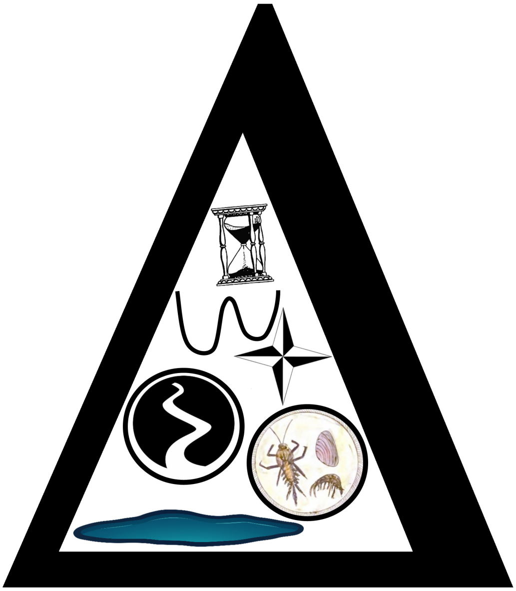
Acta Universitatis Agriculturae Sueciae

Doctoral Thesis No. 2021:38
Faculty of Natural Resources and Agricultural Sciences

Resilience and stability of freshwater invertebrate communities across space and time

Hannah Fried-Petersen



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Hannah Fried-Petersen
Faculty of Natural Resources and Agricultural Sciences
Department of Aquatic Sciences and Assessment
Uppsala

SWEDISH UNIVERSITY
OF AGRICULTURAL
SCIENCES

DOCTORAL THESIS
Uppsala 2021

Acta Universitatis Agriculturae Sueciae
2021:38

Cover: *Change*
(Illustration: H. Fried-Petersen)

ISSN 1652-6880
ISBN (print version) 978-91-7760-754-0
ISBN (electronic version) 978-91-7760-755-7

Uppsala
Print: SLU Service/Repro, Uppsala 2021

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Abstract

Understanding ecosystem response to environmental change is one of the biggest challenges in ecology. Studies of the biological factors and environmental drivers underpinning change in communities through space and time are essential for predicting responses to increasing anthropogenic pressures on ecosystems. Ecosystems encompass numerous interactions within and across levels of biological organization and are inextricably linked to human societies. This thesis addresses ecosystem change from the perspectives of ecological and social-ecological resilience, ecosystem stability, and adaptive capacity. Drawing on ecological resilience theory, promising methods for assessing social-ecological resilience were identified. Following this, the concept of adaptive capacity was refined, operationalized, and distinguished from ecological resilience and stability. Indicators of adaptive capacity, namely compositional stability, functional redundancy, and response diversity were measured in invertebrate communities in Swedish freshwater. I quantified drivers of stability across time and space in Swedish lakes and documented positive correlations between functional redundancy and response diversity at a broad spatial scale in Swedish streams. These indicators were influenced by physiochemical variables, and pervasive anthropogenic disturbances in the landscape. The results highlight the importance of studying long-term and spatially extensive changes in biotic communities using a framework that integrates different aspects of ecosystem resilience to environmental change.

Keywords: Ecological resilience, stability, adaptive capacity, social-ecological systems, spatial ecology, functional ecology, aquatic invertebrates, disturbances

Author’s address: Hannah Fried-Petersen, Swedish University of Agricultural Sciences, Department of Aquatic Sciences and Assessment, Uppsala, Sweden

Motståndskraft och stabilitet hos evertebratsamhällen i sötvatten över tid och rum

Sammanfattning

Att förstå ekosystems reaktion på miljöförändringar är en av de största utmaningarna inom ekologi. Studier av de biologiska faktorer och drivkrafter som ligger till grund för förändring i samhällen över rum och tid är nödvändiga för att förutsäga effekterna av ett ökande antropogent tryck på ekosystem. Ekosystem omfattar många interaktioner inom och över nivåer av biologisk organisation och är oupplösligt kopplade till mänskliga samhällen. Den här avhandlingen behandlar ekosystemförändringar ur perspektiven ekologisk och socioekologisk motståndskraft, ekosystemstabilitet och anpassningsförmåga. Med utgångspunkt i ekologisk motståndskraftsteori identifierades lovande metoder för att bedöma socioekologisk motståndskraft. Efter det förfinades begreppet anpassningsförmåga, operationaliserades och separerades från ekologisk motståndskraft och stabilitet. Indikatorer för anpassningsförmåga, nämligen kompositionsstabilitet, funktionell redundans och responsdiversitet, mättes i evertebratsamhällen i svenska sötvatten. Jag kvantifierade drivkrafter för stabilitet över tid och rum i svenska sjöar och dokumenterade positiva samband mellan funktionell redundans och svarsdiversitet i bred rumslig skala i svenska vattendrag. Dessa indikatorer påverkades av fysiokemiska variabler och genomgripande antropogena störningar i landskapet. Resultaten belyser vikten av att studera långsiktiga och rumsligt omfattande förändringar i biotiska samhällen med hjälp av en ram som integrerar olika aspekter av ekosystemets motståndskraft mot miljöförändringar.

Nyckelord: Ekologisk motståndskraft, stabilitet, anpassningsförmåga, socioekologiska system, rumslig ekologi, funktionell ekologi, vattenlevande evertebrater, störningar

Författarens adress: Hannah Fried-Petersen, Swedish University of Agricultural Sciences, Department of Aquatic Sciences and Assessment, Uppsala, Sweden

Dedication

To Yimen and Noa: to the moon and back ↔ ☾

Contents

List of publications

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

I. W.C. Chuang, A. Garmestani, T.N. Eason, T.L. Spanbauer, **H.B. Fried-Petersen**, C.P. Roberts, S.M. Sundstrom, J.L. Burnett, D.G. Angeler, B.C. Chaffin, L. Gunderson, D. Twidwell, C.R. Allen (2018). Enhancing quantitative approaches for assessing community resilience. *Journal of Environmental Management*, 213, pp. 353-362.

II. D.G. Angeler, **H.B. Fried-Petersen**, C.R. Allen, A. Garmestani, D. Twidwell, W.C. Chuang, V.M. Donovan, T. Eason, C.P. Roberts, S.M. Sundstrom, C.L. Wonkka (2019). Adaptive capacity in ecosystems. *Advances in Ecological Research*, 60, pp. 1-24.

III. **H.B. Fried-Petersen**, Y.G. Araya-Ajoy, M.N. Futter, D.G. Angeler (2020). Drivers of long-term invertebrate community stability in changing Swedish lakes. *Global Change Biology*, 26, pp. 1259-1270.

IV. **H.B. Fried-Petersen**, D.G. Angeler, A. Truchy, B.G. McKie (Manuscript). Land-use and hydrological alterations affect functional redundancy and response diversity of macroinvertebrates in Swedish streams.

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

The contribution of Hannah Fried-Petersen to the papers included in this thesis was as follows:

I. HFP was involved in developing the ideas central to this paper and specifically in writing the sections on ecological resilience and quantitative approaches for assessing ecological resilience.

II. HFP was involved in idea development, structuring of the paper and extensive input in the writing stage.

III. HFP was responsible for idea development and analytical design, analysis of the data, and writing of the manuscript with support of all authors.

IV. HFP shared responsibility for the idea development and analytical approach, and had main responsibility for data analysis and writing of the manuscript with support from all authors.

Additional papers

In addition to the papers included in the thesis, the author has contributed to the following peer-reviewed publications and PhD thesis manuscripts:

I. D.L. Baho, C.R. Allen, A.S. Garmestani, **H.B. Fried-Petersen**, S.E. Renes, L. Gunderson, and D.G. Angeler (2017). A quantitative framework for assessing ecological resilience. *Ecology and Society*, 22 (3):17.

II. D.L. Strayer, B.V. Adamovich, R. Adrian, D.C. Aldridge, C. Balogh, L. E. Burlakova, **H.B. Fried-Petersen**, L.G. Tóth, A.L. Hetherington, T.S. Jones, A.Y. Karatayev, J.B. Madill, O.A. Makarevich, J.E. Marsden, A.L. Martel, D. Minchin, T.F. Nalepa, R. Noordhuis, T.J. Robinson, L.G. Rudstam, A.N. Schwalb, D.R. Smith, A.D. Steinman, J.M. Jeschke (2019). Long-term population dynamics of dreissenid mussels (Dreissena polymorpha and D. rostriformis): a cross-system analysis. *Ecosphere*, 10 (4).

III. S.E. Renes, E.S. Lindström, **H.B. Fried-Petersen**, S. Langenheder, C.R. Allen, D.G. Angeler, B.G. McKie (Manuscript). Ecological memory and the functional responses of microbial communities to disturbance.

IV. S.E. Renes, B.G. McKie, **H.B. Fried-Petersen**, S. Langenheder, D.G. Angeler, E.S. Lindström (Manuscript). Microbial community composition under disturbance: deterministic or stochastic responses?

1. Introduction

"It is a wonderful feeling to recognize the unity of a complex of phenomena that to direct observation appear to be quite separate things."

