures, processes and functions, has remained elusive and challenging to quantify. In this thesis, two methods were used to assess the resilience of aquatic communities to different stressors and management practices. Time series modelling and discontinuity analysis were used to quantify scaling structures and dynamics, both relevant for ecological resilience. The aims of this work were to: (i) evaluate the performances of two time series modelling approaches: Asymmetric Eigenvector Maps (AEM) and Moran's Eigenvector Maps (MEM), and determine which is best suited to study ecological resilience, (ii) assess the efficiency of liming as management technique to restore lakes to pre-acidified conditions, (iii) investigate if acidified lakes (degraded systems) are more vulnerable to environmental change compared to near-pristine circumneutral lakes, and (iv) investigate regional climatic effects on the resilience of shallow lakes using an experiment along a latitudinal gradient that manipulated nutrients and ecosystem size.

AEM consistently outperformed MEM with differences in modelled scale-specific patterns. These results suggest that the outcomes are dependent on the modelling approach and that AEM might be better suited to assess resilience when temporal trends are relevant. Liming improved species richness and diversity, but resulted in communities that are neither typical of acidified nor of circumneutral lakes. The resilience attributes were similar across all lakes; however both limed and acidified lakes had higher proportions of species with stochastic dynamics. These findings suggest that liming is unable to break the feedbacks that maintain the system in an acidified state. Acidified and circumneutral lakes were found to be equally vulnerable to environmental change as both lake types had similar resilience characteristics. Similar resilience attributes were also observed in the experiment across countries, except when severe drought conditions occurred that apparently led to lower resilience.

Keywords: Resilience, Scales, Time series modelling, Discontinuity analysis, Environmental change, Management, Vulnerability, Phytoplankton, Benthic invertebrates, Zooplankton

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Sammanfattning på svenska

Ekologisk resiliens definieras som förmågan hos ekosystem att motstå störningar utan att förlora sin ursprungliga struktur, ingående processer och funktioner. Ekologisk resiliens är fortfarande en utmaning att kvantifiera främst på grund av att många skalor är involverade med komplexa interaktioner dem emellan. I denna avhandling har två statistiska metoder använts för att bedöma resiliens hos akvatiska ekosystem som utsatts för olika typer av mänsklig miljöpåverkan och förvaltningsmetoder. Tidsseriemodellering och diskontinuitetanalys användes för att kvantifiera skalornas strukturer och dynamik, båda relevanta för resiliens. Målen var att: (i) utvärdera vilken av två tidsseriemodelleringsmetoder: Asymmetric Eigenvector Maps (AEM) och Moran's Eigenvector Maps (MEM), som är främst lämpad för att studera ekologisk resiliens. (ii) Bedöma effekterna av kalkning som förvaltningsmetod för att återställa sjöar som har skadats av surt nedfall: (iii) Undersöka om sådana försurade sjöar är mer sårbara för framtida miljöförändringar jämfört med sjöar med mera neutralt pH och bevarad buffringsförmåga. (iv) Undersöka hur resiliensen i sjöar påverkas av klimateffekter, ekosystemstorlek och näringsämnespåverkan vilket gjordes genom att, i stora tankar, manipulera växtnäring och ekosystemstorlek i en latitudgradient över flera länder.

Resultatet var beroende av modelleringsmetod och AEM överträffade MEM med skillnader i modellerade skalspecifika mönster och bedöms därför vara bättre lämpad att för att bedöma resiliens när underlagsmaterialet innehåller data med tidsserier. Kalkade sjöar hade högre artrikedom och diversitet, men resulterade i samhällen som varken var typiska för försurade sjöar eller neutrala sjöar. Resiliensen var däremot likartad i alla tre typer av sjöar; men både kalkade och försurade sjöar hade fler arter med stokastisk dynamik. Detta tyder på att kalkning inte kan bryta de återkopplingar som upprätthåller ekosystemet i ett försurat läge. Försurade och neutrala sjöar bedömdes vara lika känsliga för miljöförändringar eftersom båda sjötyperna hade liknande resiliensegenskaper. Likartade resiliensegenskaper observerades också i det storkaliga experimentet, utom i ett fall där svår torka ledde till lägre resiliens.

Dedication

To my family for their unconditional support…

The complexity of things – the things within things – just seems to be endless. I mean nothing is easy, nothing is simple.

Alice Munro

Contents

List of Publications

This thesis is based on the following papers, referred to by Roman numerals in the text:

I Baho, D.L., Futter, M.N., Johnson, R.K. and Angeler, D.G. (2015). Assessing temporal scales and patterns in time series: comparing methods based on redundancy analysis. *Ecological Complexity* in press. DOI: 10.1016/j.ecocom.2015.04.001

II Baho, D.L., Drakare, S., Johnson, R. K., Allen, C. R. and Angeler, D.G. (2014). Similar resilience attributes in lakes with different management practices. *Plos One* 9(3), e91881.

III Angeler, D.G., Baho, D.L., Allen, C.R. and Johnson, R.K. (2015). Linking degradation status with ecosystem vulnerability to environmental change. *Oecologia* in press. DOI: 10.1007/s00442-015-3281-y

IV Baho, D.L., Tavsanoglu, U.N., Sorf, M., Stefanidis, K., Drakare, S., Scharfenberger, U., Agasild, H., Beklioglu, M., Hejzlar, J., Adrian, R., Papastergiadou, E., Zingel, P., Sondergaard, M., Jeppesen, E. and Angeler, D.G (2015). Macroecological patterns of resilience inferred from a multinational, synchronized experiment. *Sustainability* 7(2), 1142-1160.

Papers I-IV are reproduced with the permission of the publishers.

The contribution of Didier L. Baho (DLB) to the papers included in this thesis was as follows (other acronyms: SD; Stina Drakare, DGA, David G. Angeler):

I DLB carried out the statistical together with DGA. All authors conceived and wrote the paper

II DLB analyzed the data together with DGA. All authors conceived and wrote the paper

III DLB analyzed the data with DGA. All authors conceived and wrote the paper

IV All authors carried out the experiment. The regular sampling in the Swedish site was performed by DLB, SD and DGA. DLB carried out the statistical analysis and wrote the paper together with DGA

Abbreviations

ANOSIM	Analysis of similarity
ANOVA	Analysis of variance
Lc	Linear combination
NMDS	Non-metric multidimensional scaling
PERMANOVA	Permutational multivariate analysis of variance
RDA	Redundancy analysis

1 Introduction

Mankind, despite being present on a minute geological time scale of Earth's history, has had profound effects on the global environment (Lewis & Maslin, 2015; Zalasiewicz *et al.*, 2011). The increasing magnitude of humans as a major driver of global environmental change started in the early 1600s (Lewis & Maslin, 2015).

