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Resilience of aquatic ecosystems

What is it? Can it be measured? Why is it important?

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Omslagsfoto: Anonymous internet source showing metaphorically the increasing human pressures on the world´s ecosystems and their resilience.

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It is undeniable that ecosystems are exposed to multiple and often interacting forms of human stress. It is unclear if and for how long ecosystems, including freshwaters, which are an important asset to societies, will be able to cope with stressors. There is scientific evidence that an ecosystem´s capacity to cope with stress is not infinite, meaning that they can ultimately undergo catastrophic regime shifts, whereupon valuable services for humans are at stake. It follows that our ability to predict global change outcomes is riddled with high uncertainty.

Current management schemes are suboptimal to address this uncertainty, because environmental goals and the indicators to assess these do not embrace the complexity that is inherent to ecosystem dynamics. Ecological theory, especially resilience theory, has advanced in recent years, allowing to empirically measure this complexity. However, the rapid advance in theory, together with the scientific language used to convey new ideas, has not been conducive to practical application of these theories. The main aim of this report is to narrow this divide, and show how an empirical assessment of attributes responsible for the complex dynamics of ecosystems, that is resilience attributes, can be made tractable. In turn, management and environmental policy can be refined, ultimately providing new opportunities to cope with lingering environmental sustainability issues.

Sammanfattning

Sjöar och vattendrag är viktiga för den biologiska mångfalden i Sverige och bidrar också med viktiga ekosystemtjänster till oss människor. Det råder enighet i den vetenskapliga litteraturen att sötvatten är bland de mest sårbara ekosystemen på grund av klimatförändringarna, och svenska sötvatten är inte undantagna från dessa förändringar. Ytvatten kan vara utsatta för kombinerade effekter av till exempel biologiska invasioner, global uppvärmning och återhämtning från försurning. Tillsammans ger dessa effekter komplexa och ofta oväntade förändringar i den abiotiska och biotiska miljön. En grundläggande fråga uppstår: är våra sötvattenekosystem kapabla att anpassa sig till dessa förändringar? Oftast används hotade populationer för att studera hur känsligt ett ekosystem är för miljöförändringar. Även om populationsbaserad kunskap är värdefull, misslyckas denna metod med att korrekt beskriva den komplexa och flerdimensionella dynamiken som karakteriserar ett ekosystem. Följaktligen föreligger stor osäkerhet om hur sjöar och vattendrag kommer att anpassa sig till denna typ av komplexa förändringar i miljön. Det behövs information för att bedöma sårbarheten ur ett ekosystemperspektiv: Vilka är riskerna för ett oönskat regimskifte i akvatiska ekosystem? Vilka faktorer är viktiga för att sådana skiften ska kunna uppstå? Kan vi hantera dessa faktorer för att avvärja regimskiften och istället främja de typer av ekosystem som vi önskar?

I denna rapport diskuteras ett ramverk för att ta itu med dessa frågor. Ramverket har sina rötter i resiliensteori. Takten i den vetenskapliga utvecklingen av resiliensteorin har kanske varit för snabb för att matcha användbarheten av teorin i praktiken. Nu är tiden mogen för att börja använda resiliensteorin i praktiska ekologiska frågeställningar.

Rapporten gör detta genom att ge en översikt av de två tillgängliga metoder som används för att kvantifiera resiliens dvs. hur komplex ekosystemstrukturen och funktionen hos ett ecosystem är . Mycket av arbetet bygger på långtidsdata från nationella övervakningsprogram som ger unika möjligheter att bedöma resiliens med hög ekologisk realism. Tyvärr är en analys baserad på långtidsdata inte möjlig i många ekosystem. Därför presenteras också en metod som möjliggör en analys av ett ekosystems resiliens då man bara har tillgång till data från ett provtagningstillfälle.

Metoder finns alltså som gör en bedömning av ekosystemens resiliens möjlig. Denna rapport beskriver därför framtida prioriteringar som kan bidrar till en effektiv användning av systemsårbarhetskonceptet inom ekologin och resursförvaltning.

Summary

Swedish lakes and fluvial ecosystems host an important part of global biodiversity and provide essential ecosystem goods and services (recreational, provisioning, regulating, supporting) to humans. There is consensus in the scientific literature that freshwaters are among the most vulnerable ecosystems in the face of on-going climate change, and Swedish freshwaters are not exempt from these changes. There is evidence that Swedish surface waters are exposed to the interactive effects of, for instance, species invasions, global warming and recovery from acidification that induce complex and often unexpected changes in the abiotic and biotic environment. A fundamental question arises: are Swedish freshwater ecosystems capable to adapt to these changes?

Despite the simplicity of this question, our current scientific approaches to deal with these questions are to a large extent inadequate. Consequently, much uncertainty exists about the long-term responses of lakes and streams to global change. Ecologist and managers often target populations of conservation interest to inform about impending threats from global change. While valuable, population-based approaches fail to accurately represent the complex and multidimensional dynamics inherent to ecosystems. Consequently, many management conundrums linger. Information is needed to assess vulnerability from a systemic perspective: What is the risk of an undesired regime shift in aquatic ecosystems upon which critical ecosystem services may be lost? Which factors are key to facilitate such shifts? Can we manage these factors to stave off regime shifts and foster desired ecosystem states?

In this *Synthesis Report*, I provide managers and stakeholders with a framework to address these questions. The framework is rooted in resilience theory, which has been advanced in recent years. However, the pace of scientific progress in resilience theory has been perhaps too fast to match practitioners' capacities to implement it. Therefore time is ripe to showcase how alternative management opportunities with an ecosystem focus, rather than a focus on components of ecosystems, can refine and ultimately benefit management.

I demonstrate this providing an overview about available statistical and modelling methods that allow quantifying attributes of ecosystem structures and functions on which their resilience depends. Much of the work builds on long-term data from National monitoring programs, providing unique opportunities to assess resilience with high ecological realism. Not only does this highlight that new monitoring programs should be created, or current programs be kept up; given the uniqueness of the monitoring program worldwide, Sweden can become a leading country to implement a resilience-based management approach of ecosystems. While using long-term monitoring data is definitely strength, resilience can be evaluated also without such data. Alternative approaches using, for instance, body mass data and scrutinizing non-linear relationships of body mass distributions within communities and populations widens the spectrum of tools to evaluate resilience.

While tools are available that make an evaluation of ecosystem resilience appealing, and thus an assessment of system-level vulnerabilities to global change feasible, the implementation of a resilience approach is not without burden. I will therefore also outline future priorities to overcome the obstacles that currently hinder an objective assessment of systemic vulnerabilities to global change.

1. Introduction

Freshwater ecosystems occupy less than 1% of the Earth´s surface and comprise only 0.01% of its aquatic resources, yet these habitats are biodiversity hotspots that are home to 10% of all known species (Dudgeon *et al.*, 2006; Strayer & Dudgeon, 2010). Freshwaters also provide essential ecosystem goods and services to humans (e.g. fishing, recreational, regulating services) (Postel & Carpenter, 1997). However, there is strong scientific consensus that freshwater ecosystems, including streams, rivers, lakes, riparian areas and other wetlands, are highly vulnerable to projected environmental change impacts (e.g., Firth & Fisher, 1992; Poff *et al.,* 2002; Glen, 2010; Boon & Raven, 2012; Capon *et al.*, 2013). There is thus special interest for countries like Sweden that host an important number and diversity of freshwater ecosystems, and that are an important asset to their societies and cultures, to understand this vulnerability.

Current rates of environmental change are unprecedented based on the last 10 000 years of palaeoclimatological evidence. Global mean surface temperature increased by 0.74 °C during the 20th century, and modelling approaches using different CO_2 emission scenarios suggest that temperature will increase another 0.6 to 4 °C by 2099 (IPCC 2007), depending on the willingness of humans to reduce current CO_2 emissions. The pace of climate change is probably too fast to allow many aquatic organisms to adapt to future environmental conditions. Many species are thought to be at risk because their ability to adapt through natural selection may be limited, and because their habitats may be significantly altered or reduced to allow for the colonization of suitable habitat through dispersal and migration (Poff *et al*., 2002). Furthermore, the synchronisation between life-cycle events and seasonal changes in habitats may be disrupted (Winder & Schindler, 2004; Harper & Peckarsky, 2006), limiting the ability of organisms to reproduce. Thus, worst-case scenarios depict increasing rates of species extinctions and loss of aquatic biodiversity that can reduce ecosystem service provisioning to human societies.

Awareness of the threats of global change on freshwaters has stimulated research into the vulnerability to global change of aquatic ecosystems and their constituent communities. More than 650 studies, including experimental, observational and modelling studies, covering different climatic, landscape and biogeographical contexts and spatial and temporal scales, have been published since 2010 (search string "freshwaters, vulnerability, climate change" in google scholar; September 2013). These studies provide insight into potential future ecological changes resulting from climate change, including broader ecosystem-level responses, i.e. altered patterns in host-parasite interactions (Marcogliese, 2001; Paull, LaFonte & Johnson, 2012), body size structure (Yvon-Durocher *et al.*, 2011), and foodwebs (Meerhoff *et al.,* 2012; Shurin *et al*., 2012; Ledger *et al.*, 2013). They also highlight a lingering double whammy that researchers and managers have recognised as an important impediment to a sound aquatic resources management and conservation in the future: 1) high uncertainty in the prediction of ecological responses, and 2) low possibility of generalization of climate change impacts across freshwater ecosystems (e.g., Wilby *et al.*, 2010).

Insight from past changes in Earth´s climate highlights that the ecological consequences of climatic change may not become manifested until critical thresholds are exceeded (Angeler, 2007; Willis *et al*., 2010; Minckley, Shriver & Shuman, 2012), meaning that rather than gradual changes, ecosystems may undergo non-linear, rapid transitions to new states in the future (i.e., catastrophic regime shifts; Scheffer & Carpenter, 2003). Efforts are made to develop early warning indicators of regime shifts in ecosystems (Van Nes & Scheffer, 2007; Carpenter *et al.*, 2011; Seekell *et al.*, 2012; Veraart *et al.*, 2012). However, for most ecosystems it is uncertain to predict if the risk of a regime shift with a consequent loss of ecosystem services exists, when and how long it will take to happen (Hughes *et al.*, 2013) or if it can be recognised early enough for management to steer systems away from such regime shifts (Biggs *et al.*, 2009). This uncertainty arises partly from the complex ecological responses that climate change triggers in the environment. Interacting climatic and other, non-climatic, anthropogenic factors (pollution, habitat fragmentation, species invasions) are often highly context dependent, causing synergistic or antagonistic ecological responses. Biogeographical, altitudinal and climatic contexts may further modulate outcomes. This limits our possibility to infer general patterns of climate change in the aquatic environment.