-Albert Einstein (1901)

In a letter to a friend, Einstein was referring to his successful unification of the microscopic physics of capillaries with the macroscopic physics of gravity (Wilson 1998). Attempts to unite seemingly disparate fields or branches within a field are at odds with the trend towards fragmentation of knowledge. Indeed, even within fields with clear similarities, difference in language, modes of analysis, and standards of validation have led to opposing “teams”, so entrenched in their own *modus operandi* that they can fail to see productive synergies.

There are hints of this division in the relationship between the fields of ecological stability and ecological resilience. In 1976, Buzz Holling defined stability and resilience as two distinct properties: resilience as “the persistence of relationships within a system”, measurable as the ability of an ecosystem to absorb changes of state variables, driving variables, and parameters, and persist, and stability as the ability of a system to return to an equilibrium state after a temporary disturbance. According to these definitions, an ecosystem can be resilient and still fluctuate greatly, i.e. have low stability (Holling 1973). Inherent to both these definitions and more recent ones is the single equilibrium focus of stability (Donohue et al. 2016), and the multi-equilibrium focus of resilience (Gunderson 2000). Despite the fact that these concepts are distinct but not incompatible, the fields of ecological stability and ecological resilience have diverged in concepts, definitions, and metrics, which hinders potentially fruitful work in both

(Allen et al. 2019). In this thesis, I propose that the two concepts are compatible and both essential, and that they can be linked through the concept of adaptive capacity. Adaptive capacity has a single equilibrium focus in its quantification but is related to the latent potential of ecosystems to absorb and cope with disturbances, thereby recognizing the possibility of regime shifts.

All ecologists would agree with this statement: ecological systems are complex and hierarchically organized in space and time. Different fields decide at which point in the hierarchy to focus, i.e., where they draw spatial and temporal boundaries around their systems of interest. No doubt, these boundaries are an illusion but necessary in order to make inferences relevant to human understanding and decision-making. The stability and resilience "camps" tend to disagree about whether stability is nested within resilience or vice versa. This may be in part because of confusing terminology, and not an inherent incompatibility between the two fields. For example, the concept of "engineering resilience", which is synonymous with bounce-back, resiliency, and recovery, is often incorrectly used interchangeably with the aforementioned "ecological resilience" (Angeler and Allen 2016). However, there is a core difference between engineering and ecological resilience, which lies in assumptions regarding whether alternative stable states exist. Like stability, the engineering resilience camp assumes or operates as though only one stable state of an ecosystem exists, leading to characteristic measures such as return time, a process rate. From the stability point of view, resilience (by which they mean engineering resilience) is a component of stability along with resistance, recovery, and variability (Donohue et al. 2013). From the ecological resilience point of view, stability (and all its components) are measures of a system within a single regime, thus nested within the concept of ecological resilience. With the latter structure of organization, stability and ecological resilience are not incompatible, they just have different boundaries of ecosystem organization.

Adaptive capacity, which arises from numerous interactions within and across the biological hierarchy, includes structural and functional patterns and processes, and different aspects of ecological stability. The term is defined and used inconsistently across scientific disciplines, and even within ecology. The working definition for this thesis is "the latent potential of an ecosystem to alter ecological resilience in response to change" (Angeler et al. 2019). The sources of adaptive capacity that confer resilience in an ecosystem are manifold, for example: connectivity, biodiversity by way of the insurance hypothesis, habitat variability and condition, refugia and support areas, natural disturbance history and adaptability, human pressures/multiple stressors, and many more (Timpane-Padgham et al. 2017). This concept thus encompasses ecological stability and relevant metrics of quantification while recognizing that systems' capacity to adapt to change can be exhausted or vulnerable, which has implications for the understanding of ecological resilience.

This thesis will move from the broadest perspective of ecological resilience, which considers both dynamics within, and shifts between, alternative "basins of attraction" and how quantification developed in this field can be useful for an even higher level of organization: social-ecological systems (SES) (**Paper I**). The perspective will then narrow to a single regime perspective and focus on the operationalization of adaptive capacity (**Paper II**), and two embedded empirical components: 1) variability (**Paper III**) and 2) functional proxies of adaptive capacity (functional redundancy & response diversity) (**Paper IV**).

Paper I is a conceptual paper that discusses theory, research development and quantitative approaches in ecological resilience and potential applications to human community resilience. Since the introduction of ecological resilience concepts to study social systems, there has been inadequate development of quantitative approaches for assessing community resilience. This paper suggests how social scientists can use tools from ecology to quantify resilience in social-ecological systems. **Paper II** clarifies the components and relevance of the concept of adaptive capacity of ecosystems, and presents testable hypotheses to evaluate its attributes.

Papers III and IV are empirical work with freshwater invertebrate communities from Swedish lakes and streams as models of complex systems, quantifying indicators of stability and adaptive capacity of these communities. **Paper III** evaluates the environmental factors influencing invertebrate community composition in Swedish lakes. Stability (measured as the inverse of variability) of these communities, based on community composition, and the environmental factors influencing this stability, is then quantified at broad spatial scales (all of Sweden) and across a long time series (23 years). Broadly, this paper assesses one component of stability and adaptive capacity in response environmental change documented for these lakes. **Paper IV** demonstrates an alternative way to assess a component of resilience using a trait-based approach to quantify the relationship between functional redundancy and response diversity (other features of adaptive capacity) of invertebrate communities in Swedish streams. The response of these two indicators to two anthropogenic disturbance gradients is examined, and we identify potential vulnerabilities of the functions provided by these communities to subsequent disturbances. Both **Papers III and IV** have a broad spatial focus which is useful for informing emerging fields of spatial resilience and spatial regimes (Allen et al. 2016, Sundstrom et al. 2017).

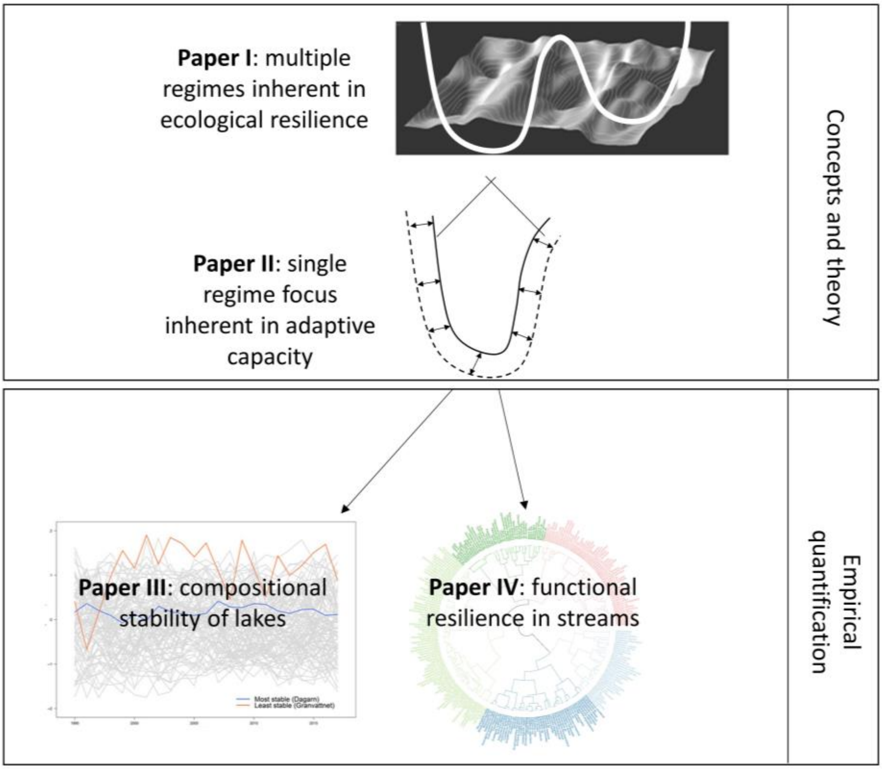


Figure 1. Diagram of the theoretical perspective of the papers in this thesis and the relationship between them. **Papers I and II** are conceptual in nature and relate to ecological resilience and adaptive capacity, respectively. Adaptive capacity is nested within ecological resilience in that it shapes dynamics within one “basin of attraction”, depicted here as a “cup”. The empirical **Papers III and IV** quantify two different attributes of adaptive capacity: compositional variability (as a component of stability), and two functional indicators of adaptive capacity with relevance for ecological resilience.

Table 1. Working definitions of terms relevant for this thesis

Term	**Definition**	**Reference**
Ecological resilience	"The capacity of an ecosystem to absorb repeated disturbances or shocks and adapt to change without fundamentally switching to an alternative stable state."	Holling, 1973
Engineering resilience	The time an ecosystem needs to return to an equilibrium or a steady state after perturbation (aka recovery rate).	Holling, 1996
Adaptive capacity	"Latent property of an ecological system to respond to disturbances in a manner that maintains the system within its current basin of attraction by altering the depth and/or width of that basin."	Gunderson 2000, Angeler et al. 2019
Ecological stability	A multidimensional concept including asymptotic stability, engineering resilience, resistance, robustness, persistence and variability, all of which are related.	Donohue et al., 2013; Pimm, 1984
Social-ecological system	A linked system of people and nature, emphasising that humans must be seen as a part of, not apart from, nature.	Berkes, Folke, & Colding, 1998
Variability	Denotes the tendency of a variable to change in time.	Arnoldi et al., 2019
Functional redundancy	The number of species that share or overlap in their ecological role within an ecosystem.	Rosenfeld, 2002
Response diversity	The range of susceptibility/tolerance to drivers of change of functionally equivalent species.	Elmqvist et al., 2003
Functional effect group	Groups of co-existing species, whose ecological effects are similar, based on the traits which determine these effects.	Laliberté et al., 2010

1.1 Concepts and theory

The first two papers of this thesis relate mainly to two concepts: ecological resilience and adaptive capacity. The definition of ecological resilience used in this thesis is "the capacity of an ecosystem to absorb repeated disturbances or shocks and adapt to change without fundamentally switching to an alternative stable state" (Holling 1973). Inherent to ecological resilience is the capacity of ecosystems to undergo regime shifts, meaning that ecosystems can exist in more than one regime (Figure 1). Adaptive capacity focuses on dynamics within a specific regime and is defined as the latent property of an ecological system to respond to disturbances in a manner that maintains the system within its current basin of attraction by altering the depth and/or width of that basin (Gunderson 2000, Angeler et al. 2019). For the purposes of this thesis, we consider adaptive capacity a component of ecological resilience.