Anthropogenic activities have profoundly disturbed biogeochemical cycles (nitrogen, phosphorus and carbon), land use and biodiversity (Vitousek *et al.*, 1997), which significantly threaten the capacity of ecosystems to fulfil their critical role (Nyström *et al.*, 2000). For instance, the production of fertilizers for agricultural purposes is responsible for converting 120 million metric tons of nitrogen gas into ammonia and extracting approximately 20 tons of phosphorous annually, which overshadows natural fluxes (Rockström *et al.*, 2009; Mackenzie *et al.*, 2002; Vitousek *et al.*, 1997). Eventually, large quantities of nitrogen and phosphorus reach surface waters and oceans causing major environmental problems such as eutrophication (Conley *et al.*, 2011; Mackenzie *et al.*, 2002). Other activities, such as the combustion of fossil fuels and the conversion of forest and grassland into agricultural land, lead to a steady increase of atmospheric carbon dioxide concentrations from approximately 280 ppm recorded in 1800 to a current level of 400 ppm (Ward *et al.*, 2015; Petit *et al.*, 1999; Vitousek *et al.*, 1997), this increase is unprecedented for the past 800,000 years (Ciais *et al.*, 2013; Masson-Delmotte *et al.*, 2013). Carbon dioxide, a greenhouse gas, is an important climate regulator and the observed increased will contribute to substantial climate change in the next century, where the global temperature is predicted to increase by 3^{o}C (Rockström *et al.*, 2009; Solomon *et al.*, 2007; Vitousek *et al.*, 1997). The current rate of biodiversity loss, as consequences of the conversion of ecosystems to agricultural or urban areas, translocations of species (voluntarily or accidentally) and poor management practices (Sala *et al.*, 2000;

Peterson *et al.*, 1998), is unprecedented (Mace *et al.*, 2005). Biodiversity loss not only concerns species extinctions but equally involves the disappearance of ecological functions they once fulfilled, which might have relevance for society regarding the provisioning of ecosystems goods and services (Balvanera *et al.*, 2006; Hooper *et al.*, 2005).

Freshwater ecosystems, including streams, rivers, wetlands and lakes, cover approximately 0.8% of Earth's surface, nevertheless this tiny proportion has disproportionate high ecological, cultural, economic and scientific value (Dudgeon *et al.*, 2006). These essential ecosystems are highly vulnerable to human activities, for instance from eutrophication, acidification, invasive species, land-use change and climate change (Kernan *et al.*, 2010a; Dudgeon *et al.*, 2006; Danis *et al.*, 2004). Thus, there is an increasing need of understanding how these ecosystems cope with or become vulnerable to stressors. Amongst freshwater ecosystems, lakes are generally used as conceptual models, as they have discrete boundaries and distinguishable connections with bordering ecosystems (Vadeboncoeur *et al.*, 2002), contain multiple species capable of tracking environmental changes (Stendera & Johnson, 2008; Cairns *et al.*, 1993; Marmorek & Korman, 1993) and have proven to be valuable to understand abrupt changes in ecosystem's structure and function (Scheffer & Carpenter, 2003; Scheffer *et al.*, 2001).

1.1 Resilience theory

The term resilience has at least two definitions with contrasting properties (Peterson *et al.*, 1998; Holling, 1992; Holling, 1973). *Engineering resilience*, the most commonly referred definition, simply measures the time required for a system to return to its original position following a perturbation (Pimm, 1984). *Ecological resilience*, on the other hand, emphasizes the ability of ecosystems to absorb disturbances and re-organize to maintain essentially the same function, structure and feedback of the system (Holling, 1973). Ecological resilience includes a broad range of biological mechanisms that assist ecosystems to sustain critical structures, functions and processes when undergoing changes (i.e. adaptive capacity) (Carpenter *et al.*, 2001).

Ecological, in contrast to engineering resilience, acknowledges that systems do not have a single steady state but that systems can move into an alternative domain of attractions (i.e. regime shifts) when reaching a certain disturbance threshold (Muradian, 2001). For instance, shallow lakes in temperate regions can undergo a shift to an alternative domain: excessive nutrient enrichment due to human activities can induce a shift from a desired clear water state to a degraded and thus undesired turbid water state. The degraded state is dominated by high algal biomasses (often of toxic species) that adversely impact ecosystem services such as fisheries, recreation and water supply (Scheffer & Carpenter, 2003; Scheffer *et al.*, 2001). Once an enrichment threshold is reached, the desirable clear water state loses its integrity and reorganizes in a new stable regime. Costly management interventions are needed to break the feedbacks of the degraded state to revert the lake to a desired clear water state (Jeppesen *et al.*, 2007a; Jeppesen *et al.*, 2007b; Carpenter & Cottingham, 1997). This illustrates a crucial limitation of the engineering definition of resilience, which can be misleading in the sense that a degraded state would revert to a desired state without management measures if given enough time (Angeler *et al.*, 2014; Holling, 1996). Consequently, the ecological definition of resilience is better suited to mechanistically comprehend how ecosystems can maintain and adapt to environmental change or become critically vulnerable to changes.

1.1.1 Cross-scale resilience, functional redundancy and response diversity

The original ecological definition of resilience, defined as a "measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables" by Holling (1973), has evolved into multiple definitions; from a clear descriptive concept to increasingly vague normative concepts, which no longer restricts to the boundaries of ecological systems, but extends the concept to include socio-economical systems (Brand & Jax, 2007). This evolution and extension of the original definition of resilience raised some fundamental questions, for instance how to measure resilience and what ecological (or socio-economical) features to consider (Brand & Jax, 2007). The concepts of cross-scale resilience, functional redundancy and response diversity can address the above-mentioned concerns at least for ecological systems.

The cross-scale resilience model, proposed by Peterson *et al.* (1998), postulates that resilience of ecosystems depends partly on how species, and the ecological role they fulfil, are distributed within and across scales of space and time. Resilience is anticipated to increase when species with overlapping functions occur at the same scale, as well as how frequent these functions ensue across scales (Allen *et al.*, 2005).

Overlapping of function at a single scale relates to the concept of functional redundancy (Loreau, 2004; Yachi & Loreau, 1999), which recognizes that a number of species can go extinct before particular functions in an ecosystem are permanently impaired. However, unlike the cross-scale resilience model, the functional redundancy concept fails to recognize that ecological processes are partitioned by scale (Angeler *et al.*, 2014; Allen & Holling, 2008).

Response diversity, which refers to the variability of responses to environmental changes among species having equivalent ecosystem functions, has some implications for resilience (Elmqvist *et al.*, 2003). Response diversity reflects the potential of species within functional groups to compensate for the loss of one or more species when facing disturbances (Walker *et al.*, 1999), thus helping the system to re-organize and maintain similar functions while undergoing changes (Elmqvist *et al.*, 2003).

1.2 Quantifying resilience

The cross-scale resilience model provides a comprehensive framework to quantify resilience, more specifically by scrutinizing the scales present in a system (Nash *et al.*, 2014). There are different methods to quantify and assess scaling patterns from ecological systems, namely discontinuity analyses and modelling approaches that make the scaling structure in time series or spatial data explicit.