The aim of this report is to provide a framework that allows aquatic ecologists and managers target, and eventually reduce, the uncertainties related to predictability and generalization of vulnerabilities of freshwater ecosystems to global change. The framework of this report is rooted in resilience theory, which builds the cornerstone of environmental sustainability research (Walker & Salt, 2006; Folke *et al.*, 2010). Resilience theory has undergone significant progress in recent years, allowing for measuring and quantifying the attributes of ecological complexity that confer ecosystems stability in the face of disturbances. I demonstrate this providing an overview about available statistical and modelling methods that allow quantifying core concepts of resilience. Much research on climate change vulnerability has centred on determining sensitivities and extinction risks of species and populations. The framework provided here shows how such information can be incorporated in a broader evaluation of systemic vulnerabilities to climate change. I define systemic vulnerabilities as the sensitivity of aquatic ecosystems to undergo regime shifts in the future that are potentially irreversible and therefore focus vulnerability from an ecosystem perspective. The increased likelihood of regime shifts at local, regional and even global scales with climate change motivates this rationale (Folke *et al.* 2004; Rockström *et al.*, 2009; Hughes *et al.*, 2013).

I provide a brief overview of our current knowledge of vulnerability to global change in aquatic systems in general, and put this general context specifically into the Swedish scene to highlight patterns of global change that affect Swedish aquatic ecosystems. I then present core concepts necessary for understanding resilience, and outline how current information of species vulnerabilities can be used to assess systemic vulnerabilities to global change. Using case studies, I show how informed management decisions can be made. Finally, I discuss future priorities to overcome the obstacles that currently hinder an objective assessment of systemic vulnerabilities to climatic change.

2. Vulnerability: a brief overview of current knowledge

Concerned by the putatively high extinction risk of aquatic taxa in the warmer future and their negative consequences for biodiversity and ecosystem service provisioning, aquatic ecologists have intensively studied thermal responses to climate change at the organism-level. Also other, non-climatic factors have been assessed that can modulate outcomes and complicate inference. The literature accumulated in recent years is vast, so I focus on key insights gained on vulnerability to climate change, rather than providing an exhaustive review of the literature. I specifically emphasise the key issues (uncertainty, limited predictability) that provide the rationale for studying systemic vulnerability, and highlight how current knowledge about trait responses to climate change can be incorporated in its assessment.

2.1. Warming, thermal tolerances and vulnerability

Insight on structural changes in communities and ecosystems can be strengthened through an assessment of functional attributes, and thermal traits of organisms have proven useful for identifying taxa that are most sensitive to warming. Many studies therefore have a vulnerability focus on the organism level, investigating how physiological adaptations to thermal conditions affect species fitness, their distributions in landscapes and consequently local and regional community structure.

According to expectation, many studies have reported a decline of cold-adapted species. Compelling evidence for this comes from a time series analysis of the fish fauna across European lakes. Jeppesen et al. (2012) have shown that cold-adapted fish species show strong patterns of decline and these patterns were evident both in the warmer south and the cooler north of Europe. This suggests no specific biogeographical contingency of fish vulnerability, highlighting a major challenge for conserving fish diversity at broad spatial scales. Thermal traits have also predicted well community responses and geographical range patterns in stream invertebrates (Chessman, 2012), highlighting *a priori* the possibility to assess potential range contractions of cold-adapted species and expansions of taxa with higher thermal tolerance. However, recent studies found that aquatic species can adapt either evolutionarily (Reed *et al.*, 2011) or through phenotypic plastic responses (acclimation) (Galbraith, Blakeslee & Lellis, 2012) to climate change that can alter their thermal tolerances, but such responses can vary because thermal optima show high variability even within single populations of freshwater organisms (Cottin *et al.*, 2012). Also, some studies have found that native species suffer higher extinction risks with climate change than invaders in freshwater fish and invertebrate communities (Moyle *et al.*, 2013; Domisch *et al.*, 2013), but even for exotic species invasion success will be uncertain (Britton *et al.*, 2010). It is clear from these examples that, although a quantification of temperature and population-level vulnerability provides insight into the consequences of global warming, a focus on warming alone does not capture the full picture of potential change (Koehn *et al.*, 2011). Climate change triggers complex changes in the abiotic and biotic environment, leading to multifaceted forms of impact and context specific responses in the environment (Covich *et al.*, 2004; Gillson *et al.*, 2013). These inevitably increase further uncertainty and limit predictability.

2.2. Vulnerability beyond temperature: increasing uncertainty

The increased uncertainty can be exemplified with the limited generalization of climate change impacts even within an ecosystem type. For instance, Bush *et al.* (2012) found that invertebrate communities in mountain and coastal streams covering a broad latitudinal gradient in Australia were affected by distinct degrees of climatic factors, spatial isolation, anthropogenic activities and sea-level rise. This suggests that coastal and mountain streams will need different climate change mitigation strategies. In a similar vein, the lake study by Danis *et al.* (2004) showed that future climate change impact differs even within an ecosystem type. They highlighted different responses in deep lakes due to different responses in mixing patterns that can affect evolutionary old deepwater fauna in some but not all deep lakes.

A high variability in vulnerability patterns within ecosystem types may not be surprising given the multiple dimensions along which system intrinsic (size, volume, morphometry, biological factors) and extrinsic factors (landscape settings, human use) interact. This variability will likely be exacerbated in the warmer future with the mounting pressure on aquatic environments to cover basic resource demands of increasing human populations (Vorosmarty *et al*., 2000; Baron *et al.*, 2002; Dudgeon, 2010). Recognising this challenge, researchers have begun not only to focus on temperature-related traits of organisms, but also to assess traits that characterise the broader suitability of habitat for organisms; for instance, flow conditions in streams, dietary and habitat specialisation, and body size (Chessman, 2009, 2013; Rosset & Oertli, 2011). Climate change creates environmental situations where specific stressors (e.g. insecticides) (Kattwinkel *et al.*, 2011), direct changes in habitat template (Jacobsen *et al.*, 2012) or indirect effects like changes in water clarity (Angeler, 2013) can outweigh temperature-related effects. A multi-trait approach is therefore very useful for identifying the most pressing stressors in freshwaters (Statzner & Beche, 2010; Kittel *et al*., 2011). In turn, this may inform about the vulnerability of ecosystems to these stressors and provide basic knowledge for their management.

3. Vulnerability: the Swedish context

Sweden started a long-term monitoring program of multiple habitats and trophic levels of lakes to follow the effects of anthropogenic acidification of regionally representative lakes in relation to lakes with a higher acid neutralizing capacity (Johnson 1999). These monitoring efforts are unique worldwide, both in the spatial extent of ecosystems covered and the constant and standardized sampling of abiotic variables and biotic communities through time. Sweden certainly has an international leading role in this regard. Thanks to this initiative it is nowadays possible to track environmental change with high ecological realism, and assess trends of change in abiotic and biotic variables that transcend the initially targeted effects of acidification.

Figure 1 shows integral changes in the abiotic environment of lakes. It is clear that international policy to mitigate anthropogenic acidification effects in the environment has been successful in terms of decreasing the deposition of acidifying compounds to surface waters, resulting in decreasing sulphate concentrations and concomitant increases in pH and alkalinity. Trends in water temperature are less clear, but it is obvious that lakes are becoming more nutrient poor, while organic matter content increases leading to higher water colour and reduced transparency (Figure 1).

There is evidence that these changes in the abiotic environment are conducive to biological changes as well. These changes are manifested, for instance, in the spread of an invasive, bloom-forming flagellate, *Gonyostomum semen* (Raphidophyta) (Angeler *et al.*, 2012). Several biodiversity impact assessment studies have shown that *Gonyostomum* does not affect overall species richness, but contributes to alter community composition (Angeler *et al*., 2010), especially in habitat-specific ways (Angeler & Johnson, 2013). *Gonyostomum* impacts may go beyond alteration of structural and functional ecosystem attributes of lakes to also affect services that are important for humans. For example, *Gonyostomum* blooms have negative impacts on the recreational services of lakes, causing allergic skin reactions in swimmers and increase maintenance costs in water treatment plants (Cronberg *et al*.1988; Hongve *et al.,* 1988). Invasions, like the case with *Gonyostomum*, can interact with other stressors to change ecosystem structures and processes further. There is for example evidence that invertebrate communities in lakes change due to changes in temperature regime (Burgmer *et al*., 2007), and other studies have shown that changes go beyond the local scale of lakes to also alter regional diversity patterns. For instance, Angeler (2013) studied how diversity changes between lakes (beta diversity). He found that all lakes contribute more equally to regional diversity over time. That is, each lake contains a set of species that is unique for this specific lake and which is not share across the lakes. This uniqueness of diversity observed in each lake suggests that all lakes become potential targets of management actions to conserve biodiversity on a regional scale. The broader implication for management was that a regional conservation strategy is not only logistically difficult; it will also be a financially expensive expectation in the future.