1.1.1 Ecological resilience

Lewontin (1969), Holling (1973), Sutherland (1974), and May (1977) first described the mathematics of non-linear ecological responses to disturbances, thus developing a theoretical framework to demonstrate how ecosystems can exist in multiple alternative stable states (Falk et al. 2019). These models implicitly defined resilience as the domain of response prior to an irreversible threshold change. Concepts of ecological resilience have increased in the scientific and environmental management literature as more ecosystems reach to or beyond their limits of recovery (Beisner et al. 2003, Biggs et al. 2018). Resilience is tied directly to the sustainability of natural systems and the services they provide and accordingly, has relevance for linked social-ecological systems and their management.

Perhaps not surprisingly given its complexity, resilience has come to mean different things in different fields (Brand and Jax 2007). Since the concept of ecological resilience was introduced to study social systems, it has often been oversimplified and used interchangeably with engineering resilience or recovery/return time. As a result, there has been inadequate development of quantitative approaches for assessing human community resilience while recognizing the possibility of multiple regimes in social-ecological systems. **Paper I** draws from ecological resilience theory and quantification to identify promising quantitative approaches for assessing linked ecological and (human) community resilience.

1.1.2 Ecological stability and adaptive capacity

Ecological stability is multifaceted and many methods of quantification have been developed, including spatial and temporal variability, compositional and/or functional turnover, persistence, and resistance (Donohue et al. 2013). There are also several types of stability, including the stability to pulse or press disturbances, extinctions, and invasions (Ives and Carpenter 2007). Systems can be unstable even without environmental disturbances (Ives and Carpenter 2007), because of internal factors such as trophic interactions and demographic stochasticity (McCann et al. 1998, Borer et al. 2012). Such external and internal factors often operate simultaneously in a given system, determining the degree of ecological stability. Ecological stability is useful for studying disturbance impact and response patterns from a process-oriented viewpoint. Adaptive capacity takes this notion one-step further by accounting for a whole range of systemic features (e.g., hierarchical organization, cross-scale interactions, and ecological memory) that are tightly interlinked. This is evident in the definition of adaptive capacity as "the property of an ecosystem that describes the change in stability landscapes and resilience is referred to as adaptive capacity" (Gunderson 2000). This definition inspired our recent definition of adaptive capacity, considered as the "latent property of an ecological system to respond to disturbances in a manner that maintains the system within its current basin of attraction" used, in **Paper II**, as an overarching framework for quantification.

1.2 Quantification metrics

Resilience is a key emergent property, underpinned by multiple mechanisms that govern the response to disturbance, operating along axes of space, time, and biological hierarchy. Quantification is needed to operationalize the concept of resilience of ecosystems and for corresponding management implications, but it has largely remained a conceptual phenomenon until recently (Lam et al. 2020). Central to the ideas of ecological resilience are the presence of (a) thresholds between ecosystem states and (b) the ability of the ecosystem to cope with disturbances and stay within a given regime (adaptive capacity). **Paper I** briefly reviews early warning indicators, relevant for predicting regime shifts, which are central to quantitative metrics related to thresholds. The quantitative measures developed in this thesis relate to (b), or adaptive capacity in ecosystems. Specifically, we evaluate variability as a component of stability (**Paper III**), and functional redundancy and response diversity (**Paper IV**) in order to gain insights into drivers of change and potential vulnerabilities in these systems.

1.2.1 Community ecology

Multiple individuals of interacting species comprise an ecological community and community ecology is the study of these interactions, and the abiotic factors affecting them, on many spatial and temporal scales (Mittelbach and McGill 2019). Who´s there (and when and where), what are they doing, and why? Again, it is clear that biological systems are hierarchically organized; ecological communities are composed of interacting genes, individuals, and populations. Selection, drift, dispersal, and speciation combine to determine biodiversity patterns, such as species-area relationships, relative abundance distributions, and diversity-disturbance relationships (Mittelbach and McGill 2019). In order to quantify subsets of resilience and its attributes (adaptive capacity and stability), **Papers III and IV** study and make inferences at the level of communities. Resilience undoubtedly intersects with and manifests at all levels of biological organization so what is the specific relationship then between community ecology and ecological resilience theory? In John Lawton´s paper “Are There General Laws in Ecology?” (1999) he argues that macroecological patterns reflect the fact that, at large scales, the “noise” of species- and system-specific details “averages out”. The use of long-term and broad scale community ecology data allows for a focus on pattern (resilience, adaptive capacity) while still being able to make inferences about underlying processes (community composition, variability, species abundances, taxonomic and functional diversity, etc.).

1.2.2 Compositional stability

Accurately quantifying stability and understanding its drivers is a fundamental, yet notoriously elusive enduring challenge for ecology (Elton 1946, Donohue et al. 2016). Pimm (1984) considered there to be five components of ecological stability: asymptotic stability, variability, persistence, resistance, and recovery (engineering resilience; Pimm 1984). Variability is an attractive facet of stability because it is empirically accessible, applicable across levels of biological organization and spatial scales, and can be indicative of the vulnerability of a system (Arnoldi et al. 2019). Variability reflects the inherent ability of a dynamical system to endure a variety of perturbations, and it provides a measure of predictability across a broad environmental context. Indeed, quantifying the stability of ecological communities at broad scales is a critical step in understanding, predicting, and managing consequences of environmental change. **Paper III** quantifies the stability of invertebrate communities in Swedish lakes across a broad spatial scale and long time series and examines multiple possible drivers of this stability. This paper uses compositional/ taxonomic data of invertebrate communities because they are sensitive to environmental change, a commonly used group in biomonitoring, and because they play key functional roles (e.g., leaf litter decomposition) in ecosystems (Bonada et al. 2006).

1.2.3 Functional redundancy and response diversity

In community ecology, trait-based or functional approaches to studying biodiversity involve understanding communities based on what organisms do, as opposed to taxonomic approaches, which are underpinned more directly by the organisms´ evolutionary history (Petchey and Gaston 2006). As a result, functional composition provides clearer mechanistic insights into the impacts of disturbance on ecosystem functioning (Robroek et al. 2017, Aspin et al. 2018). Changes in species composition are not necessarily coupled to changes in functional trait composition (Fukami et al. 2005, Gallagher et al. 2013). This may be due to various mechanisms, one of which is functional redundancy. Functional redundancy refers to the number of species that share or overlap in their ecological role, as defined by their effect traits (i.e., traits that determine how species affect or contribute to ecosystem functions) (Yachi and Loreau 1999, Naeem and Wright 2003). High functional redundancy confers resilience of specific ecosystem functions to a broad range of disturbances if there is diversity in degrees of susceptibility/tolerance to drivers of change of these functionally equivalent species (response diversity; Elmqvist et al. 2003). **Paper IV** evaluates functional redundancy and response diversity of invertebrate communities in broadly-distributed southern Swedish streams. Correlations between these metrics as well as their relationships with two anthropogenic disturbance gradients are examined in order to make inferences about adaptive capacity and resilience of the functions provided by these groups of functionally redundant species across environmental gradients.

2. Framework and objectives

The broader goals of this thesis are to 1) summarize, broaden and operationalize concepts related to ecological resilience, adaptive capacity, and stability and 2) to develop quantitative indicators of these concepts and explore the environmental variables driving changes in these metrics. The novelty of this work is the transdisciplinary approach to ecological resilience in **Paper I**, and the clarification of and framework for testing adaptive capacity in **Paper II**. **Paper III** is novel in the quantification of one aspect of stability (taxonomic variability) and its drivers at a broad spatial and temporal scale**,** and **Paper IV** in the examination of the relationship between two functional indicators of resilience and their relationships with two disturbance gradients at a broad spatial scale. The thesis as a whole unites these papers under the metaphorical umbrella of ecological resilience.

The specific aims of the thesis were to:

- Review quantification of ecological resilience and applications for social-ecological systems (**Paper I**).
- Refine the definition of adaptive capacity and operationalize the concept (**Paper II**).
- Develop indicators of stability and adaptive capacity based on taxonomic and functional metrics (**Papers III and IV**).
- Examine the environmental drivers of stability and adaptive capacity of invertebrate communities in Swedish freshwater systems (**Papers III and IV**).