Discontinuity analysis is a powerful tool to infer dominant scales and cross-scale interaction from ecological systems (Allen *et al.*, 2005). The analysis is based on the notion that species' body sizes mirror the scale at which species operates, where species groups of similar-sized individuals along body size distribution can presumably exploit resources at these specific scales (Holling, 1992). Thus, each body size group reflects distinct scales based on resource availability in the system, and the number of body size groups indicates the number of dominant scales present in the system (Holling, 1992). On the other hand, discontinuities (gaps) comprise zones of transitions where resources are either scarce or highly variable (Allen & Holling, 2008; Allen *et al.*, 2005). Hierarchical cluster analysis (HCA), Bayesian classification and regression tree (BCART), classification and regression tree (CART), and gap rarity index (GRI) can be used to evaluate discontinuities (Stow *et al.*, 2007). A conceptual overview of the discontinuity approach is shown in Figure 1.

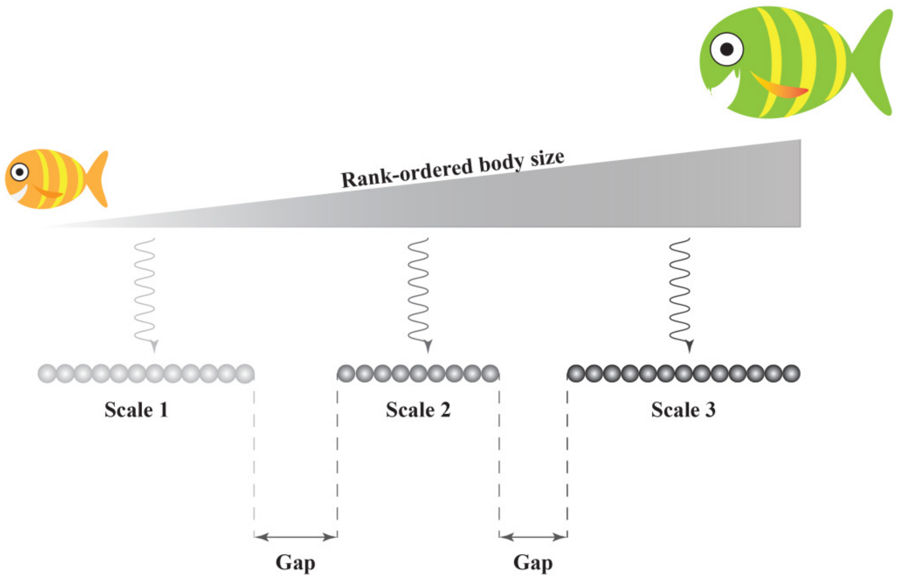
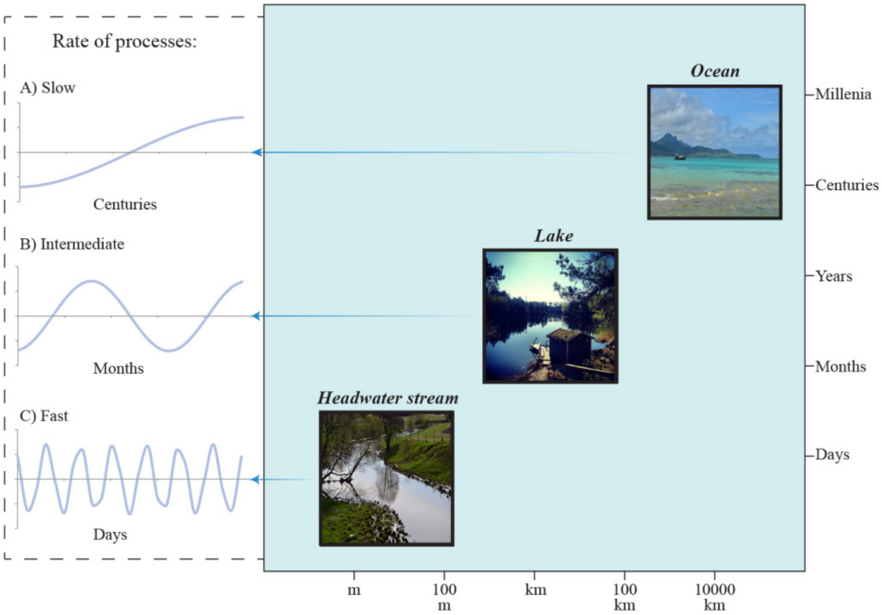


Figure 1. Illustration of discontinuity analysis. Individual species in a community (e.g. fish) are rank ordered with respect to their body sizes (from smallest to largest). Aggregations (grey dots) depict groups of species with homogenous body sizes that arise from discrete scale-specific processes in the environment. Gaps represent transitional areas between scales where no body sizes occur.

One major limitation of the discontinuity analysis is that it relies primarily on body size and such data are not readily available for organisms with modular growth, for example: plants and corals (Angeler *et al.*, 2015), but recent statistical developments can detect discontinuities using species' distributions or abundances across space or through time. For instance, Angeler *et al.* (2009) described a time series modelling approach that identifies temporal cross-scale structure. Time series modelling is particularly appealing as it can evaluate the degree by which key environmental factors affect the system's organization (Angeler *et al.*, 2011). For example, the study of Angeler *et al.* (2013a) found that temporal patterns of some invertebrate species groups corresponded to fast environmental changes, whereas others were related to slow environmental changes. In addition, time series modelling allows the detection of species associated with stochastic dynamics; that is species (usually rare species) that do not contribute to within- and cross-scale patterns (Göthe *et al.*, 2014). Species with stochastic dynamics have some relevance for resilience as they can potentially substitute others that went extinct following a major disturbance, and thus contribute to the adaptive capacity of the system, assisting in their reorganization and prevent the system from moving to an alternative state (Carpenter *et al.*, 2001; Walker *et al.*, 1999). In contrast to the discontinuity analysis, the time series modelling facilitates the detection temporal processes at discrete spatial scales, where some processes generally occur faster on a smaller spatial scale whereas others are slower and extend over larger spatial scale as shown in Figure 2.

Figure 2. A conceptual representation showing the dynamics at which processes occur at discrete spatial and temporal scales in three aquatic systems. A headwater stream is a very dynamic system where processes occur rapidly on a small spatial scale (Horne & Goldman, 1994), processes in a lake occur at intermediate speed related to the water residence time (Horne & Goldman, 1994), and slow processes occurring on larger spatial scale such as ocean circulation (Duplessy, 1999).