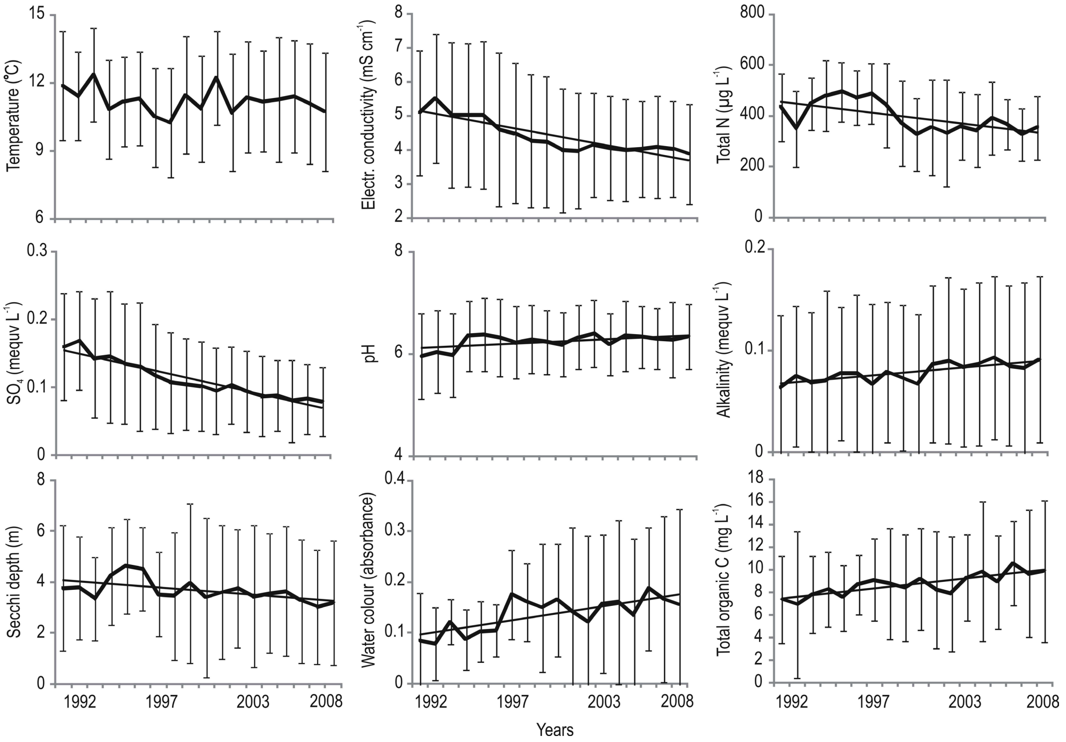

Figure 1: *Temporal patterns of selected water quality variables between 1992 and 2009 in lakes across Sweden. Shown are the overall patterns (means ± SD) from 26 lakes analysed for this study. Trend lines indicate significant monotonic change over time identified by generalised least square regressions. The figure is taken from Angeler (2013)*

Despite these recent research results highlighting future challenges for management of surface waters in Sweden, it is unclear how abiotic and biotic lake conditions will further change with ongoing global change. More specifically, uncertainty exists whether ecosystems can adapt to these changes in the long-term or whether their adaptive capacity eventually erodes, leading to undesired and potentially catastrophic regime shifts on local and regional scales. This motivates more research into possibilities to cope with this uncertainty from a scientific perspective, which then can be used to make informed decisions for management and policy development.

4. Assessing vulnerability: the next steps

Two mutually non-exclusive key challenges emerge for aquatic resource management, based on our current knowledge of climate-change-related vulnerabilities of freshwaters. Can we reduce uncertainty to identify realistic ecosystem vulnerabilities to climate change? How can we incorporate current knowledge in the systemic assessment of vulnerabilities and improve inference? In this section, I will discuss a framework that provides ecologists and managers with the possibility to reduce uncertainty in vulnerability assessments without sacrificing the complexity needed to understand ecosystem structure and processes. I discuss the underpinning theories in the context of resilience. Resilience theory has gained traction in recent years because it makes the attributes that characterise ecological complexity quantifiable, allowing for an assessment of critical ecosystem attributes that mediate their ability to cope with disturbances.

4.1. Resilience theory in a nutshell

Different definitions of resilience have been published, and aquatic ecologists have so far studied resilience following the engineering (Gaudes, Artigas & Munoz, 2010; Gerisch *et al.*, 2012; Robinson, 2012) and ecological (Bogan & Lytle, 2011; Ireland *et al.*, 2012; Angeler *et al.*, 2013) definitions of resilience in the global change vulnerability context. Discerning between these definitions is necessary because both emphasise different ecological phenomena that need to be considered for assessing systemic vulnerabilities to climate change.

Holling (1973) defined ecological resilience as a measure of the amount of change or disruption that is required to transform a system from being maintained by one set of reinforcing processes and structures to that being maintained by a different set of processes and structures. Inherent to this definition is that ecological systems can undergo non-linear change or shift between alternative states (i.e. regime shifts). In the ecological literature, the existence of alternative states of ecosystems has been exemplified by the simple ball-in-cup heuristic (Figure 2A). This definition differs radically from engineering resilience, which is considered a measure of return time following perturbation (Figure 2B). Engineering resilience is based on the premise that a system will perform a specific task consistently and predictably around an equilibrium regime, and thus a system will re-establish performance quickly should a disturbance occur. However, ecosystems can operate in multiple basins of attraction and therefore do not have an equilibrium regime, and ecological resilience is therefore more relevant for understanding ecosystem dynamics, especially in the global change context. The following example makes these differences clear.

It is recognised that climate change will likely trigger more frequently non-linear changes (regime shifts) in aquatic ecosystems (Meerhoff *et al.*, 2012). Shallow lakes are well-known models of such shifts that upon excessive nutrient enrichment, for instance, shift from a clear-water state dominated by submerged macrophytes (desired state) to another state characterized by turbid water, frequent algal, often toxic, blooms and reduced ecosystem service provisioning (degraded or undesired state) (Carpenter & Cottingham 1997; Scheffer, 1997). Both states are stable, and major management intervention is required to shift a lake from the degraded to the desired state. In this case an engineering view of resilience would always, and incorrectly, predict that a lake in a turbid state would inevitably return to the clear state without management interaction.

Ecological resilience is a broader concept than stability, because it explicitly considers a compartmentalization of ecological structures and processes by scale that are commensurate in space and time (Holling, 1992; Angeler, Göthe & Johnson 2013; Allen *et al*., 2014). These scaling relationships can be described, for instance, at the individual zooplankton scale range where predation and competition occur in cm^3 to m^3 in space and hours to days in time; a lake scale range with surface areas from multiple m^2 to km^2 and water renewal times lasting years to decades; to a landscape scale range that covers hundreds to thousands of km^2 that has formed over centuries and millennia. A multi-scale spatiotemporal view of ecological systems is useful because the impacts of climate change can differ depending on the scale of observations (Angeler, Drakare & Johnson, 2011; Nash *et al.* 2014), allowing for the identification of the kind of stressor and the magnitude of their impact across scales. An explicit view of scaling relationships in ecological systems permits quantifying several mutually non-exclusive core concepts and issues that are thought to confer systems resilience. These core concepts are briefly outlined.

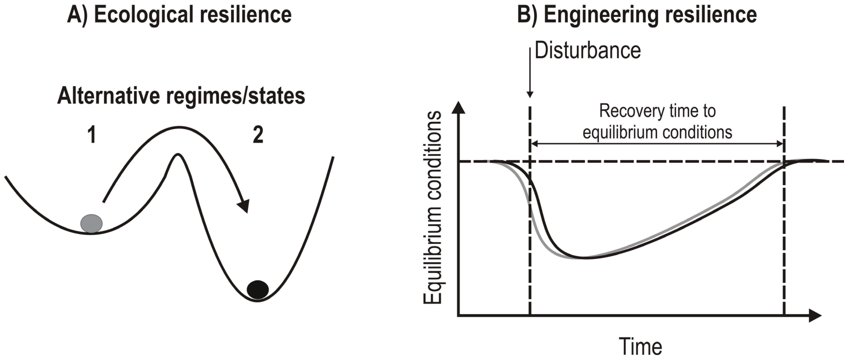

Figure 2*: Comparison of different resilience concepts: Ecological (A) vs. engineering resilience (B). Ecological resilience considers that ecological systems can exist in alternative system states or regimes, while engineering resilience only focuses on recovery time to equilibrium conditions after disturbances. For further explanations see text.*

4.2. Core concepts

Important to the understanding of the following key concepts is the notion that ecosystem processes (flux of matter and energy; primary productivity) depend on functional attributes of species within ecosystem and their responses to disturbances rather than on structural community attributes, e.g. species richness (Hooper & Vitousek, 1997; Nyström, 2006; Mori, Furukawa & Sasaki, 2013). Implicit to the systemic assessment of vulnerabilities is the quantification of the distributions of functions at multiple scales of space and time. Understanding how functions are distributed within and across scales, and positive interactions between functions and processes, has implications for the resilience of ecosystems.

4.2.1. Cross-scale resilience, functional redundancy and the insurance effect

Peterson *et al*. (1998) have described the cross-scale resilience model, which builds on the premise that the resilience of ecological processes, and ultimately of ecosystems, depends in part on the distribution of functions within and across scales of space and time. At either a single scale, resilience increases due to a redundancy of ecological functions at the same scales (Allen, Gunderson & Johnson, 2005). In this model, resilience is also thought to be strengthened if functions are present at different scales. The cross-scale resilience model relates to the concepts of functional redundancy or the insurance hypothesis (e.g., Yachi & Loureau, 1999; Mori *et al.*, 2013). These concepts have received much research attention to elucidate the relationships between biodiversity and ecosystem functioning. However, much of this research has neglected that ecological processes are compartmentalized by scale as posited by resilience theory. Thus, incorporating biodiversity-ecosystem functioning approaches into empirical testing of the cross-scale resilience model will likely allow for a more mechanistic understanding of biodiversity and their role in ecosystems and potentially result in refined management information.

4.2.2. Response diversity

The within and cross-scale distribution of species and their role for resilience can be further scrutinized with the concept of response diversity (Elmqvist *et al.*, 2003). Rather than focusing on the redundancy of a specific function, this concept emphasizes the variation in responses to environmental change by species within a functional group. In other words, response diversity considers the functional make up of a species accounting for multiple traits (Mori *et al.*, 2013) that modulate species responses through, for instance, distinct colonization, growth, competition and dispersal abilities. If for example all species within a functional group have similar trait configurations, it can be expected that all respond similarly to disturbance. In this case response diversity, and therefore resilience, is low, meaning that an entire functional group can be wiped out by a disturbance event. Thus, the ability to quantify response diversity within and across scales of ecological systems would provide further insight into their relative resilience to climate change.

4.2.3. The role of rare species

In ecological systems most species are rare, being represented by only a few individuals or restricted to selected habitats, but the role of rare species, and their potential loss in ecosystems are unclear. Mouillot *et al.* (2013) have recently shown that highly distinct combination of functional traits are supported predominantly by rare species that differed from those of common species in coral reefs, alpine meadows and tropical forests. They concluded that a loss of these rare species, even within high diversity systems, would have disproportionate, negative effects on ecosystem functions in these systems.