3. Methods

Here I present an overview of the key methods used in this thesis. Note that **Papers I and II** are primarily conceptual, and therefore their methods of development are only very briefly described. For more details on empirical methods, please see **Papers III and IV**.

3.1 Social-ecological resilience and adaptive capacity

The topics and collaboration network for **Papers I and II** came out of the Complexity working group. With contributors all over the US and in Uppsala, Sweden, this group of international transdisciplinary scholars met once a month from 2015 to 2018 to discuss all things related to complex adaptive systems (CAS; Levin, 1998) A main focus of CAS theory is to understand the dynamics of aggregate patterns that result from the interaction of system components. As social-ecological systems are CAS, some members of the working group (social scientists, an environmental lawyer, data scientist, and various breeds of ecologists) worked on this synthesis to provide recommendations for a more holistic assessment of social-ecological systems (**Paper I**). Likewise, a diverse group with experience in all stages of environmental management, from empirically focused biology to policy development and management recommendations, collaborated to refine the concept of adaptive capacity and develop hypotheses to assess its attributes (**Paper II**).

3.2 Lake data

The Swedish national surface water monitoring program began in the 1960s and is unique in its temporal and spatial extent and open-access policy (Fölster et al. 2014). Lake eutrophication was the main concern in the beginning but the program has continually expanded and today includes regular long-term monitoring of water chemistry and biodiversity in 67 watercourses and 106 lakes, and a low-intensity sampling program of an additional 4800 lakes. The monitoring program is overseen and regulated by the Swedish Agency for Marine and Water Management (SwAM: https://www.havochvatten.se/en). The Departments of Aquatic Sciences and Assessment and Aquatic Resources at the Swedish University of Agricultural Sciences (SLU) are responsible for chemical analyses and taxonomic identification. Data are open access and no permission is required for their use (http://miljodata.slu.se/mvm/).

Paper III was based on autumn sampling of environmental and invertebrate community data from 105 lakes between 1995 and 2017. The studied lakes are medium sized (area = 0.03–14 km^2, mean = 1.5 km^2) and are considered to be trend lakes, that is, largely unaffected by point effluents and heavy soil usage other than forestry (Fölster et al. 2014). The lakes are broadly distributed throughout Sweden, north and south of the Limes Norrlandicus (LN). The LN is a strong and stable biogeographical and climatic divide between northern and southern Sweden in terms of air temperature, precipitation (duration of snow cover), vegetation (e.g., boreal/alpine in the north vs. hemiboreal in the south) and soil type. It has been used to define two ecoregions in Sweden, shown to differ in invertebrate abundance and community structure (Sandin and Johnson 2000).

3.2.1 Sampling

Invertebrates were sampled from vegetation free, hard-bottom littoral habitats according to standardized sampling protocols (Fölster et al. 2014). Samples were collected in autumn; the northernmost lakes were sampled in early autumn and the southernmost in late autumn. Five standardized kick samples were taken using a hand net (mesh size 0.5 mm). Sampling consisted of disturbing the substratum along a 1-m-long section for 20 s. Samples were immediately preserved in 70% ethanol (final concentration) and later processed in the laboratory by sorting using × 10 magnification. Invertebrates were identified to the lowest feasible taxonomic unit (usually species) and counted using light and dissecting microscopes. To ensure that inferences were based on a reasonable number of occurrences, we excluded taxa found in less than 5% of the samples.

Water quality data were obtained from surface water samples, which were taken at 0.5 m depth at a mid-lake station in each lake. Samples were collected with a Ruttner sampler and kept cool during transport to the laboratory, where they were analysed for alkalinity and total phosphorus. All chemical analyses were conducted at the Department of Aquatic Sciences and Assessment (Swedish University of Agricultural Sciences) following International Organization for Standardization (ISO), or European standards (EN) (Wilander, A., Johnson, R.K. and Goedkoop 2003). Autumn water chemistry measurements were matched by year and lake to the autumn invertebrate samples.

3.3 Stream data

Paper IV was based on analyses of benthic macroinvertebrates sampled in 134 stream reaches in southern Sweden (below the Limes Norrlandicus). Data were compiled by the Swedish Environmental Protection Agency project WATERS (www.waters.gu.se). The objective of the project, concluded in 2016, was to develop and improve the assessment criteria that are used to classify the status of Swedish inland waters in accordance with the EU Water Framework Directive. The taxonomic data from this project were matched with trait information retrieved from the database compiled for European freshwater invertebrates by Tachet et al. 2010. Anthropogenic disturbance gradients were based on land-use data from CORINE Land Cover inventory (https://land.copernicus.eu/pan-european/corine-land-cover), and hydrological variables based on the Dundee Hydrological Regime Assessment Method (DHRAM, Black et al. 2005).

3.3.1 Sampling

Invertebrates were collected during the autumn in riffle habitats, i.e., stretches of faster water flow over shallower benthic habitats dominated by hard rocky substrates. Five replicate samples were taken, using standardized kick sampling with a hand net (0.5 mm mesh size). For each sample, the bottom substratum was disturbed for 20 seconds along a 1 m stretch. Invertebrates were preserved in 70% ethanol in the field and processed in the laboratory by sorting against a white background with 10x magnification. Invertebrates were identified to the finest taxonomic unit possible (generally genus or species, but subfamily for Chironomidae and order for some Oligochaeta) and counted using dissecting and light microscopes. The sampling year range was restricted to between 2006 and 2013 in order to maximize the number of streams and quality of data for the analysis while keeping the timeframe as restricted as possible. Within this range, we used abundances from the most recent year of sampling for each stream, and means of these abundances if the stream was sampled more than once that year.

3.3.2 Trait data

Trait information for each species was retrieved from the database compiled for European freshwater invertebrates by Tachet et al., 2010 (https://www.freshwaterecology.info/). In order to quantify functional redundancy, we selected three relevant biological traits that regulate the effects of organisms on their environment: body size, feeding habits (or functional feeding group), and locomotion (Frainer et al., 2018). Body size is related to the metabolic capacity of each species, and thus their energetic requirements (Brown et al. 2004). Feeding habits, or functional feeding group (FFG), reflects to which specific resource processing function the invertebrates contribute (e.g. breakdown of leaf litter or consumption of algal resources) (Wallace and Webster 1996). Locomotion reflects how mobile a species is and where in the ecosystem it operates (e.g. crawling on the substrate or swimming in the water column) and hence where in the ecosystem it is likely to influence functioning (Bonada et al. 2007). All the biological traits constituting functional effect traits are scored based on organism morphology – i.e. biomass is based on their mean body size, feeding group on mouthpart morphology, and locomotion on locomotary structures.

As response traits used to quantify response diversity, we selected seven ecological traits reflecting species environmental tolerances and ecological flexibility. In contrast to the morphologically-based effect traits, ecological or response trait data are based primarily on the optimum and distribution of trait values along an environmental gradient (Garnier et al. 2016). A fuzzy coding approach was used for both types of traits and affinities for each category were standardized as percent affinities within a trait.

3.3.3 Anthropogenic gradient characterization

We studied the effects of two anthropogenic disturbance gradients (agricultural land-use and hydrological modifications) on functional redundancy and response diversity. Previous research has documented extensive impacts of intensifying agricultural land-use and hydrological modifications on the diversity and composition of freshwater invertebrates (McKie and Cranston 2001, Johnson and Almlöf 2016, Kjaerstad et al. 2018), and the ecosystem processes they regulate (Young and Huryn 1999, Matthaei et al. 2010, Woodward et al. 2012, Piggott et al. 2012, Frainer and McKie 2015).

To characterize the agricultural land-use gradient, we used catchment-level land use data from the year 2006 from CORINE Land Cover inventory (© European Union, 2006).

Relevant hydrological variables were selected based on the Dundee Hydrological Regime Assessment Method, which classifies the extent of anthropogenic hydrological modification and the associated risk of damage to in-stream ecology using a scheme compatible with the requirements of the Water Framework Directive (DHRAM, Black et al. 2005). The method computes 32 parameters that can be broadly classified into five groups: flow magnitude, frequency, duration, timing and rate of change. For our study the parameters were computed from modelled discharge data obtained from the Swedish Meteorological and Hydrological Institute (SMHI; http://www.smhi.se/). PCA was used to reduce dimensionality and extract the two most important variables for characterizing hydrological modifications i.e. those most highly correlated to PCA 1 and PCA 2 (change in duration of high pulse with respect to natural flows, and the 30-day maximum flow, respectively).

We used the aforementioned variables (catchment land-use, change in duration of high pulses, and 30-day max. flow) in an overall PCA to characterize and reduce the dimensionality of the two pressures, in order to analyse each gradient separately. PCA was run on standardized variables (subtracting the mean and dividing by SD). Stream scores along the first two principal components were subsequently used to represent level of agricultural land-use and hydrological modification, respectively.

3.4 Measuring stability and quantifying functional redundancy and response diversity

In order to summarize lake invertebrate community composition and estimate intra- and inter-lake variability (our measure of stability) for **Paper III**, we performed a DCA on raw littoral invertebrate abundance data. One DCA was performed for all 105 lakes across the study period (years 1995–2017), although not all lakes were sampled for all 23 years during the designated fall sampling period (minimum of 10 years, max of 23, and mean of ~20 years). Rare taxa were downweighted to decrease the influence of extremely rare species on the DCA ordination, since we were particularly interested in overall changes in community composition across time. We performed subsequent statistical analyses on the lake scores (in a northern and southern ecoregion) for the first two DCA axes, which summarize the first and second most variation in invertebrate community composition.