2 Objectives of the thesis

The objective of this thesis was to increase our understanding about how structural and functional properties operating at distinct scales confer ecological resilience and to quantify the latter. The specific aims, using the Swedish lake monitoring data and a pan-European mesocosm experiment, were to:

1. Evaluate the statistical performance and outcomes of two time series techniques, to determine which method is best suited to study ecological resilience (Paper *I*)

2. Quantify and assess the resilience characteristics of lake ecosystems that have been exposed to different stressors (Paper *II*, *III* and *IV*) and assess the influence of management interventions on resilience (Paper *II*)

3. Evaluate if degraded systems (acidified lakes) are more vulnerable to environmental change compared to near-pristine circumneutral lakes (paper *III*)

4. Investigate regional climate effects on the resilience of shallow lakes with contrasting nutrients and size across a latitudinal gradient including Sweden, Estonia, Germany, The Czech Republic, Turkey and Greece (Paper *IV*)

3 Materials and methods

3.1 Lake selection for the observational studies (Papers *I-III*)

A long-term lake monitoring program of multiple habitats and across different trophic levels was initiated in Sweden, in the late 1980s (Fölster *et al.*, 2014, www.slu.se/aquatic-sciences). Lakes of similar size and located in the same mixed forest (boreal) ecoregion of southern Sweden, were selected for this study (Table 1). Historically, this area has had high acidic deposition; where lakes with high acid buffering capacity were marginally affected, whereas those with low buffering capacity became culturally acidified. Extensive liming management interventions were used in many cases as an attempt to restore lakes to pre-acidification conditions (pH and alkalinity).

3.1.1 Sampling

Water quality and biological variables were sampled and analyzed based on standard protocols throughout the study period.

Water quality and biological samples were taken usually once to four times annually from February to early November at a mid-lake station in each lake. Samples were collected from 0.5 m depth using a Plexiglas® sampler and kept cool during transport to the laboratory for further analysis. Samples were analyzed for variables related to acidity (pH, alkalinity, sulphate and chloride concentrations), nutrients (total phosphorus, total nitrogen, organic nitrogen, soluble reactive phosphorus, and silicon), water clarity (Secchi disc depth, water colour, and total organic carbon), ionic strength (electrical conductivity) and temperature. The water quality analyses were conducted at the Department of Aquatic Sciences and Assessment, Swedish University of Agricultural

Sciences following International (ISO) and European (EU) standards when available (Fölster *et al.*, 2014).

Table 1. *Summary of the geographic properties of the studied lakes*

Lake	Coordinates		Lake size (km^2)
Acidified lakes			
Brunnsjön	56°59’58” N	15°72’80” E	0.11
Grissjön	58°76’12” N	15°14’21” E	0.23
Harasjön	57°00’60” N	13°57’92” E	0.58
Härsvatten	58°01’89” N	12°03’03” E	0.19
Rotehogstjärnen	58°81’37” N	11°61’24” E	0.17
Storasjö	56°94’65” N	15°27’12” E	0.38
Circumneutral lakes			
Allgjuttern	57°94’66” N	16°09’63” E	0.16
Fiolen	57°09’06” N	14°52’95” E	1.63
Fräcksjön	58°14’68” N	12°18’11” E	0.27
Humsjön	58°61’99” N	14°47’58” E	0.25
Stora Envättern	59°11’36”N	17°35’35” E	0.37
Stora Skärsjön	56°67’01” N	13°06’53” E	0.33
Limed lakes			
Ejgdesjön	58°88’41” N	11°47’09” E	0.83
Gyltigesjön	56°75’18” N	13°17’40” E	0.40
Gyslättasjön	57°10’67” N	14°48’34” E	0.33

Phytoplankton was sampled from the epilimnion using a 2 m long Plexiglas® tube sampler (diameter of 3 cm). In lakes with surface area > 1 km^2 a single mid-lake site was used for sampling. In lakes with surface area < 1 km^2, five random epilimnetic water samples were taken and pooled into a composite sample, from which a subsample was taken. Samples were preserved with acid Lugol’s solution. Phytoplankton was identified to the lowest possible taxonomic unit (usually species) and enumerated using an inverted microscope following a modified Utermöhl technique (Olrik *et al.*, 1989). Biovolumes (mm^3 L^{-1}) were calculated using geometric shapes based on recommendations of Blomqvist and Herlitz (1998).

Benthic invertebrates were sampled along a single wind-exposed, vegetation-free littoral habitat of each lake in late autumn (late October - early November). Five replicated samples were taken using standardized kick sampling with a hand net (mesh size 0.5 mm) by disturbing the substratum over a 1-m-long stretch for 20 s at a depth of about 0.5 m. Samples were preserved in 70 % ethanol prior to sorting and identification in the laboratory.

Invertebrates were enumerated and identified to the lowest feasible taxonomic unit using a dissecting microscope.

3.2 Pan-European mesocosm experiment (Paper *IV*)

One lake from each of six countries (Sweden, Estonia, Germany, Czech Republic, Turkey and Greece) was selected based on water quality criteria that reflect natural abiotic characteristics of shallow, nutrient-poor lakes across Europe. The following criteria were used: water depth (< 5 m), alkalinity (< 4 meq/L), water colour (< 20 mg Pt/L), electrical conductivity (< 500 mS/m) and total phosphorus concentration (< 25 µg/L) to identify suitable lakes (Table 2) and for setting up the experiment. The experiment was carried out simultaneously in the respective locations, using a standardized sampling method, and ran for approximately six months (May to early November 2011), corresponding to the ice-free period in the northern countries (Landkildehus *et al.*, 2014).

Table 2. *Location of the selected lakes used to accommodate the experiment.*

Country	Lake	Coordinates		Altitude
Sweden	Erken	59°49’59” N	18°33’55” E	11
Estonia	Võrtsjärv	58°12’17” N	26°06’16” E	35
Germany	Müggelsee	52°26’00” N	13°39’0” E	32
Czech Republic	Vodňany	49°09’14” N	14°10’11” E	395
Turkey	Gölet	39°52’38” N	32°46’32” E	998
Greece	Lysimachia	38°33’40” N	21°22’10” E	16

3.2.1 Experimental design

The experiment manipulated two nutrient levels (low, high) and two water levels (shallow, deep) that were replicated four times, resulting in a total of 16 mesocosms in each country. The mesocosms consisted of cylindrical impermeable fiberglass tanks (diameter 1.2 m and 4 mm thick), with two different heights 1.2 and 2.2 m for the shallow and deep treatments, respectively. The mesocosms were secured to floating pontoon bridges that were made of wooden boards and floating materials and were anchored to a fixed position in the respective lake. The mesocosms were randomly arranged in two rows, which were separated by a boardwalk to facilitate sampling. Once the mesocosms were attached to the pontoons, a mixture of gravel and mud from a nearby mesotrophic lake was added as bottom substrate, this mixture was earlier allowed to settle so as to equilibrate total phosphorus fluxes between the sediment and the water phase. Thereafter mesocosms were filled with filtered nutrient-poor water to attain 1020 and 2150 L, corresponding to shallow and deep water levels, respectively.