These results have important implication for the resilience of ecosystems because they contribute an important facet to response diversity. In ecosystem modelling these rare species can show stochastic dynamics (Angeler *et al.*, 2013). However, because patterns of cross-scale structure are explained by dominant taxa, stochastic species are often discarded from the inference process. In other resilience assessment methods (i.e., discontinuities in animal body size; Allen & Holling, 2008) species dominance patterns, and therefore the role of rare and dominant species, are not accounted for. There is evidence that after disturbances rare species with stochastic dynamics may replace dominant species, contributing to the maintenance of functions in ecosystems (Walker, Kinzig & Langridge, 1999). It is clear that rare species with presumably stochastic dynamics comprise an important facet of resilience, adaptive capacity. Thus, inference about the vulnerability of ecosystems to climate change can be optimised if assessment is based both on within- and cross-scale patterns explained by dominant species and the stochastic dynamics shown by rare species.

5. From theory to measurement

The cross-scale resilience model highlights that the identification of the scales of structure present in a system is non-trivial. There are several methods available to measure scale-specific patterns in ecological systems, but these methods differ in their assumptions, which need to be considered when assessing resilience and comparing results based on different methods. I will specifically deal with discontinuity analysis and time series modelling in this report, because these methods have been used extensively in the analyses of real data; therefore, results derived from studies using these methods have high ecological realism compared to theoretical models and simulation studies. Table 1 provides a brief overview of the methods and highlights pros and cons of each method.

5.1. Discontinuity analysis

Classification and regression tree analyses and their Bayesian implementations (Chipman, George & McCulloch, 1998), kernel density estimation (Havlicek & Carpenter, 2001) and the gap rarity index (Restrepo *et al.*, 1997) have been used to evaluate discontinuities in animal body-mass distributions. Holling (1992) hypothesized that the discontinuous organization of ecological systems is ultimately mirrored in the structure of animal communities, positing that behavioral, life history and morphological attributes of animals adapt to discontinuous environmental patterns because these patterns reflect opportunities for food, shelter and other resources. Indeed, Holling (1992) found a correlation between breaks in distributions of animal body mass, an integrative variable allometric with many ecological attributes (Peters 1983), and discontinuities in structures and processes in the boreal forest of Canada. He interpreted aggregations of species (or modes) along body mass distributions as scales at which resources and structure are available to organisms that have evolved to exploit resources at these specific but not at other scales (Figure 3). This means that species within the same body mass aggregation interact in their resource use, but they do less so with species in other aggregation groups. In contrast, gaps (discontinuities or troughs) in the distribution (Figure 3) reflect the transition between structuring processes, and thus scaling regimes (i.e. scale breaks). At these transitions there is no ecological structure or resource pattern with which animals can interact, or there is great variance and instability in the structures or patterns.

***Table 1**: Comparison of methods available for assessing cross-scale structures necessary for studying systemic vulnerabilities to climate change.*

Method	Data sets	Advantages	Limitations
Discontinuity analyses (GRI, CA, CART, BCART, KDE)	Univariate, rank-ordered, log-transformed data (e.g., body size or mass)	- Data easy to obtain either from available sources or through measurement. - Simple assessment of non-linear (scale-specific) structures in data.	- Species dominance patterns not explicitly accounted for. - Resilience assessment limited to the evaluation of cross-scale patterns. - Limiting assessment of ultimate factors causing discontinuities.
Time series and spatial modelling (Canonical ordinations[a,b]; wavelet analyses[c])	Multivariate; species abundance and/or presence-absence data	- Species abundances accounted for. - Separating the role of dominant and rare species. - Evaluation of complementary aspects of resilience and adaptive capacity. - Relating patterns to dynamic environmental change.	- Data acquisition labour intensive, high resource demand. -Higher analytical complexity relative to discontinuity analysis. -Scales and patterns of structure contingent on sampling frequency and length. - Limited availability of adequate long-term data.

Abbreviations: GRI, Gap Rarity Index; CA, Cluster Analysis; CART, Classification and Regression Trees; BCART, Bayesian CART; KDE, Kernel Density Estimates (see text).

[a] Angeler, Viedma & Moreno (2009), an example for time series modelling; [b] Dray *et al*. (2006), showing the modelling framework for assessing spatial resilience; [c] Keitt & Fischer (2006), time series modelling.

Holling´s discontinuity hypothesis has been expanded theoretically, and empirical analyses have shown that the location of species within body mass aggregations is non-random with regard to several ecological phenomena (Figure 3). Increased variability at transitions between scales, measured with discontinuities in animal body size distributions, has been associated with nomadism (Allen & Saunders 2002, 2006), species invasions and extinctions (Allen *et al.* 1999, Allen 2006), and population dynamics (Wardwell & Allen 2009). Nomadism is often found in ecosystems that exhibit high variability in resource abundance in time and space, so nomadism reflects some form of spatial process to cope with this resource variability. In the absence of such spatial processes, higher resource variability can induce higher population fluctuations, and in turn increase the extinction risk of organisms (Pimm 1991). Increased environmental variability may further enhance the effects of competition, amplifying the extinction probability (May 1973). The propensity of declining species to have body masses proximate to discontinuities suggests that high variation in resource abundance and location in space and time is a hardship for some species. This hardship is further increased when proximity to discontinuities comprises an opportunity for invasive species that can drive native species of similar size to extinction if they are able to better use resources.

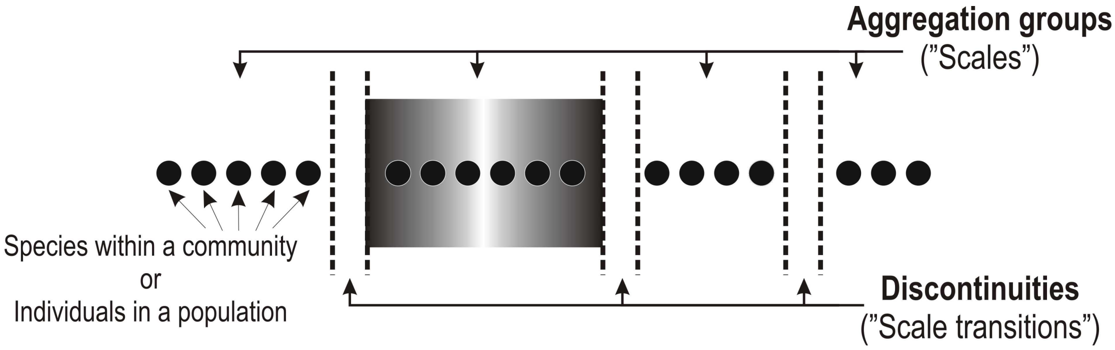

Figure 3: *Conceptual overview of the discontinuity approach. Species (individual dots) within a community are rank-ordered (from low to high) with respect to body mass (log-transformed). Discontinuities or gaps (vertical dotted bars) are identified statistically and separate species into aggregation groups of species with similar body masses. These aggregation groups putatively mirror scale-specific structure and processes in ecosystems, while the discontinuities reflect transition zones or "scale breaks". The figure shows that the original community based approach can be extended to population-level analysis. The shaded area in the second body mass aggregating reflects zones of higher ecological variability (edges; grey areas) and stability (center; white areas).*

That animal body mass distributions from ecosystems are discontinuous now is widely accepted. Although numerous mechanistic hypotheses have been forwarded to account for this (Allen *et al.* 2006), a version of the Textural Discontinuity Hypothesis has the most support (Nash *et al.* 2014). However, basic uncertainty remains regarding some specifics of the hypothesis. Evidence is compelling that discontinuous body mass distributions reflect discontinuous structures in the environment, and in some cases the identity of some of that structure is clear (Nash *et al.* 2013). The discontinuities themselves have been characterized as both "forbidden zones" that comprise hardships for species; that is, where either no resources exists or where their distribution is highly variable in space and time complicating their acquisition. The association of heightened variability in animal populations at the population and community levels as manifest by variability in population abundance, nomadism, invasions and extinctions has been documented for a number of systems (Allen & Holling 2008).

Discontinuity analyses have been used to identify the number of dominant scales that are present in animal communities or other complex system (Allen *et al.*, 2005; Allen & Holling, 2008). Although body mass is an important trait of animal species, the lack of sufficient body mass data for other organism groups (e.g., plants) has led to a bias of discontinuity research towards a few taxa. Also, because body mass integrates processes acting at distinct evolutionary and ecological time scales, our ability to discern among the relative importance of ultimate factors generating discontinuous body mass distributions is limited. Furthermore, species abundances are not accounted for in discontinuity analysis of body mass, so the role of dominant *vs* rare species cannot be separated (Table 1). Therefore, using data independent of body mass, such as population variability, to identify discontinuities and cross-scale structure may increase the robustness of discontinuity analyses (Table 1). Time series analysis has been advocated as such a robust alternative.

5.2. Time series modelling

Ecosystems are usually measured and managed at scales that are tractable to humans, usually at scales that extend between tens to thousands of meters, and frequencies ranging weeks to decades. Time series modelling allows us to identify the scales of temporal frequencies in complex systems, and makes it possible to track the imprints of environmental change over time (Keitt & Fischer, 2006; Angeler, Drakare & Johnson, 2011; Angeler, Allen & Johnson, 2013). For example, analysis of long-term data has revealed discrete groups of species that exhibit distinct temporal frequencies, with some responding to slow environmental variables and others responding to fast variables (e.g., Angeler, Allen & Johnson, 2013).

Methodologically the identification of community patterns at different temporal frequency scales is relatively simple and based on an automated calculation, which minimizes the risk of introducing a researcher-based bias in model construction. The original method has been described by Angeler *et al.* (2009). A description of an updated approach can be found in Angeler *et al.* (2013), and Figure 4 provides a simplified schematic of how the method works. Briefly, in this updated version temporal variables are extracted by AEM analysis (Asymmetric Eigenvector Maps, Blanchet et al. 2008, Borcard et al. 2011). The AEM analysis produces a set of orthogonal temporal variables that are derived from the linear time vector that comprises the length of the study period (i.e., time steps in years, months or days that comprise the temporal window for community measurements in each ecosystem) and that can be used as explanatory variables to model temporal relationships in community data. The type of AEM variables computed for time series analysis was designed for spatial analysis to account for linear trends in the response variables, but has also been used in time series modelling (Angeler *et al.*, 2013). Because time comprises a directional process, AEM is suitable for modeling both components of linear temporal change and fluctuation patterns at different frequency scales in communities.

The AEM analysis yields a series of variables with positive eigenvalues from the conversion of the linear time vector, each of which corresponds to a specific temporal structure and scale in community dynamics: the first AEM variable models linear trends and the subsequent variables capture temporal variability from slow to increasingly shorter fluctuation frequencies in the community data over the study period. For each ecosystem, a parsimonious temporal model for community dynamics can then be constructed by running a forward selection on the AEM variables. Because AEM analysis is efficient in covering linear trends no detrending of models is necessary.