To quantify functional redundancy and response diversity of benthic macroinvertebrates sampled in 134 stream reaches in southern Sweden, we used the trait data described in section 3.3.2. Functional redundancy was calculated based on the three effect traits (body size, FFG, locomotion). We computed a Gower dissimilarity matrix from the trait data of all species. We then applied Ward’s minimum variance clustering on the Gower dissimilarity matrix in order to classify species into Functional Effect Groups (FEGs). We used a dendrogram to visually represent this clustering. Defining the number of FEGs for the subsequent analyses was a critical step. We identified five clusters based on a fusion level diagram and expert inspection of the dendrogram to ensure that the groupings were not taxonomically bound. We classified the FEG membership of all species sampled in each stream and measured the functional redundancy as the number of species sampled within an effect group. Of those functionally redundant species, we used their corresponding response traits to calculate the response diversity of that FEG in that stream. Response diversity was quantified by measuring the multivariate functional dispersion (FDis; Laliberté et al. 2010) of the sampled species in response trait space, using a Gower dissimilarity matrix of species computed from response traits (see Figure 3 from Section 4.3.2).

3.5 Statistical analyses

All statistical analyses were performed in R versions 3.4.2 and 3.5.1 (R Development Core Team, 2018). The complete descriptions of the different statistical methods used can be found in the individual papers, and for **Paper III** published data and code can be found in a Zenodo archive at http://doi.org/10.5281/zenodo.3384632.

3.5.1 Lake stability

The statistical analyses were designed to 1) study the factors affecting the yearly Detrended Correspondence Analysis scores (as summaries of community composition) of the studied lakes and to 2) quantify stability at the lake level and examine larger regional patterns in lake stability. For the first aim, we used four mixed-effects models to study how lake latitude, lake size, species richness, alkalinity, and total-phosphorus affected community composition, modelled separately for each ecoregion: DCA 1 south, DCA 2 south, DCA 1 north, and DCA 2 north. Alkalinity, TP, and species richness were modelled as fixed effects and lake size and latitude as fixed covariates. All models included random intercepts for lake and year identity.

For the second aim related to lake stability, we used the variation in yearly DCA scores within lakes and across years as a measure of individual lake stability. To estimate the within-lake variation in yearly DCA scores, we extended the above-mentioned mixed-effects models to include lake-specific ‘residual variation.’ To examine potential drivers of this stability, we extended the heterogenous residual models to include predictors for lake-specific residual variances. Specifically, we modelled stability as a function of latitude, lake mean richness across years, lake size, mean TP, and mean alkalinity.

We fitted all models described using a Bayesian framework implemented in R with the RJAGS package (Plummer 2016). We ran 3,050,000 iterations per model, from which we discarded the initial 50,000 (burn-in period). Each chain was sampled at an interval of 3,000 iterations, which resulted in a low autocorrelation among thinned samples. Posterior means and 95% credible intervals were estimated across the thinned samples for the mean effects (fixed effects), (co)variances, and heterogeneous residuals.

We considered estimates of fixed effects and covariates to be significantly different from zero when their associated 95% credible intervals did not overlap zero. We assessed the statistical support for a nonzero value of the heterogeneous residuals differently because variance components are bound to be positive. We therefore determined the probability that an estimated variance was different from the null expectation based on permutation tests (Good 1994, Araya-Ajoy and Dingemanse 2017).

3.5.2 Stream functional redundancy and response diversity

In order to address whether and how functional redundancy (FR) and response diversity (RD) are correlated, and if this correlation changes across functional effect groups, we calculated Pearson’s Rank correlation coefficients for the overall correlation between FR and RD, and individually for each FEG. To look at the effects of the two disturbance gradients on FR and RD overall, we fitted four linear mixed effect models that had FR or RD as response variables, PCA 1 or PCA 2 as fixed effects, and stream identity as a random effect. We used a further four linear mixed effect models to study how each disturbance gradient affected FR and RD in each FEG. For this, we fitted models that had as response variables FR or RD and as fixed effects FEG, disturbance gradient, and their interaction. All models had stream identity as random intercepts to account for pseudo-replication. For all models, we estimated mean effects sizes and 95% credible intervals to determine the magnitude of the effect of the agricultural land-use and hydrological modification gradients on functional redundancy and response diversity overall and for each functional group. We considered effects sizes to be statistically significant (i.e., in the frequentist's sense) when their associated 95% credible intervals did not overlap zero.

4. Results and discussion

4.1 Review quantification of ecological resilience and applications for social-ecological systems

The earliest surviving written record of scientific use of the word resilience in the English language is believed to be from the 1620s when Sir Francis Bacon used it to describe the “act of rebounding” (Alexander 2013). It comes from the Latin verb *resilire*, meaning to rebound or recoil. Since then, various fields ranging from business and economics to psychopathology, disaster management, and ecology have refined and reshaped the term according to their own paradigms. Even within the field of ecology, resilience has come to have two quite different meanings. The first, also known as engineering resilience, essentially preserves the original sense of the word and in an ecological context refers to the rate or speed of recovery of an ecosystem following a disturbance (Pimm 1984). The second definition was developed by C.S. Holling to include the concept of alternative states or regimes, characterized by different structures and dynamics (Holling 1973). From this definition came the term ecological resilience, or the amount of disturbance an ecosystem can withstand before switching to an alternative regime. Since Holling’s landmark paper in 1973, much progress has been made in the resilience field. Quantitative assessments of ecological resilience have been developed with varying degrees of success for detecting and predicting thresholds (Dakos et al. 2015, Burthe et al. 2016) and for measuring ‘specific resilience’ (Carpenter et al. 2001, Baho et al. 2017). Attempts have also been made to propose how to measure the generalized resilience of systems (Baho et al. 2017). The aim of **Paper I** was to motivate the application of quantitative ecological resilience methods to human community resilience to provide a more holistic assessment of social-ecological systems.

Social-ecological systems reflect a highly interconnected relationship between human communities and ecosystems. These systems are dynamic and interdependent, and understanding/quantifying their components is a “wicked problem” that, given increasing global anthropogenic pressures in the 21st century, is getting more wicked (DeFries and Nagendra 2017). Adding to the complication is the development of simultaneous yet separate quantification of resilience in human communities and ecosystems. There are no widely accepted or commonly used quantitative approaches for assessing community resilience, and the existing methods reflect an engineering resilience perspective and thus do not account for the possibility of multiple regimes or the dynamic and multifaceted characteristics of complex systems. While there has been progress towards systematically incorporating ecological resilience into the understanding of social-ecological systems (Li et al. 2020), the qualitative treatment of some community resilience attributes and the limited applicability of quantitative indicators limits its applicability as a concept. This calls for more innovative solutions, which are designed to deal with uncertainty, feedbacks within and across temporal and spatial scales, and natural variation in linked social-ecological systems.

4.1.1 Indicators of ecological resilience

The concept of ecological resilience, and its accompanying quantification methods, incorporates dynamic feedbacks across space and time, non-linear change (thresholds), and the range of natural variation in a system (Holling and Meffe 1996). Quantifying ecological resilience has focused in large part on the detection of temporal early warning signals (EWS) that indicate an impending regime shift rather than directly measuring the innate degree of system resilience at a given point in time. These indicators can be very useful when a system is approaching a transition even in the absence of adequate knowledge about the mechanisms involved. However, the biggest challenge in the application of EWS comes from the difficulty in identifying the most appropriate variable to measure and the relevant spatiotemporal scale for monitoring and analysing. Additional problems arise because resilience assessments based on signatures of a specific variable might not reflect the general resilience of an ecosystem, which emanates from broader interactions of biological and environmental components (Baho et al. 2017). Attempts to directly measure resilience include efforts to map a basin of attraction and the location of a system within the basin using the three parameters of resilience defined by Walker et al. (2004); namely, latitude, resistance, and precariousness. However, this method is not yet applicable to real multivariate systems, as it requires thousands of initial conditions and extremely long time series (Mitra et al. 2015). Network theory is another method that has been used to analyse how the topology of an ecological network is more or less resilient to the loss of nodes (Dunne et al. 2002) and has recently been used to develop models that incorporate multiple dimensions (Gao et al. 2016, Kéfi et al. 2016), but suffers from an inability to explicitly incorporate scales other than indirectly via trophic level. Perhaps the simplest and most common method to quantify ecological resilience is that of the cross-scale resilience model and its attendant discontinuity hypothesis, which explicitly incorporates scales (Nash et al. 2014). In **Paper I**, we discuss methods currently used for quantifying ecological resilience that appear promising for community resilience—early warning signals, the cross-scale resilience model, and spatial resilience.