Four days following the addition of water, the mesocosms were inoculated with plankton (phytoplankton and zooplankton) and sediments (which presumably harbour resting stages) that were collected from five nearby lakes using standardized protocols. Submerged aquatic plants, namely the Eurasian water-milfoil (*Myriophyllum spicatum*) were planted in each mesocosm. The mesocosms were also stocked with planktivorous fish. Three-spined stickleback (*Gasterosteus aculeatus*) was used in most countries, whereas juvenile roach (*Rutilus rutilus*) was used in Sweden due to legal restrictions on the translocation of species between habitats, and Greece where mosquito fish (*Gambusia affinis*) was used due to scarcity of sticklebacks. Since different fish species were used, stocking was thus based on fish biomass (4-20 grams per tanks).

Finally, the phosphorus concentrations were adjusted to 25 µg TP/L and 200 µg TP/L, corresponding to the low and high nutrient treatments, respectively. Nitrogen, on the other hand, was added to reach a ratio of phosphorus to nitrogen of 1:20. The two nutrient levels simulated oligotrophic and hypertrophic conditions, respectively. Nutrient additions were only required for the high nutrient treatments when the experiment started, thereafter monthly nutrient additions were needed in both nutrient treatments (low and high) to account for nutrients loss.

3.2.2 Sampling

Zooplankton was sampled from the mesocosms directly after the introduction of fish. Thereafter monthly samples were taken, using a Plexiglas® tube sampler. Samples over the entire water column were taken and pooled. A well-mixed subsample of 5 L was filtered using a plankton net with a mesh size of 20 µm. Zooplankton were transferred and preserved in a 50 mL bottle containing Lugol's solution. Measurements of temperature, water level, and nutrients were synchronized with the zooplankton sampling events. At the end of the experiment, an integrated sample, corresponding to the entire duration of the experiment, was prepared by mixing subsamples (25% of the original volume) from each monthly sample. Using the integrated samples, zooplankton taxa were identified to the lowest possible taxonomic unit (species). Similarly, body size and biomass were calculated using geometric conversions following a standardized protocol.

3.3 Data used

In paper *I*, a long-term (1988-2012) water quality data set, comprising 23 variables from three circumneutral headwater lakes (Allgjuttern, Fräckjön and Stora Skärsjön) was used to compare the statistical performances and outcomes of two time series methods.

In Paper *II*, phytoplankton time series data (1997-2009) were used to comparatively assess the relative resilience in acidified (Brunnsjön, Härsvatten, Rotehogstjärnen), circumneutral (Allgjuttern, Fräcksjön, Stora Skärsjön) and limed lakes (Ejgdesjön, Gyltigesjön, Gyslättasjön), using a time series modelling technique.

In paper *III*, long-term data (1988-2012) from benthic invertebrates were used to assess if degraded systems (acidified lakes; Brunnsjön, Grissjön, Harasjön, Härsvatten, Rotehogstjärnen and Storasjö) were more vulnerable to environmental changes compared to near pristine systems (circumneutral lakes; Allgjuttern, Fiolen, Fräcksjön, Humsjön, Stora Envättern and Stora Skärsjön), using the same time series modelling technique as in paper *II*.

In paper *IV*, zooplankton data from the mesocosm experiments along a latitudinal gradient were used to assess the impact of the experimental manipulations and regional climatic conditions on the resilience of shallow lakes.

3.4 Statistical analyses

Most statistical analyses that are relevant for the main and specific objectives of this thesis were performed in R version 3.0.2 (R Development Core Team, 2012). The complete descriptions of the different statistical methods used can be found in the individual papers.

In paper *I*, the performances of two time-series methods, Asymmetric Eigenvector Maps (AEM; Blanchet *et al.*, 2008) and Moran's Eigenvector Maps (MEM; Dray *et al.*, 2006), were compared. These two time series are based on redundancy analysis (RDA), but differ in their statistical assumptions. The methods can be outlined as follows:

1. AEM and MEM first extract a set of orthogonal temporal variables (AEMs and MEMs) from the time vector that covers the length of the study period, that are later used as explanatory variables to model

temporal relationships of the response variables (i.e. water quality variables or species data).

2. Significant temporal variables (AEMs and MEMs) are selected, through forward selection procedures, and are linearly combined in the RDA models to extract temporal patterns from the response variable matrices. The resulting temporal patterns are overlaid on significant RDA axes that are tested through permutation tests. Finally, the R software creates linear combination (lc) score plots that depict the modelled temporal patterns, which are associated with each significant RDA axis.

The main difference between the two types of time series models is that MEM cannot handle linear trends and thus requires detrending of response variables (Legendre & Legendre, 2012; Blanchet *et al.*, 2011).

Spearman's rank correlations were used to compare the outcomes, i.e. the modelled temporal patterns of AEM and MEM. The relationship between the individual water quality variables and the temporal patterns from each RDA axis were also explored using Spearman's rank correlation analysis.

In paper *II*, phytoplankton community structure was characterized across three different lake types: acidified, circumneutral and limed lakes, using common metrics (total biovolume, richness, diversity and evenness). Diversity and evenness were calculated following the recent recommendations of Jost (2007) and Tuomisto (2012;2010). Repeated measures analysis of variance (rm-Anova) was performed in Statistica v.5 (Statsoft Inc, Tulsa, OK, USA) to test for the effects of lake type, time and lake type x time interactions on phytoplankton community metrics. Tukey's HSD test was carried out when a significant treatment (lake type) was observed.

Multivariate analysis was also carried out on phytoplankton communities using permutational multivariate analysis of variance in PERMANOVA version 1.6 (Anderson, 2001), based on Bray-Curtis dissimilarity matrices and 9999 unrestricted permutations of square root transformed species biovolume matrices. The relative resilience (using the cross-scale resilience model; Peterson *et al.*, 1998) of phytoplankton communities was assessed using the AEM time series modelling approach. Once the cross-scale structure of resilience was identified, the within-scale attributes of resilience was explored using Spearman's rank correlations. Correlation was used to investigate the relationships between individual phytoplankton species and the temporal patterns (lc scores) of each significant RDA axis. Species that did not statistically correlate with any of the significant RDA axes were considered as stochastic species.

In paper *III*, a similar approach as in paper *II* was used to identify cross-scale attributes of resilience and species with stochastic dynamics. In addition, taxa that correlated with the temporal patterns and stochastic dynamics were assigned into feeding groups (filterers, gatherers, grazers, omnivores, shredders and predators), based on their feeding preferences using the online database http://www.freshwaterecology.info/ (Schmidt-Kloiber & Hering, 2015) to score their preferences. Filterers filter fine suspended materials from the water, gatherers fine particles from the sediment and from detrital materials that has been colonised by bacteria (Wallace & Webster, 1996). Grazers feed mainly on biofilms found on stones and vegetation (Wallace & Webster, 1996). Shredders are able to chew and feed on coarse particulate organic matter, and predators feed on living prey (Wallace & Webster, 1996). Taxa that scored identically among different feeding groups were designated as omnivores. Once feeding groups were assigned functional richness, functional diversity and function evenness within- and across-scale was also determined following the recent recommendations of Jost (2007) and Tuomisto (2012;2010).