In a next step, Redundancy Analysis (RDA) is used to related AEM variables to the community data. The RDA retains significant AEM variables and these are linearly combined to extract temporal patterns from the Hellinger-transformed species matrices; that is, the RDA identifies species with similar temporal patterns in the species × time matrix and uses their temporal patterns to calculate a modeled species group trend for these species based on linearly combined AEMs. The significance of the temporal patterns of all modeled fluctuation patterns of species groups revealed by the RDA is tested by means of permutation tests. The RDA relates each modeled temporal fluctuation pattern with a significant canonical axis. The R software generates linear combination (lc) score plots, which visually present the modeled temporal patterns of species groups that are associated with each canonical axis. Counting the number of significant canonical axes, the cross-scale aspect of community dynamics important for resilience can be quantified (Angeler et al. 2013). The temporal patterns identified at each scale can then also be correlated with environmental data. This allows for assessing environmental correlates of scale-specific community dynamics.

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

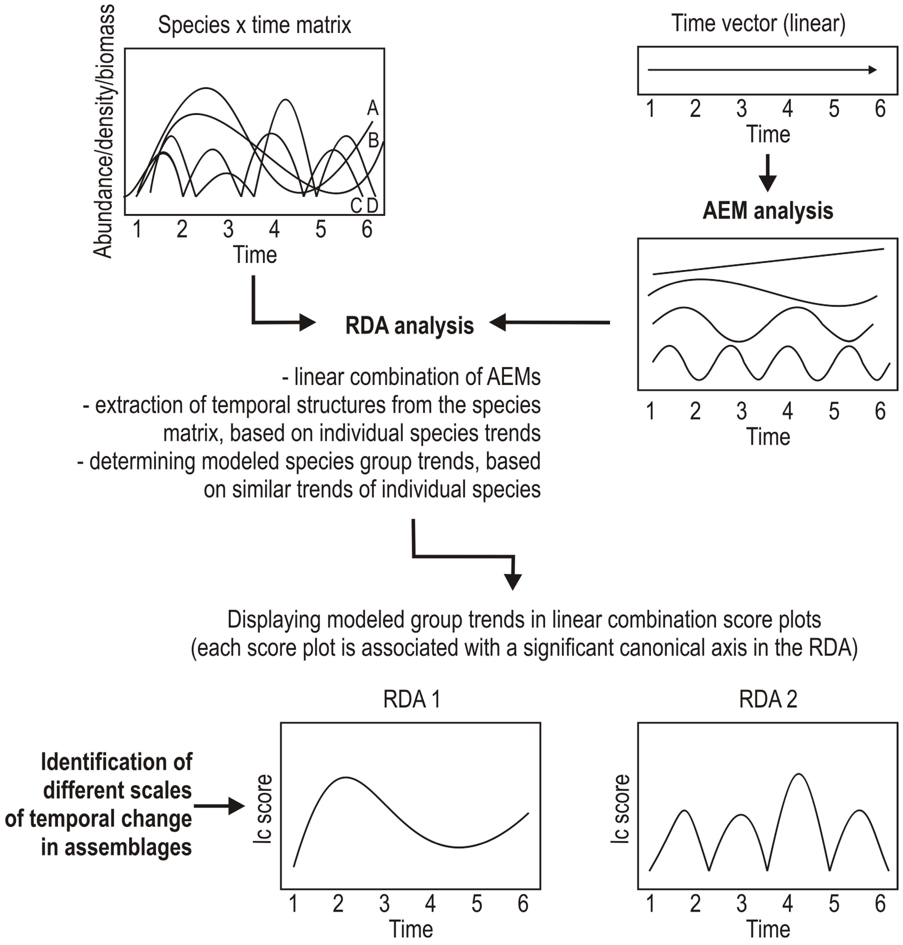

Figure 4: *Flow chart outlining the steps involved in time series modelling. First, a linear time vector is converted into AEM (Asymmetric Eigenvector Maps) variables, which are then related to the species × time matrix of a specific ecosystem by means of RDA (Redundancy Analysis). The RDA identifies species with similar temporal trends in the species × time matrix and calculates a modeled species group trend from their collective patterns. Significant modeled trends are associated with significant RDA axes, and these trends are visually shown in linear combination score plots. Because RDA axes are independent from each other, they represent temporal patterns at independent scales.*

5.3. From individual ecosystems to entire landscapes

Multiscale, hierarchical spatial modelling (e.g. Dray *et al.*, 2006) allows extending assessment of resilience from the ecosystem to landscape scales, providing opportunities for testing the vulnerability of entire networks of ecosystems or regional landscapes to global change (Cumming, 2011; Angeler *et al.*, unpublished manuscript). This spatial modelling approach is similar to the method outlined in 5.2. with the exception that instead of a single ecosystem, multiple sites are considered in the analysis. That is, instead of a linear time vector comprising sampling intervals in a single system, in the spatial analysis models are constructed on the basis of the geographical coordinates of multiple sites. Both time series modelling and its spatial analogue hold much promise, but the scales of pattern and structure that can be discerned have upper bounds set by the limit of the temporal extent or number of sites covered in the data series, and lower bounds set by the temporal frequency or spatial resolution of sample collection.

6. Case studies

6.1. Subarctic lakes in Sweden

Ecosystems at high altitudes and latitudes are expected to be particularly vulnerable to the effects of climate change (Wrona *et al.*, 2006). Angeler, Allen & Johnson (2013) assessed the responses of littoral invertebrate communities to changing abiotic conditions in subarctic Swedish lakes with long-term data (1988–2010) and compared the responses of subarctic lakes with those of more southern, hemiboreal lakes. They used the time-series modeling approach described in 5.2. to identify dominant and distinct temporal frequencies in the data to track community change at distinct temporal scales (Figure 5). They also determined the distribution of functional feeding groups of invertebrates (predators, gatherers, grazers, omnivores, shredders that play important roles in ecosystem processes) within and across temporal scales to evaluate resilience based on the predictions made by the cross-scale resilience model (Peterson *et al.*, 1998; see also section 4.2. of this report).

Two patterns of temporal change within the invertebrate communities were identified that were consistent across the lakes (Figure 5). The first pattern was one of monotonic change (slow group in Figure 5) associated with changing abiotic lake conditions due to global change mediated impacts on water clarity. The second pattern was one of showing fluctuations largely unrelated to gradual environmental change (fast group in Figure 5). Thus, two dominant and distinct temporal frequencies (temporal scales) were present in all lakes analysed. Although the contribution of individual feeding groups varied between subarctic and hemiboreal lakes, they shared overall similar functional feeding group attributes (richness, evenness, diversity). The redundancies of functions within and between the observed temporal scales were similar across lakes, highlighting similar resilience characteristics in subarctic and hemiboreal lakes (Figures 6 and 7). An important finding was that a replacement of cold-stenothermic with warm-tolerant species maintained the functional underpinnings of resilience in subarctic lakes. This case study shows how inference about climate change impact can be strengthened when a compartmentalization of ecological functions by scale is accounted for in assessment studies.

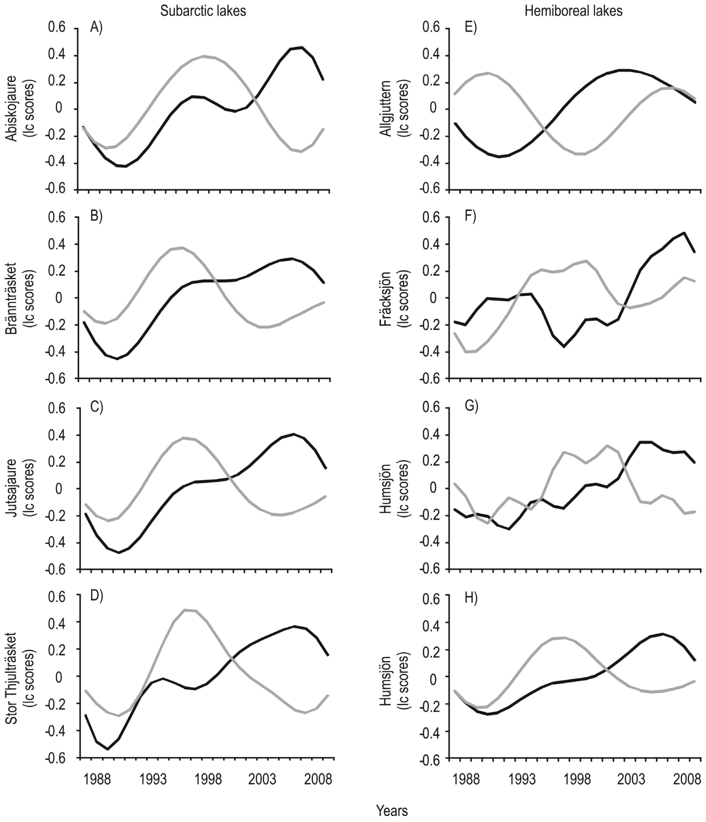

Figure 5: *Temporal patterns of two species groups associated with RDA 1 ("slow" group; black lines) and RDA 2 ("faster group"; grey lines) obtained from multivariate time series modelling of invertebrate communities in subarctic (A-D) and hemiboreal (E-H) lakes. These patterns are determined from species x time matrices (i.e. the analysis is taxonomy based). Inference about functional characteristics is made a posteriori by identifying species that describe the "slow" and "fast" temporal patterns and their functional feeding group characteristics.*