4.1.2 Early Warning Signals

Effectively and objectively detecting and evaluating erosion of the buffering capacity of an ecosystem is critical if managers wish to target the most vulnerable systems. Since Carpenter and Brock (2006) advanced the idea of broadly applicable statistical signatures prior to critical transitions, the EWS literature has proliferated (Litzow and Hunsicker 2016). Theory surrounding EWS is predicated on empirical evidence that generic symptoms occur across many types of ecosystems as they approach a tipping point (Dakos et al. 2015). This is the foundation for the study of EWS which attempt to identify critical thresholds and quantify the resilience of a system in relation to that threshold. EWS are appealing due to their potential to detect impending thresholds across a range of complex systems as they appear to reflect fundamental tendencies of complex systems (Scheffer et al. 2015). The mechanisms driving regime shifts do not need to be measured in order to calculate an early warning signal, which is a strength of such signals (Scheffer and Van Nes 2007). However, critical transitions between alternative regimes are notoriously difficult to predict because some systems may show little to no change before a threshold is reached (at which point management intervention is often too late), noise may interfere with signal detection (Scheffer et al. 2009), and univariate indicators (which are the basis of most EWS) may not necessarily reflect the fundamental process(es) driving a potential regime shift (e.g., Eason et al. 2014, Spanbauer et al. 2014). Also, EWS have been shown to fail in detecting regime changes across multiple taxon groups in marine and freshwater environments (Burthe et al. 2016). Brock and Carpenter (2012) describe this challenge as a fundamental issue for EWS. A further complication is that EWS may only signal regime shifts in certain cases (Dakos et al. 2015, Eason et al. 2016). For instance, there is evidence to suggest that EWS are only present in systems with nonlinear dynamics that exhibit hysteresis (Litzow and Hunsicker 2016). Nevertheless, generic indicators of ecological resilience are important tools in the study of complex systems, and in some cases can be used to detect and predict regime shifts.

Two broad classes of EWS indicators have been developed to address the following types of ecosystem fluctuations: 1) systems that remain close to an equilibrium and generally only experience small fluctuations around that equilibrium, and 2) systems that experience larger fluctuations due to more environmental variation such that they generally operate far from any equilibrium. The classes of indicators that have been developed for the aforementioned patterns of organization are known as critical slowing down and flickering, respectively (Scheffer et al. 2015).

4.1.3 Discontinuity hypothesis, cross-scale resilience, and time series modelling

Early warning indicators are intended to predict/identify regime shifts based on generic signals that occur across ecosystems, such as critical slowing down, flickering, or a loss of system organization (Fisher Information). It has been argued that the reason some EWS do not provide adequate warning is because they are not scale-specific, or they focus on the wrong scale (Nash et al. 2014). That is, EWS do not account for the hierarchical organization of ecosystems, an inherent property whereby patterns and processes are manifested and operate at different scales of space and time. Nor do they inform us about the specifics regarding a system's resilience. In other words, an EWS may tell us how close a system is to a threshold or bifurcation, but not about the specific properties of that resilience. These may be changing at a particular range of scales in response to changing environmental conditions or other disturbances or drivers, which due to cross-scale feedbacks may push the system closer to a bifurcation (the equivalent of reducing its resilience). Current approaches to identify scales are based on the discontinuity hypothesis (Holling 1992) and complement EWS. The underlying assumption is that the discontinuous organization of ecological systems is mirrored in the structure of biological communities. Holling (1992) posited that this pattern arises because behavioral, life history, and morphological attributes of organisms adapt to discontinuous environmental patterns in opportunities for food, shelter, and other resources. Holling (1992) found a correlation between breaks in distributions of animal body mass, an integrative variable that is in allometric relationship to many physiological and ecological attributes (Peters 1983), and discontinuities in structures and processes. Aggregations of species in body mass distributions reflect the scales at which resources and structure are available to organisms that have evolved to exploit resources at those specific scales (Nash et al. 2013, Stirnemann et al. 2015). In contrast, gaps (discontinuities or troughs) in the distribution reflect the transition between structuring processes and thus hierarchical levels in an ecosystem (i.e. thresholds Wiens 1989). At these transitions, there is no ecological structure or resource pattern with which organisms can interact, or there is great variance and instability in the structures or patterns (Allen and Holling 2008). Many systems have been successfully examined for discontinuities and/or multimodalities in animal body mass distributions, in line with the discontinuity hypothesis (Wardwell et al. 2008, Thibault et al. 2011, Sundstrom et al. 2012, Nash et al. 2014, Raffaelli et al. 2016).

Once discontinuities are identified, the distribution of functional groups within and across these aggregations can reveal the relative resilience of a system of delimited spatial and temporal bounds (Allen et al. 2005). A system with high within-scale diversity of function and high cross-scale redundancy of function is expected to have a higher capacity to buffer disturbances and remain in the same regime, or basin of attraction (Allen and Holling 2002). Evidence continues to accumulate showing that it is functional richness across multiple scales rather than species richness that is critical for buffering capacity and the long-term persistence of ecosystems (Soliveres et al. 2016). Using discontinuity analysis to identify the intrinsic scales of biological communities may be combined with EWS to pinpoint sensitive scales that may provide earlier warning signals of an impending threshold (Spanbauer et al. 2016).

Time-series modelling approaches to quantify resilience build upon discontinuity theory and are designed to quantify the specific resilience of a community, such as a phytoplankton community’s response to liming (Baho et al. 2014). Discontinuity analysis can be used to make the within and cross-scale distribution of organisms explicit, which is the first step towards the quantification of resilience in the time-series modelling approach. Subsequently, dominant temporal frequencies in a particular community are identified and the distribution of species (and consequently their functions) within and across these spatiotemporal scales can indicate the community’s ability to buffer against disturbances and thus its resilience (Angeler et al. 2013).

4.1.4 Spatial resilience

Spatial resilience is the contribution of spatial attributes to the feedbacks that generate resilience in complex systems (Allen et al. 2016). Spatial resilience can be an important means of assessing resilience when long-term data are not available, or when inference broader than a local case study is desired. Structures and processes that influence resilience operate within and between multiple spatial scales (Nyström and Folke 2001, Cumming 2011, Zurlini et al. 2014, Allen et al. 2016). Characteristics that interact across spatial scales, such as spatial diversity and heterogeneity of components and processes that comprise systems, and spatial connectivity within and between systems (Cumming 2011) govern spatial resilience. System memory also plays a role: restoration to the previous state post-disturbance is more likely if spatially connected areas maintain pre-disturbance components and processes (Nyström and Folke 2001, Cumming 2011). Identification of spatial regimes and quantification of spatial resilience is relatively new, but several methods appear promising (e.g. Sundstrom et al. 2017b, Roberts et al. 2019b). Advancements have been made by extending early warning signals into spatial contexts (Kéfi et al. 2014). Network theory has potential for assessing spatial resilience at local scales (i.e., at individual nodes such as cities) and at broad scales (i.e., between nodes such as cities within a region; Allen et al. 2016b). Estimating cross-scale resilience and discontinuity patterns in space can assess the distribution and scale at which ecological functions occur across spatial extents (Göthe et al. 2014), providing warnings of low resilience when functional redundancy across scales is reduced (Peterson et al. 1998, Göthe et al. 2014). Spatial modeling can also help untangle the relative importance of dominant and rare species. This has been suggested to contribute to a more detailed picture of resilience as rare species can maintain critical functions in ecosystems by replacing dominant species after perturbations (Angeler et al. 2015).

4.1.5 Ecological resilience methods in SES

Resilience is an emergent property of complex systems, therefore no single metric can encapsulate it (Angeler and Allen 2016). Attempting to understand and quantify an emergent property such as resilience of a social-ecological system poses two issues: the fallacy of division and the inverse fallacy of composition. Aristotle (384–322 BC) first addressed these two fallacies in his text *Sophistical Refutations* (Woods and Walton 1989) and a basic understanding of these two principles can be useful when trying to understand the complex nature of deriving quantitative measures of social-ecological resilience. A fallacy of division happens when one reasons that what is true for the whole (in this case, the social-ecological system), must also be true for all or some of its parts (patterns and processes occurring at lower scales in a hierarchically structured system). The fallacy of composition is the converse and occurs when one attributes a property of a constituent part of a complex system to that system as a whole. Addressing the overall resilience of a SES at an unspecified scale to unspecified disturbances (general resilience) is very difficult and therefore attempts to address resilience have focused on lower levels in the hierarchical structure of a SES (specific resilience). This invokes the fallacy of composition and means that when measuring resilience of a specific group to a specific pressure (e.g., phytoplankton response to nutrient loading) conclusions do not necessarily apply for all groups and all pressures. The implications are that single resilience metrics reflects unique aspects of system resilience. In order for resilience theory to be most useful for understanding SES resilience, the simultaneous consideration of multiple metrics to quantify resilience is required (Folke et al. 2005, Roberts et al. 2019).

That being said, there are metrics developed in ecological resilience that have been useful for assessing the complexities inherent in human community resilience. They bridge ecological and community resilience to better assess and manage change in coupled human and natural systems. Indeed, despite the aforementioned challenges combined with often insufficient data and the lack of long term temporal studies (Nyström and Folke 2001, Hicks et al. 2016), some ecological resilience indicators have been applied to assess community aspects of resilience in SESs (Quinlan et al. 2016, Peterson et al. 2018, Biggs et al. 2018). Human communities and the ecosystems they inhabit and to which they are coupled cannot be disentangled, and therefore a more holistic understanding of how the resilience of each is deeply intertwined is the topic of **Paper I**. This undertaking is not intended to be exhaustive but highlights the types of synergies and cross-disciplinary cooperation needed to begin to understand our increasingly complex and interconnected world.