In paper *IV*, discontinuity analysis, based on Bayesian Classification and Regression Trees (BCART developed by Chipman *et al.* (1998) and freely available: http://www.rob-mcculloch.org/code/CART/index.html), was used to infer within- and cross-scale resilience from body size and biomass data of zooplankton. BCART identifies groups of maximum homogeneity from rank ordered (log transformed body size and biomass) data, which presumably operate in distinct scaling regimes (Allen *et al.*, 2005; Holling, 1992). The number of homogenous or aggregation groups identified and the number of species present in each group facilitate the assessment of cross- and within-scale attributes of resilience. In addition to within- and cross-scale attributes of resilience two additional metrics were assessed: the length of each aggregation group determined as the difference between the highest and lowest log-transformed body size and biomass of species belonging to a specific group and the distance (gap size or discontinuities *sensu* Allen *et al.* (2005)) between each successive aggregation groups.

The cross-scale, within-scale, aggregation length and gap size were analyzed using a mixed model ANOVA, to determine the treatments (water depth and nutrients) and climate effects and their interaction terms. Non-metric multidimensional scaling (NMDS) with Euclidean distance matrix was used to explore similarities of the overall resilience structure (combining cross-scale structure, within scale structure, aggregation length and gap size). Analysis of Similarity (ANOSIM; 999 permutations) was used to complement the NMDS analysis to investigate treatments (water depth, nutrient level) and climate effects on the four resilience indices.

4 Results and discussion

4.1 Time series modelling technique selection (Paper *I*)

The two time series modelling approaches, AEM and MEM, revealed significant temporal structures of the water quality variables in all three studied lakes. The overall variance explained by AEM models was consistently higher (adjusted R^2 values; Allgjuttern 0.78, Fräcksjön 0.78 and Stora Skärsjön 0.60) than MEM models (Allgjuttern 0.66, Fräcksjön 0.64 and Stora Skärsjön 0.33). AEM revealed temporal dynamics at four, five, and three significant temporal scales for Allgjuttern, Fräcksjön and Stora Skärsjön, respectively, whereas MEM showed temporal dynamics at four scales for Allgjuttern, four for Fräcksjön, and two for Stora Skärsjön (Figure 3). The temporal dynamics depicted by the two models differed. Similarly, Spearman rank correlation analysis showed that the temporal patterns generated by AEM were usually not correlated to those modelled by MEM. The only exception was found in Allgjuttern, where a significant negative correlation (Spearman's rho: -0.67, $P < 0.001$) between modelling methods was found for the temporal pattern associated with RDA axis 2. Furthermore, Spearman rank correlation analysis indicated that more water quality variables correlated with the significant canonical axes from AEM than from MEM, where on average 17 water variables were correlated with the first RDA axis from the AEM model, compared with three from MEM.

These results suggest that choice of a time series model will affect insights and interpretations of temporal dynamics of complex system and ultimately the ecological resilience. AEM was found to outperform MEM, by explaining higher proportions of variance. This finding agrees with earlier studies by Blanchet *et al.* (2011; 2008). Previous studies have suggested that AEM is best suited to study directional processes (Legendre & Gauthier, 2014; Blanchet *et al.*, 2011; Blanchet *et al.*, 2008), for instance the long term environmental changes (due to land use changes, acid deposition and climate) that are known to occur in the selected lakes (Angeler & Johnson, 2012; Monteith *et al.*, 2007; Evans *et al.*, 2005; Renberg *et al.*, 1993).

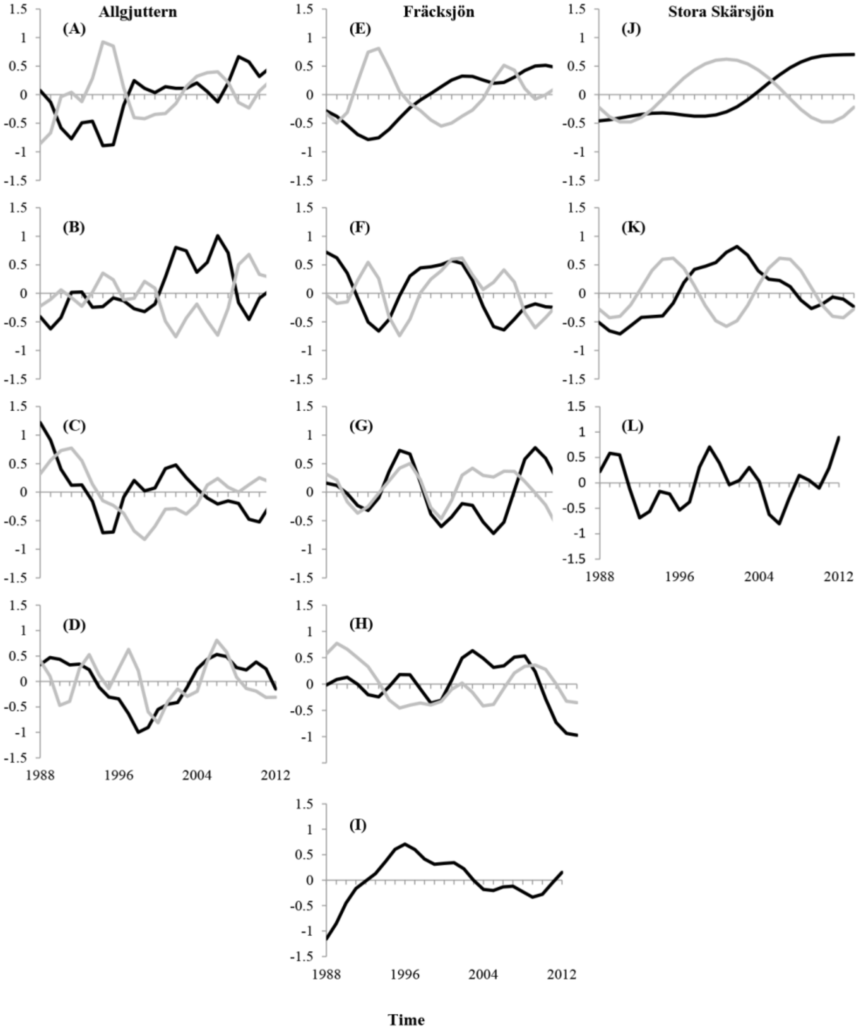


Figure 3. Time series models showing modelled fluctuation frequencies of water quality variables from Allgjuttern (a-d), Fräcksjön (e-i) and Stora Skärsjön (j-l) at different temporal scales (RDA axes). Shown are the patterns based on the linear combination (lc) scores of significant AEM variables (black lines) and MEM variables (grey lines).

Detrending, a mandatory prerequisite of the MEM model, has been criticized to remove key ecological patterns from analyses (Wartenberg *et al.*, 1987; Hill & Gauch, 1980) as observed in the first RDA axes of MEM models. Detrending can be especially problematic when assessing complex systems dynamics, as the impacts of environmental change are scale specific (Nash *et al.*, 2014), with ecosystem changes often unfolding over decades, centuries or millennia (Sheffield *et al.*, 2012; Renberg *et al.*, 1993). Thus, detrending-based methods, including MEM, can lead to ecological misinterpretations of the underlying temporal structures and resilience in ecological systems, where an understanding of scale-specific patterns and processes is crucial (Allen et al., 2014; Nash et al., 2014).