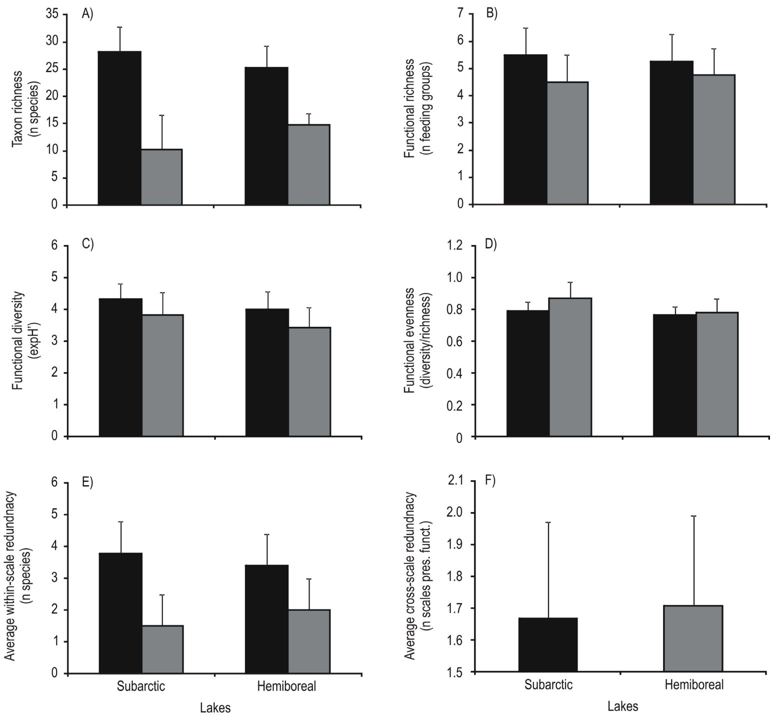

Figure 6: *Comparison of structural (taxon richness; A) and functional (B-D) community metrics, and average within-scale redundancy in "slow" species groups (black bars) and "faster" species groups (grey bars) for subarctic and hemiboreal lakes. Shown is also the average cross-scale redundancy (the number of scales in which the studied feeding groups are present) for subarctic and hemiboreal lakes (F). Shown are means ± standard deviations of four subarctic and four hemiboreal lakes.*

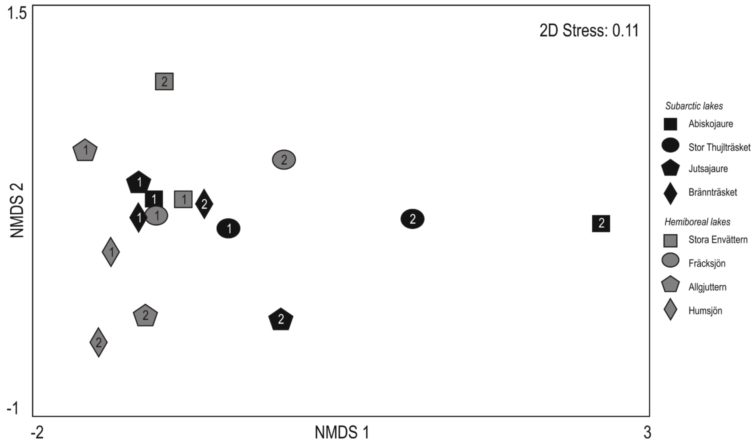

Figure 7: *Nonmetric multidimensional scaling ordination (Bray-Curtis based) showing similarities of functional feeding group attributes across slow (symbols with 1) and faster (symbols with 2) species groups in subarctic and hemiboreal lakes. The graph shows an overlap of functions within and between subarctic and hemiboreal lakes, which similar to the patterns found in the univariate analysis (Figure 6), highlights similar resilience attributes.*

6.2. Acidified Swedish lakes

The subarctic lakes study aimed at identifying resilience characteristics between lake types that have potentially different vulnerabilities to global change (that is, without knowing *a priori* how human action has affected these lakes). However, many cases exist where human footprints already have had a negative effect on ecosystems. A case in point is anthropogenic acidification, leading to a biodiversity loss in many lakes that were sensitive to acidification due to their low acid buffering capacity. There is evidence that acidification caused a regime shift of many lakes, and despite the implementation of international policy to mitigate the impact of acidification, many lakes have resisted to return to previous conditions due to weak chemical and biological recovery (Johnson & Angeler, 2010; Angeler & Johnson, 2012). In scientific terms this resistance to return to a previous ecosystem state has been referred to as hysteresis.

Hysteresis can maintain degraded ecosystems in a stable state, preventing them from returning to desired states. However, it is unclear whether degraded, hysteretic states of an ecosystem are potentially more vulnerable to undergo further regime shifts with ongoing environmental change than undegraded states. Similar to the subarctic lakes study, Angeler, Allen & Johnson (unpublished manuscript) compared littoral invertebrate communities to changing abiotic conditions in acidified (degraded state) and circumneutral (desired, undegraded state) Swedish lakes with long-term data (1988-2012), using the time series modelling approach described in 5.2. They identified again dominant and distinct temporal frequencies in the data, allowing to track community change at distinct temporal scales. In addition to dominant temporal frequency patterns, they assessed additionally species with stochastic dynamics that were not associated with the temporal frequency patterns observed. They determined the distribution of functional feeding groups of invertebrates within and across temporal scales, and in the stochastic group of species. The distributions of functions within and across temporal scales and in the stochastic species group have been considered to confer resilience to ecosystems, despite changing environmental conditions. Three patterns of temporal change within the invertebrate communities were identified that were consistent across the lakes (Figure 8). The first pattern (RDA 1) was one of monotonic change associated with changing abiotic lake conditions. The second (RDA 2) and third (RDA 3) showed fluctuation patterns largely unrelated to gradual environmental change. Thus, at least three distinct temporal frequencies (temporal scales) were present in all lakes analyzed. As was the case in the subarctic lakes study, acidified and circumneutral lakes shared overall similar functional richness, evenness, diversity, and redundancy patterns within and across the observed temporal scales and in the stochastic species group (Figures 9 and 10). Again, these similar resilience characteristics highlight similar systemic vulnerabilities to global change between lake types. That is, although acidified lakes have already undergone a potential regime shift these results suggest that these lakes have a similar likelihood as near-pristine ecosystems to undergo further regime shifts with ongoing environmental change.

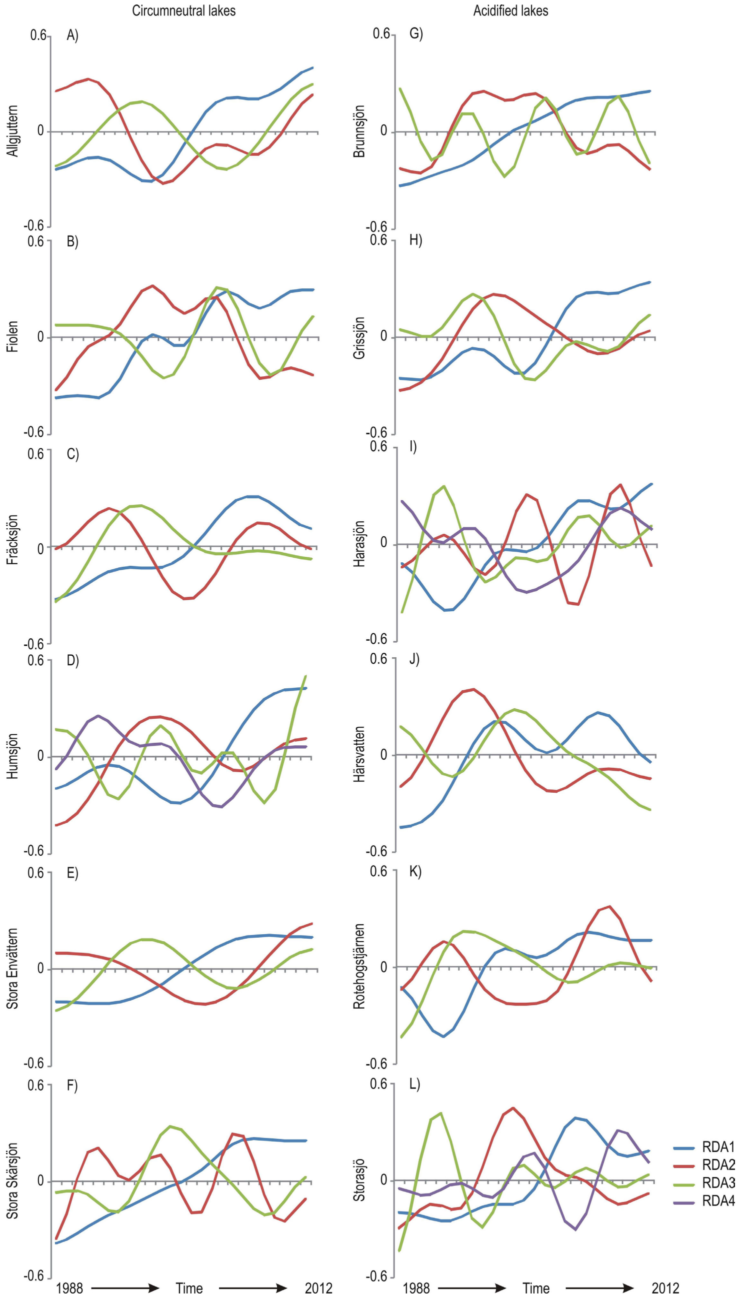

Figure 8: *Temporal patterns of species groups associated with canonical axes obtained from multivariate time series modelling of invertebrate communities in circumneutral (A-F) and acidified (G-L) lakes.*

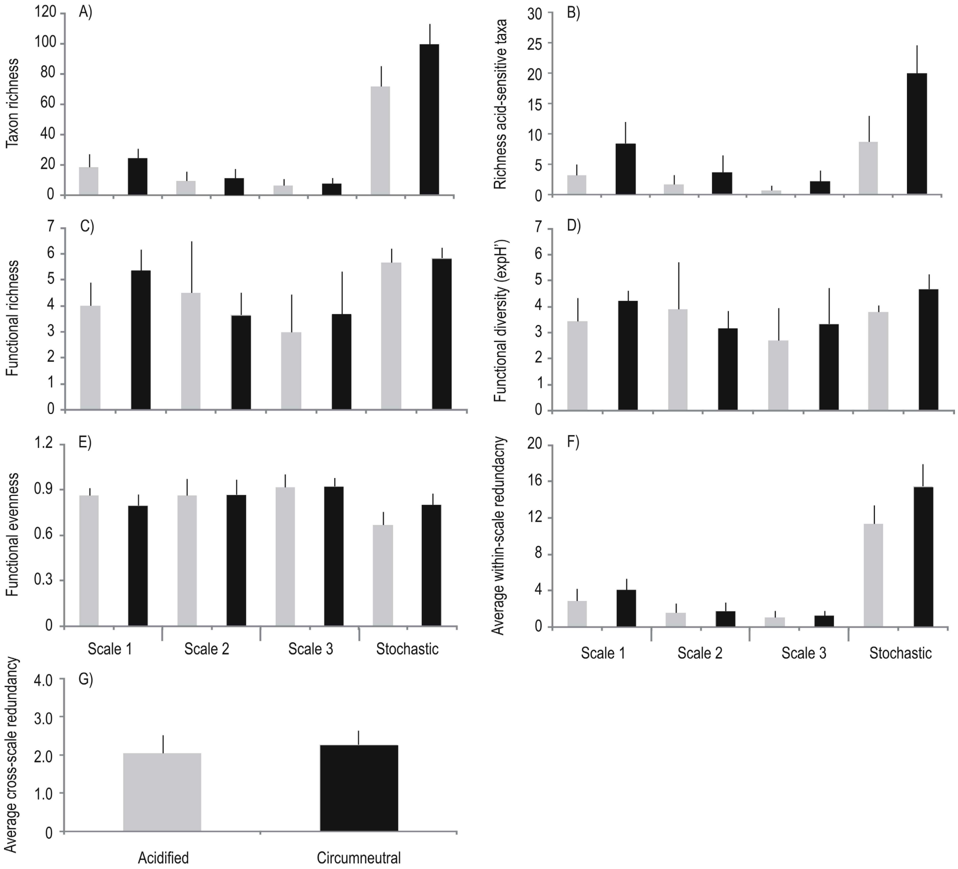

Figure 9: *Comparison of structural (total taxon richness, A; richness acid-sensitive taxa, B), functional (C-E) community metrics, and average within-scale redundancy (F) associated with the temporal patterns identified by time series modelling for acidified (grey bars) and circumneutral (black bars) lakes. Shown is also the average cross-scale redundancy for acidified and circumneutral lakes (G). Shown are means ± standard deviations of six acidified and six circumneutral lakes.*