4.2 Refine and operationalize adaptive capacity

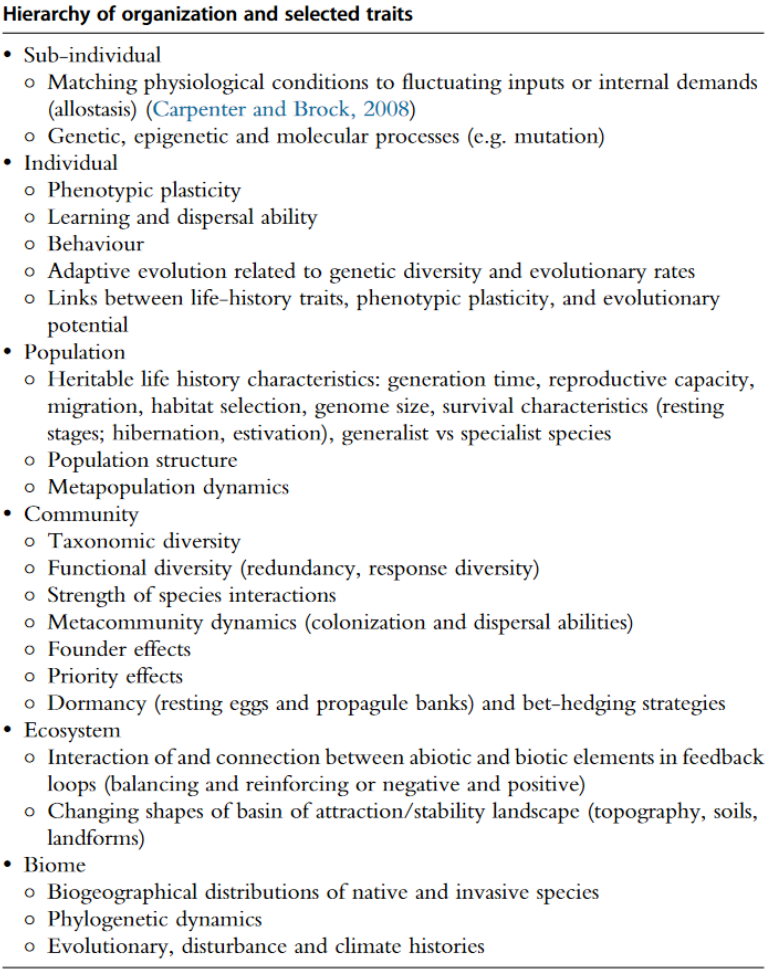
The study of *adaptation* as a response to climate is a broad and interdisciplinary field (Adger and Vincent 2005, Brooks et al. 2005) that spans many levels of biological organization and many research fields. Specifically, the term *adaptive* has been studied from an evolutionary perspective, focusing on the matching of phenotypic traits of individuals and populations to their environment. The term also has roots in ecological and systems theory concepts applied to higher scales of organization (communities, ecosystems), and to SES definitions that focus on the ability of a system to change and maintain ability to support human well- being or other specific human- centric outcomes (Seaborn et al. 2021). *Adaptive capacity* is one such system-level term often used to describe the ability of ecosystems to cope with disturbances, while implicitly recognizing that this capacity emerges from processes at lower biological levels. This term is related to ecological resilience but we contend that it is distinguishable in two ways: 1) Adaptive capacity focuses on dynamics within a specific regime while ecological resilience encompasses broader system dynamics by considering alternative regimes. 2) Adaptive capacity can be thought of as akin to fundamental niche space at the ecosystem level, describing the latent potential of an ecosystem to cope with disturbances, but meaning that current observations may not encapsulate the full adaptive capacity of the system. Ecological resilience is more akin to realized niche space, which is then understood as a measure of the amount of change needed to change an ecosystem from one set of processes and structures to a different set of processes and structures. In **Paper II**, we summarize the components that contribute to adaptive capacity and how they may interact within and across the hierarchy of biological organization. We then propose the use of an iterative hypothesis-testing framework for assessing the general adaptive capacity of ecosystem regimes, using simple indicators of ecological stability, early warning signals, and cross-scale resilience metrics based on the aforementioned biological components.

4.2.1 Components of adaptive capacity

Adaptive capacity is comprised of components that interact dynamically, only partially lending themselves to organization in discrete categories (Table 2). Ecological memory, cross-scale interactions, ecological functioning, and rare species all contribute to adaptive capacity and emanate from within and between the different levels of biological organization, which can be seen in Table 2. Ecological memory is “the capability of the past states or experiences of a community to influence the present or future ecological responses of the community” (Sun and Hai 2011). This memory of ecological communities implies a “learning process” (Carpenter et al. 2001) that facilitates persistence during future disturbance. Ecological memory can be divided into internal and external legacies (Bengtsson et al. 2003) which are in turn composed of information legacies (species traits in the community, adaptation to past disturbances) and material legacies (propagules, seed banks; Johnstone et al. 2016). All of these types of memory are underpinned by one or more level of organization, as shown in Table 2. The consideration of cross-scale interactions for adaptive capacity points out that while the impact of disturbances in ecosystems can be scale-specific, components operating at other scales might buffer the disturbances in terms of maintaining system-level functioning. Also potentially important for the maintenance of system-level functioning is the distribution and redundancy of functional traits within and across spatiotemporal scales (Laliberté and Legendre 2010, Nash et al. 2016). Rare species may contribute an important but to some extent unpredictable degree of adaptive capacity to ecosystems through their ability to replace dominant species and the functions they provide after a disturbance.

Within the field of evolutionary biology, processes conferring adaptive capacity at the individual or population level are known as *adaptive potential* and the embedded *evolvability* (Hansen et al. 2019, Seaborn et al. 2021). The roles of standing genetic variation, phenotypic plasticity, and the interaction between the two in conferring adaptive potential to changing environmental conditions is a very active area of empirical and theoretic development (e.g. Chevin, Lande, & Mace, 2010). Adaptive potential can be considered a component of biological adaptive capacity. Evolutionary models are explicit on the underlying mechanisms of adaptive potential at the individual and population level, and the demographic consequences for populations and their risk of extinction. Components of this theoretical framework may be useful for the further conceptual and operational developments of adaptive capacity at the community and ecosystem level. Linking the frameworks studying the ability of organisms to respond to environmental change at different levels of biological organization will further our understanding of the adaptive capacity of ecosystems.

Table 2. Factors that contribute to adaptive capacity across different scales of biological organization. Table from **Paper II**.



Hierarchy of organization and selected traits

- Sub-individual
  - Matching physiological conditions to fluctuating inputs or internal demands (allostasis) (Carpenter and Brock, 2008)
  - Genetic, epigenetic and molecular processes (e.g. mutation)
- Individual
  - Phenotypic plasticity
  - Learning and dispersal ability
  - Behaviour
  - Adaptive evolution related to genetic diversity and evolutionary rates
  - Links between life-history traits, phenotypic plasticity, and evolutionary potential
- Population
  - Heritable life history characteristics: generation time, reproductive capacity, migration, habitat selection, genome size, survival characteristics (resting stages; hibernation, estivation), generalist vs specialist species
  - Population structure
  - Metapopulation dynamics
- Community
  - Taxonomic diversity
  - Functional diversity (redundancy, response diversity)
  - Strength of species interactions
  - Metacommunity dynamics (colonization and dispersal abilities)
  - Founder effects
  - Priority effects
  - Dormancy (resting eggs and propagule banks) and bet-hedging strategies
- Ecosystem
  - Interaction of and connection between abiotic and biotic elements in feedback loops (balancing and reinforcing or negative and positive)
  - Changing shapes of basin of attraction/stability landscape (topography, soils, landforms)
- Biome
  - Biogeographical distributions of native and invasive species
  - Phylogenetic dynamics
  - Evolutionary, disturbance and climate histories

4.2.2 Assessing adaptive capacity

Paper II proposes a framework for assessing adaptive capacity using a reiterative approach based ideally on time series from regular monitoring, or alternatively on multiple snapshot samplings of the ecosystem. From these data changes over time can be compared, which gradually reduces the uncertainty surrounding the adaptive capacity of the ecosystem. This approach should facilitate the assessment of general system-level adaptive capacity to an unspecified disturbance or stressor by measuring surrogates of adaptive capacity based on measures of ecological stability (Donohue et al. 2013), biodiversity (Magurran 2013), and resilience (Angeler and Allen 2016).

For details on this framework, see **Paper II** and Baho et al. 2017. Most generally, the framework works by evaluating surrogates of adaptive capacity in a logical, iterative sequence based on multiple lines of evidence (e.g. taxa across distinct trophic levels; Burthe et al. 2016). These hypotheses can be framed specifically from an environmental management perspective to facilitate the quantification of adaptive capacity without sacrificing the complexity inherent in management-related assessments. These proposed hypotheses are very general, but they stress the importance of long-term and spatially extensive monitoring programs that may capture both the known and yet unknown sources of adaptive capacity in ecosystems. The explicit emphasis on learning in this framework makes clear that uncertainty about complex systems will never be fully eliminated, but it can be incorporated and reduced incrementally when an ecosystem is monitored over time and space.