AEM, unlike MEM, has been tailored to handle the unidirectional nature of time (Legendre & Legendre, 2012; Blanchet *et al.*, 2008), where earlier conditions can influence later conditions. These results combined with the logical underpinnings of the models suggest that AEM might be more suitable for assessing and interpreting resilience in ecological systems especially when temporal trends are relevant.

4.2 Resilience of managed and unmanaged lakes (Paper *II*)

Large-scale restoration programs based on liming of surface waters and catchments have been extensively used in Sweden and elsewhere to counteract negative effects of anthropogenic acidification.

Liming was found to improve the water quality and diversity of phytoplankton, equivalent to the targeted reference conditions present in circumneutral lakes (Paper *II*). The within- and cross-scale patterns were similar across limed, acidified and circumneutral lakes, implying that all lakes share similar resilience attributes. However, liming was found to lead neither to communities (PERMANOVA analysis) representative of acidified nor of circumneutral lakes.

Moreover, the results provide new insights about the effects of liming on diversity and resilience. The increase in species richness and diversity triggered by liming, were found to marginally contribute to the within- and cross-scale structure of phytoplankton, but were instead associated with stochastic dynamics. This is counterintuitive to the idea that increased resilience (higher within- and cross-scale redundancy; Allen *et al.*, 2005) is associated with higher diversity (Folke *et al.*, 2004; Carpenter *et al.*, 1999). The level of species with stochastic dynamics was higher in limed compared to circumneutral lakes. Species with stochastic dynamics can increase the adaptive capacity of the system, by harbouring an array of differential responses to disturbances (response diversity) with the potential of substituting affected species, thereby maintaining feedback and critical processes of the system. The results suggest that liming does not move acidified lakes from a degraded state, but rather comprise a particular condition of acidified states with an enhanced response capacity.

These findings suggest that liming is perhaps not an integral restoration tool, and helps to better understand the commonly observed phenomenon where communities return to an acidified state once liming is stopped (Clair & Hindar, 2005).

4.3 Vulnerability of degraded systems to environmental change (Paper *III*)

Acidified lakes are examples of ecosystems that are trapped in a degraded state (Yan *et al.*, 2003; Yan *et al.*, 1996; Marmorek & Korman, 1993) and which may be more vulnerable to environmental change than their counterparts in a desirable state (circumneutral lakes). The systemic vulnerability of acidified and circumneutral lakes to environmental changes were investigated using benthic invertebrates. More specifically, vulnerability was assessed by quantifying attributes of ecological resilience, i.e. within- and cross-scale structure and distribution of functional feeding groups as a measure functional redundancy.

Broad environmental change, including increased water colour and decreased sulphate concentration, were observed over the 25 year study period in both lakes associated with decreasing acid deposition, global warming and changes in land use (Monteith *et al.*, 2007; Evans *et al.*, 2005). If acidified lakes are indeed more vulnerable to environmental change, this should be reflected by lower resilience attributes than in circumneutral lakes. However, the results showed similar distributions of feeding groups within and across temporal scales, meaning that both lake types have similar resilience characteristics and are thus equally vulnerable to environmental change. In addition, both lake types appear to have similar adaptive capacity as indicated by species with stochastic dynamics. The observed similarity in resilience characteristics across acidified and circumneutral lakes might be attributed to compensatory effects, where tolerant species appeared to compensate for the functional loss of acid-sensitive species.

Moreover, some functional feeding groups (Figure 4) were found to be more vulnerable than others; filterers and shredders had the lowest within-scale redundancy, indicating that filterers and shredders are potentially at risk of disappearing from lakes, but these groups are generally more abundant in streams, probably due to habitat preferences (Johnson *et al.*, 2004).

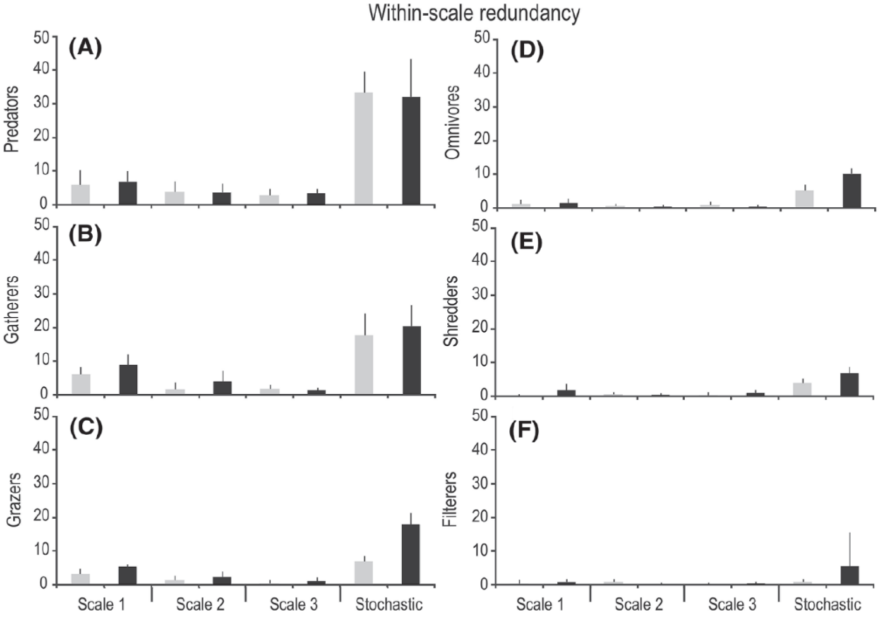


Figure 4. The within-scale redundancy, i.e. distribution of functional feeding groups; (a) predators, (b) gatherers, (c) grazer, (d) omnivores, (e) shredders and (f) filterers, associated with the temporal patterns identified by the time series model for acidified (grey bars) and circumneutral (black bars) lakes.

4.4 Effects of ecosystem size, nutrients and climate on the resilience of shallow lakes (Paper *IV*)

Climate change is considered as one of the most eminent threats to lake ecosystems (Adrian *et al.*, 2009). The effects of climate change, mediated by altered temperature and precipitation patterns (IPCC, 2007), can boost eutrophication in shallow lakes through intertwined pathways that enhance nutrient transport and availability (Kernan *et al.*, 2010b; Jeppesen *et al.*, 2009). Hence, climate change is expected to increase the likelihood of undesirable regime shifts in shallow lakes resulting in impaired ecosystem services such as fisheries, recreation and fresh water provisioning (Folke *et al.*, 2004; Smith *et* *al.*, 1999). A synchronized mesocosm experiment, along a European latitudinal gradient (Sweden, Estonia, Germany, Czech Republic, Turkey and Greece), was used to investigate the effects of two parameters; nutrients and ecosystem size that are predicted to affect the resilience of shallow lakes under future climate change scenarios. Zooplankton communities were used as model organisms, with the aim of quantifying their ecological resilience to the experimental manipulation (nutrients and water levels) across different climatic settings. Resilience was inferred from discontinuity analysis performed on both zooplankton body size and biomass. In addition to the within- and cross-scale patterns which are considered as proxies of relative resilience (Peterson *et al.*, 1998), discontinuity analysis facilitates the quantification of two additional measures (gap size and aggregation length) that are known to convey ecological clues about possible extinction (Allen *et al.*, 1999).