These results are encouraging, because although acidified lakes in a degraded state often have damaged fish communities, limiting their value for fisheries, they have often clearer waters, contributing to other recreational (boating, swimming, diving) and aesthetic services. Some of these services might be at stake if acidified lakes would be more prone to undergo further regime shifts with global change. Also this study makes clear how long-term monitoring efforts, combined with an ecological complexity approach that are often neglected in assessing global change problems, can facilitate an evaluation of systemic vulnerability. Measuring ecological resilience attributes, and comparing these attributes across organism groups and system types with presumed different vulnerabilities based on known histories of ecological degradation has potential to identify ecosystems at risk of undergoing catastrophic regime shifts. This can contribute to reduce uncertainty in the assessment of the potential sensitivity of ecosystems to global change, and facilitate the planning of management and conservation action in the long term.

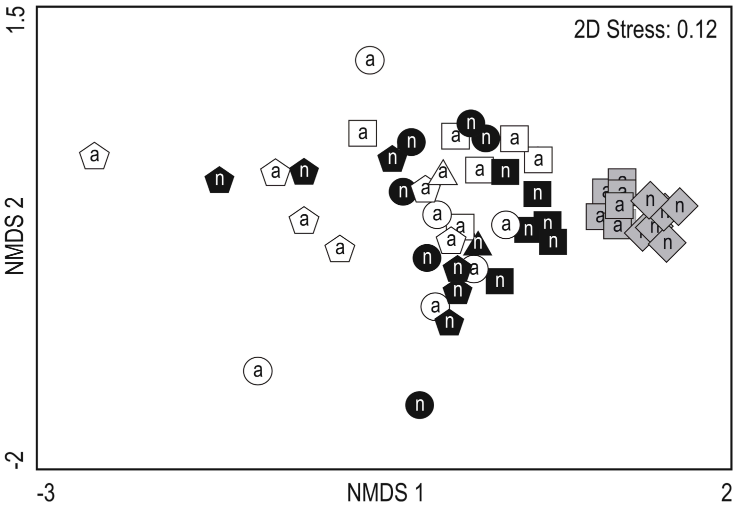

Figure 10: *Nonmetric multidimensional scaling ordination (Bray-Curtis based) showing similarities of functional attributes across species groups with slow (squares), intermediate (circles), faster (diamonds) species groups in acidified (white symbols) and circumneutral (black symbols) lakes. For lakes Humsjön and Harasjön functional attributes associated with a fourth temporal pattern (triangles) are shown. Also shown are, similarities of functional characteristics of groups of species with stochastic dynamics (grey symbols).*

6.3. Species invasions

Long-term monitoring of ecosystems as in the case studies presented above is rather an exception than a rule, meaning that for many ecosystems not enough data are available to assess resilience form a dynamic and multiscale perspective. Although time series modelling has an advantage to track patterns of environmental change explicitly, methods that allow measuring resilience on short time scales are needed. Determination of the discontinuous distribution of body mass in communities is one possibility (as in 5.1.). I am unaware of a study that has used this approach in the context of Swedish freshwaters, although Angeler et al. (2012) have used discontinuity analysis to study biomass patterns of *Gonyostomum semen* at local and regional scales during a 10-year period. I will therefore provide an example from the Florida Everglades that highlight the potential of using discontinuity analysis, specifically in the context of biological invasions.

One of the side effects of environmental change is species invasions that may have pronounced negative effects on aquatic ecosystems and landscapes. Using the vertebrate fauna of the Everglades wetland complex of south Florida (USA), Forys & Allen (2002) quantified how the loss of native species of amphibians, birds, reptiles and mammals and invasion by nonnatives may alter functional group richness within and across scales. They carried out discontinuity analyses on rank-ordered body mass data to identify groups of species that operate presumably in similar scaling regimes. They found that despite large changes in species composition due to potential extinctions and successful invasions by nonnative species, functional group richness did not change significantly within scales. There was also not any significant loss of overall redundancy of function across scales, and overall body mass pattern did not undergo substantial change as a result of invasions. As was the case with the Swedish lake studies, this highlights also the robustness of the vertebrate fauna to invasions, and the broader resilience of these communities to the plethora of anthropogenic stressors that currently affect the Everglades.

7. A conceptual model for measuring systemic vulnerabilities to environmental change

Based on these case studies and our current understanding of resilience theory we can develop a conceptual model to guide managers in endeavours to assess empirically the systemic vulnerability of freshwaters to climate change (Figure 11). The model builds on discontinuity analysis and time series modelling that have proven useful for assessing resilience. These techniques have been used in several resilience assessment studies (overview in Allen *et al.*, 2014; Nash *et al.*, 2014), facilitating comparisons across communities and ecosystems.

In a first step, the conceptual model emphasises the need to identify the scale-inherent structures in data sets for assessing systemic vulnerabilities (Figure 11). Once the cross-scale structures have been identified, the next step is to associate scaling patterns with specific taxa and evaluate the functional attributes of these species and their contributions to within and cross-scale redundancies. If multiple traits are available that allow estimating potential responses to disturbance, the functional redundancy analysis can be refined with an assessment of response diversity patterns that are compartmentalized by scale or present in species groups with stochastic dynamics.

The model is simple because it shows how complexity attributes of ecological systems that are necessary for understanding their systemic vulnerability to climate change can be evaluated in two straightforward steps. I will now show how the model can be used to address practical management questions.

7.1. Application to management

Resources for managing ecosystems are not infinite, requiring the identification of trade offs in priority settings for management. Freshwater ecologists and managers are challenged to identify ecosystems that are highly vulnerable to environmental change; more specifically, those that face an impending regime shift. The conceptual model (Figure 11) provides not only possibilities for reducing uncertainty by identifying systems that are more vulnerable to climate change; it also allows for standardized comparative analyses of systemic vulnerabilities within and across habitats that can facilitate the identification of ecosystems that should receive management priority.

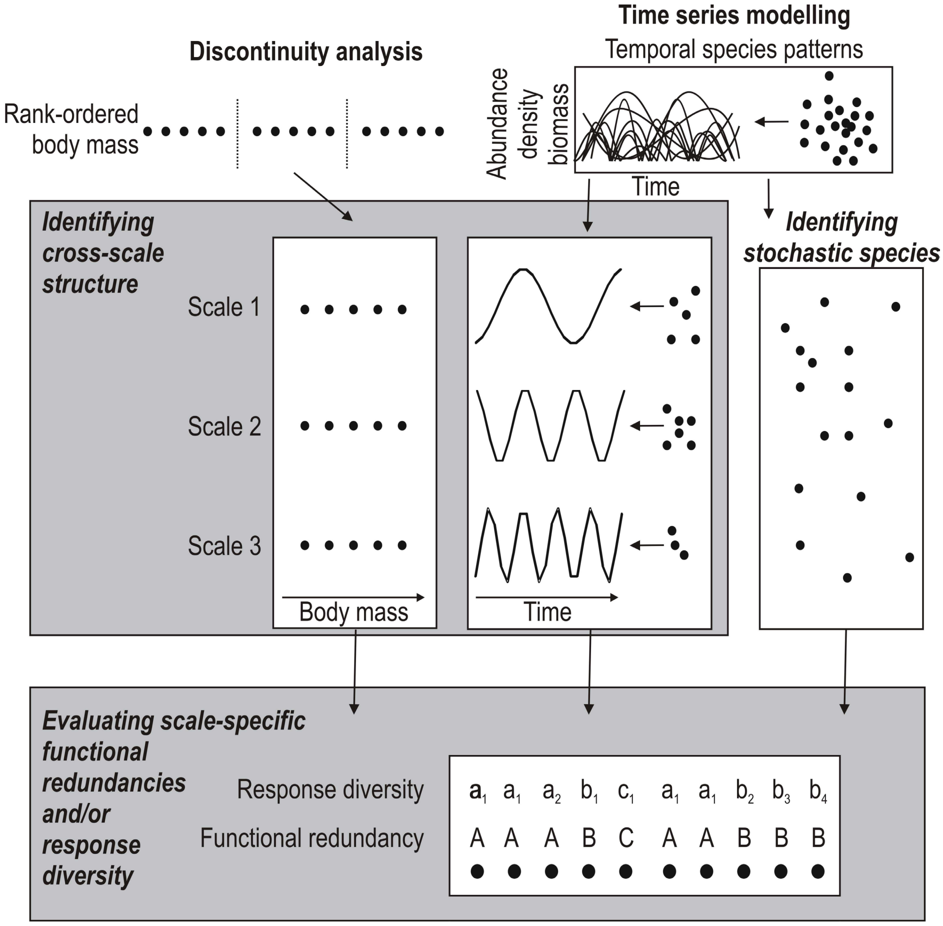

***Figure 11**: Conceptual model outlining approaches for identifying scale specific structures necessary for understanding the systemic vulnerability of ecological systems to climate change. In a first step, discontinuity analysis or time series analysis can be used to identify the cross-scale structure in data sets; time series analyses also allows identifying species with stochastic patterns that are not contributing to cross-scale structure. Discontinuity analysis is based on rank-ordered body mass data of species within a community (black dots); it aggregates species in putatively distinct scaling regimes that are separated by “scale breaks” or discontinuities (vertical dotted lines). Time series analysis extracts groups of species with contrasting temporal frequency patterns from species x time matrices, based on temporal patterns of abundances, densities or biomass. After identifying cross-scale (and stochastic) patterns, the distribution of functional attributes of the species explaining these patterns can be assessed. When a multiple trait analysis is possible, the analysis of functional redundancy within and across scales can be complemented with an estimation of response diversity that is compartmentalised by scale (and in the group of stochastic species).*

By quantifying and comparing cross-scale structures and the distribution of functional traits within and across scales, inference about the relative resilience of freshwaters can be made. We illustrate this with the following hypothetical scenarios (Figure 12). In these scenarios we incorporate species vulnerabilities, accounting for their physiological sensitivities to higher temperatures or other stressors that might contribute to their extinctions with ongoing environmental change. For simplicity, these species are symbolized by the white dots and distinguished from species with higher tolerances to environmental stress (black dots) in our scenarios (Figure 12). In the “low vulnerability” scenario, species within a community carry out the hypothetical functions A, B, and C. In this scenario, function A has the highest within- and cross scale redundancy, followed by functions B and C. All functions are carried out by “vulnerable” and “tolerant” species. Ignoring potential functional compensation processes, this scenario suggests that an extinction of vulnerable species will be less detrimental for the ecosystem, because all functions are still carried out by tolerant species, both within and across scales, once sensitive species went extinct.

If we simply reshuffle the vulnerability characteristics of species, we can obtain a contrasting scenario that reflects a putatively high systemic vulnerability to climate change. In this scenario, extinctions may decrease the within- and cross-scale redundancies of functions B, and lead to a loss of function C altogether. This highlights that the systems capacity to fulfill critical processes associated with these functions that may be relevant for ecosystem service provisioning are jeopardized. If managers can identify ecosystems with such vulnerability characteristics, management priorities can be geared towards maintenance of these functions (Figure 12).

It is not our aim to provide an exhaustive list of interventions that are potentially applicable in ecosystems to achieve this goal. As pointed out before, environmental change can have context-dependent effects and will therefore require site-specific approaches. However, the following considerations can provide guidance for tailoring specific management plans.

Our scenarios are built on current theory and empirical examples that climate change has scale-specific impacts (Angeler, Allen & Johnson, 2013; Nash *et al.*, 2014). Our scenarios highlight the need to identify the scales that are amenable to management. For example, species that operate in scaling regimes that operate over very broad spatial extents an long periods of time (i.e. those capturing climate change) may be more difficult, if not impossible, to manage in the long term. The Swedish case studies make clear how the effects of global change can be particularly strong at scales with slow dynamics that operate over broad spatial extents. Neither are current governance structures designed to, nor resources available, to cope with climate change management of freshwaters at such scales (Nilsson & Persson, 2012). It is therefore necessary to identify scales that are either unaffected by global change or that allow managing scales that are tractable within the constraints set by current natural resources governance schemes. Managing these scales can contribute to maintain or increase functional ecosystem properties at these scales, compensate for the loss of such attributes at scales that cannot be managed, and eventually foster desired ecosystem states and stave off regime shifts.

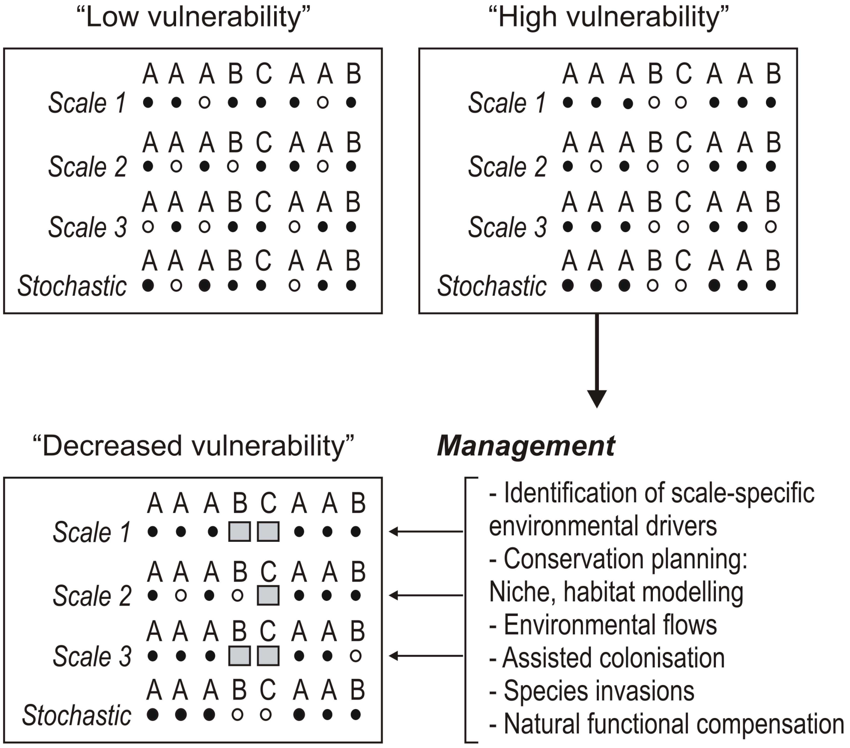

Figure 12: *Scenarios contrasting high and low systemic vulnerabilities to climate change of ecological systems, and how vulnerability can be decreased through management. For explanations see text.*

In practice, this means that management might be most effective at local to regional scales where ecological processes can be tracked at infra-seasonal to seasonal to inter-annual scales. At these scales, management can target to maintain or increase functional redundancy through assisted translocations (Olden *et al.*, 2011) to compensate for a potential loss of redundancies at unmanageable scales. Detailed spatial and temporal conservation planning (Hermoso, Ward & Kennard, 2012) and other niche (Pearson & Dawson, 2003) and habitat modelling (Keith *et al.*, 2008) can be very useful to manage the abiotic habitat template (e.g., environmental flows; Arthington *et al.*, 2010; Yen *et al.*, 2013) at these scales to optimize the viability of resident species and assisted colonizers (species symbolized with grey squares in Figure 2). Optimizing assisted colonization may be desirable because maintenance of local functions through natural colonization processes from regional sources may be limited (Thompson & Shurin, 2012). Although still debated, also the roles of exotic species merit attention (Allen *et al.*, unpublished). Exotic species can compensate for the loss of functions and increase the resilience in ecosystems, thereby decreasing their systemic vulnerability to environmental change; however, the benefits of "assisted invasions" need to be carefully balanced against other negative side effects in freshwaters.

8. Conclusion and future challenges

Managers are in need of assessment tools to understand the boarder impacts of climate change on ecological systems. The conceptual model presented here can be useful because it allows assessing the current status of vulnerability across ecosystems in a comparative way and identifying systems that should become priority targets for management. Not only would this allow to reduce uncertainty considering potential vulnerabilities to change, it would also entail a more effective use of often limited resources dedicated to freshwater management. However, a risk with status assessments is that future responses are not accounted for. This means that ecosystem that may look currently robust to change, like subarctic (Case study 1) and acidified (Case study 2) lakes or the Everglades (Case study 3), may face an erosion of resilience in the future (Forys & Allen, 2002).

It is clear that a systemic assessment of climate change vulnerabilities will require a great amount of data of sufficient temporal span and spatial extent. Exceptional data sets from long-term monitoring programs have proven very useful so far. However, the broader application of promising temporal or spatial modelling tools is currently limited by the general lack of standardized long-term (centuries, millennia) data with good spatial resolution. There is a clear need to create more long-term monitoring efforts (Maberly & Elliot, 2012; Viheervaara *et al.*, 2013), which in combination with paleontological data may allow for a better understanding of complex system responses to climatic change.

Existing data allow for studying vulnerability patterns empirically. These, in combination with specifically designed experiments (Ledger *et al.*, 2012), provide opportunities for obtaining complementary and more mechanistic information between structure, functions and process rates. Improved trait-based knowledge, especially those that can be divided in response traits to assess the system´s resistance to disturbance and effect traits to assess its recovery after disturbance (Sterk *et al.*, 2013) will further strengthen inference. Aquatic communities (microbes, plankton) are especially suitable for experimental manipulation, facilitating testing of hypothesis about the influence of perturbations on ecosystems and their structural and functional attributes.

Future scenarios of the effects of global climate change are pessimistic regarding loss of biodiversity and sustainability of ecosystem services. Politicians, scientists, and managers should exploit every tool available that could help conserve our environment. Our conceptual model for evaluating systemic vulnerabilities could be very useful for some of these tasks.

Despite this report highlighting possibilities for alternative environmental assessment and management in the future, it needs to be stressed that current legislation is not conducive to their implementation. The current environmental goal framework for surface waters in Sweden is almost exclusively based on chemical criteria (Table 2). Biological indicators, like e.g. the presence of pearl mussel (i.e. a population-based indicator) or the quality of nesting bird communities in and around waters are not well represented. If systemic measures are to be used as goal criteria, it is clear that environmental policy will need to be refined to allow for a systematic application of system-level indicators in assessment.

Indikator	**Ansvarig myndighet**
Antal isdygn	Jämtlands län
Begränsat näringsläckage – fånggrödor	Länsstyrelserna i samverkan
Begränsat näringsläckage – skyddszoner	Länsstyrelserna i samverkan
Fosfor i sjöar	Södermanlands län
Föryngring av flodpärlmussla	Länsstyrelserna i samverkan
Häckande fåglar vid vatten	Länsstyrelserna i samverkan
Nedfall av kväve	Naturvårdsverket
Nedfall av svavel	Naturvårdsverket
Skyddade sjöar och vattendrag	Havs- och vattenmyndigheten
Strandnära byggande vid sjöar och vattendrag	Havs- och vattenmyndigheten
Växtskyddsmedel	Kemikalieinspektionen

***Table 2**: Summary of environmental goals for ”living lakes and streams” (in Swedish) highlighting that goal defintions are based on almost exclusively biogeochemical criteria, and a few biological criteria (highlighted in colour) based on pearl mussel populations or bird communities. Downloaded from the website of the Swedish Environmental Protection Agency at http://www.miljomal.se/sv/Miljomalen/Alla-indikatorer/?mkmid=8&enablelocation=0&lid=0&psize=1000&fid=2&ismainonly=0*

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