The attributes of resilience were found to be similar across the experimental manipulations (nutrients and size). Such conservative patterns were also observed in marine benthic communities (Havlicek & Carpenter, 2001) and fresh water species (Raffaelli *et al.*, 2000) that were exposed to different disturbances.

However, the results from Greece deviated noticeably from the other study areas, having lower within- and cross-scale structures and wider gaps (Figure 5), which suggest an overall reduced resilience.

In contrast to the other study areas, the mesocosms in Greece suffered from strong drought conditions during the experiment, markedly reducing water levels (about 90% and 50% in the shallow and deep enclosures, respectively). The other southern site (Turkey) also suffered drought conditions by evaporation, but to a lesser extent (approximately 50% and 25% in the shallow and deep enclosures, respectively) compared to Greece, possibly due to the high altitude of the Turkish site that reduced evaporation. This might indicate the existence of a threshold, where the system shifts to an alternative state when exceeding a certain water loss threshold. Prolonged drought can decrease the resilience of an aquatic system and trigger a regime shift in biological communities (Angeler *et al.*, 2013b; Washington-Allen *et al.*, 2008).

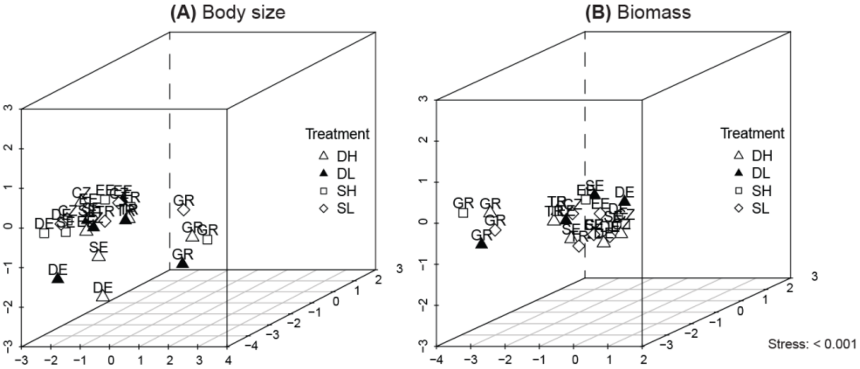


Figure 5. Non-metric multidimensional scaling (NMDS) ordination showing the overall resilience patterns (combining all four resilience indicators; within- and cross-scale structures, aggregation length and gap size) across treatments: DH; deep and high nutrient, DL; deep and low nutrient, SH; shallow and high nutrient and SL; shallow and low nutrient, and countries: SE; Sweden, EE; Estonia, DE; Germany, CZ; Czech Republic, GR; Greece and TR; Turkey.

However, the resilience patterns observed from the Greek site might have been an artefact of the planktivorous fish species (mosquito fish instead of stickleback) used in the experiment. Planktivorous fish are known to affect the resilience of aquatic ecosystem (Carpenter *et al.*, 1999) and the combination of high temperature and reduced space observed in Greece could have stimulated feeding rates and predator-prey encounters (Legler *et al.*, 2010; Wang *et al.*, 2009), thus affecting the resilience of zooplankton. This also implies that climate mediate changes through indirect pathways by affecting a set of organisms that ultimately affect the resilience of the system (Petchey *et al.*, 1999).

5 Conclusions and future challenges

The aim of this thesis was to address current knowledge gaps regarding the quantification of ecological resilience and to enhance mechanistic understanding of how resilience emerges as a function of structural and functional ecosystem properties that operate at discrete scales. The results showed that: (a) degraded acidified lakes have similar resilience characteristics as circumneutral lakes and are thus equally vulnerable to environmental change, (b) lake liming does not seem to move acidified lakes from a degraded state, (c) climate change, more specifically the expected prolongation of drought in semi-arid countries can decrease the resilience of aquatic systems and trigger regime shifts in biological communities, and (d) selection of the statistical method used to infer resilience is crucial, as differences in method requirements and assumptions can lead to different results.

Environmental change is an ongoing process that increases the uncertainty of management and conservation actions. However, the statistical methods used, including time series modelling and discontinuity analysis, are versatile and applicable to both aquatic and terrestrial systems, and have the potential to identify sensitive ecosystems and facilitate the elaboration of mitigation and remediation measures, thus decreasing the uncertainty associated with assessing the effects of environmental change. In addition, these tools provide the means to enhance communication and collaboration with social scientists who are struggling to quantify resilience (Sundstrom *et al.*, 2014). The application of these tools in socio-ecological settings is still in its infancy and has so far been used to understand the resilience of cities and firms (Garmestani *et al.*, 2008; Garmestani *et al.*, 2007; Garmestani *et al.*, 2006). This outlines the need to explore the application of these quantification tools to other non-ecological systems, which might enhance the progress of resilience theory across disciplines (Sundstrom *et al.*, 2014; Brand & Jax, 2007).

Moreover, ecological resilience assessment can benefit if for instance: ecosystems processes such as energy flow in food webs or whole system metabolism are included. Also investigating resilience in a landscape context and more generally using multiple groups of organism in resilience assessments can refine ecological theory and management applications.

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Acknowledgments

This thesis was made possible through the support of many people who deserve my gratitude, in particular:

> My supervisors: David Angeler, Stina Drakare, Craig Allen and Richard Johnson, it has been an honour and an inspiration to work with you and I am grateful that you gave me this unique opportunity.
>
> My family for their continuous support throughout the years and special thanks to Pia-Maria for her understanding and encouragements.
>
> The awesome PhD students group at the department: Alexander, Amélie, Ana, Elin, Eva, Jakob, Joachim, Jose, Kristina, Maidul, Mr Minh, Oded, Pianpian, Rikard, Salar, Steffi and Wiebke, for creating a supportive and cheerful atmosphere.
>
> The administrative staff at the department for helping out with many practical issues and all the people involved in monitoring program.
>
> Sebastian Sonesten and Tim Saari Byström for their assistance in the field.

This project was jointly financed by the by the EU FP-7 Theme 6 project REFRESH (Adaptive Strategies to Mitigate the Impacts of Climate Change on European Freshwater Ecosystems, Contract No.: 244121, www.refresh.ucl.ac.uk/) and the Department of Aquatic Sciences and Assessment at SLU, who I gratefully acknowledged.