4.3 Indicators of stability and adaptive capacity

As previously noted, ecological resilience is an emergent property of complex systems, and thus no single metric can capture it fully. Perhaps because of this overwhelming complexity, much of the literature on ecological resilience has focused on theory, definitions, and broad conceptualizations (Chambers et al. 2019), which has led to confusing terminology and a somewhat unstructured set of quantification methods. Frameworks for assessing the general resilience of systems are mostly just that, frameworks, and they rely ultimately on relatively simple, well-known, and measurable entities that are well-grounded in ecological (stability) theory (Donohue et al. 2013, Baho et al. 2017). Most quantitative assessment have been of specific resilience. That is “resilience of what to what” (Carpenter et al. 2001), e.g., the resilience of phytoplankton communities to liming (Baho et al. 2014). Many of these studies have been limited in spatial and temporal extent. Examining ecological resilience at broad scale is necessary because many environmental pressures (e.g. species invasions, nutrient and acid deposition, climate change) operate at broad spatial and temporal scales and may cause long-term loss of stability and resilience of entire landscapes (Angeler et al. 2015, Allen et al. 2016). Thus, one of the aims addressed by both **Papers III and IV** of this thesis was the quantification of adaptive capacity metrics using structural and functional aspects at broad spatiotemporal (**Paper III**) and spatial (**Paper IV**) scales.

4.3.1 Lake stability

We used the variation in yearly Detrended Correspondence Analysis (DCA) scores within lakes and across years as a measure of individual lake stability (Figure 2). We found significant differences between lakes in their compositional stability across time in both the community structure captured by DCA 1 and DCA 2 in northern and southern lakes ($p < .001$ for all four models). The mean variance across lakes in DCA 1 score was 0.33, and the range spanned from 0.15 (Lake Dagarn, most stable) to 0.62 (Lake Granvattnet, least stable). For DCA 2, the mean variance was also 0.33 with a range from 0.13 (Siggeforasjön, most stable) to 0.93 (Ymsen, least stable). This method allowed for the identification of particularly stable and particularly variable lakes, which may be of interest for management prioritization at local scales. Quantification of stability at the individual lake level allowed us quantify the factors driving this stability at broader scales and between ecoregions.

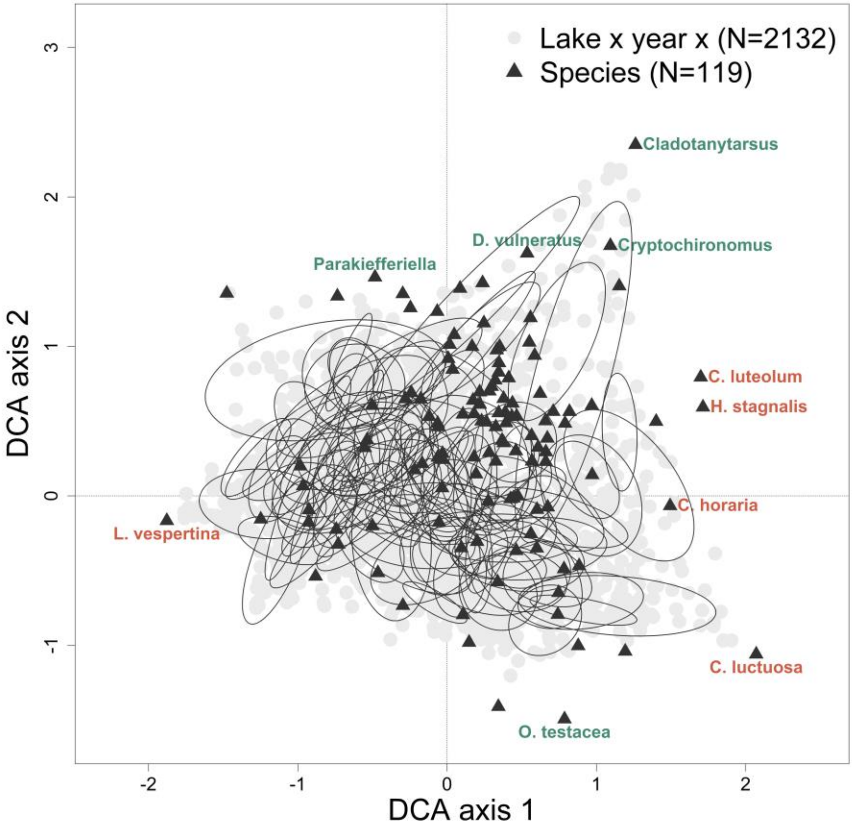


Figure 2. Detrended correspondence analysis ordination biplot for the 105 lakes across all years. Taxa locations are depicted with black triangles and lake scores (in a given year) are depicted in gray circles. Black ellipses are drawn around the standard deviation of point scores for each lake, by year. Detrended correspondence analysis (DCA) axis 1 eigenvalue = 0.38 and axis length = 3.67. Axis 2 eigenvalue = 0.25 and axis length = 3.39. The five taxa with the highest absolute loadings for DCA 1 and DCA 2 are labeled in orange and green, respectively. Figure from **Paper III**.

4.3.2 Stream functional redundancy and response diversity

Using trait data of invertebrates from 134 southern Swedish streams, we identified five functional effect groups (FEGs) based on effect traits. Very generally, FEG 1 consists of larger sized organisms with burrowing, crawling or more sessile locomotion modes, and diverse feeding modes ranging from filterers to parasites to predators to scrapers. It also includes some snail genera with “swimming” traits (indicating a readiness to enter the drift). FEG 2 is medium to large sized mobile crawling predators that predominantly engulf their prey, but also some species that hunt using suspension feeding and are temporarily attached. FEG 3 is predominantly small to medium sized crawling detritivores, ranging from shredders to gatherers, but also a few smaller crawling predators (e.g. Isoperla) which also sometimes gather. FEG 4 includes small to large sized swimming predators that predominantly suck the body contents of their prey. FEG 5 consists predominantly of small to medium sized scrapers, including smaller snails which do not readily drift (unlike those in FEG 1).

Functional redundancy for each FEG in each stream was measured as the number of species. From those identified species, response diversity was quantified as their multivariate dispersion in response trait space (Figure 3). We thus ended up with 670 measures of both functional redundancy and response diversity (5 FEGs x 134 streams). Both indices were ranked within FEG to control for inter-stream differences (e.g. as 1–134 for the 134 streams).

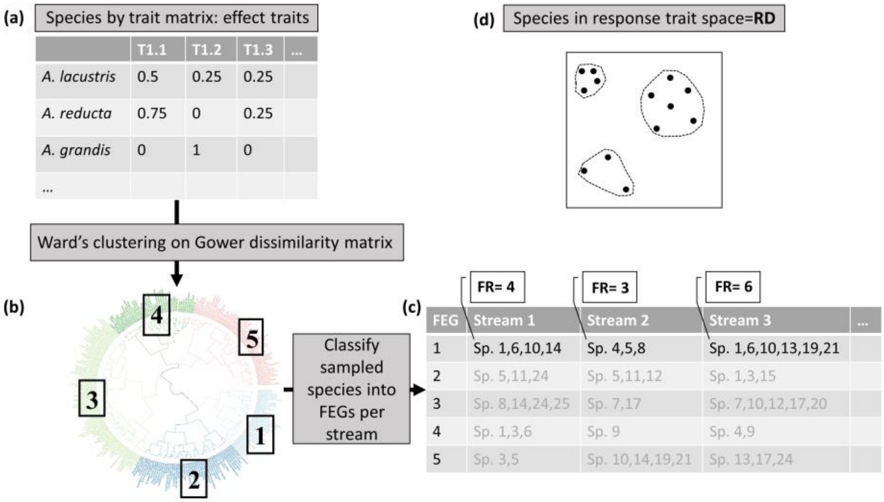


Figure 3. Schematic to illustrate how functional redundancy (FR) and response diversity (RD) were calculated in **Paper IV**. The first step is a) a species by trait matrix for the fuzzy-coded effect traits (body size, feeding group, locomotion) for all taxa. Columns represent theoretical fuzzy-coded effect traits for each taxa (row names). Functional effect groups (FEG) are defined next (b) based on a fusion-level plot of the dendrogram and expert opinion. Functional redundancy is measured (c) as the number of species sampled in each stream and in each FEG. Of those sampled species, the response diversity of each stream and each FEG is measured (d) as their functional dispersion (FDis) in trait space (based on response traits).

We examined the correlation between functional redundancy and response diversity. This is important because resilience is fostered if in addition to high levels of functional redundancy, species respond differently to disturbances (response diversity). According to the ¨insurance effect¨ hypothesis, functional redundancy among species providing similar ecological roles (i.e., having similar functional effect traits) confers adaptive capacity because declining species may be replaced by other functionally similar species (Yachi and Loreau 1999, Angeler et al. 2019, McLean et al. 2019). Adaptive capacity is also fostered if in addition to functional redundancy, species respond differently to disturbances, quantified as 'response diversity' (RD) (Nyström 2006), i.e. diversity in the types of traits that regulate species responses. Since these measures were based on two different sets of traits and different indices, their positive correlation was not a given. However, the correlation was positive both overall (i.e. correlation of the full set of 670 measures), and in each individual FEG, though not significant in FEG 5 (Figure 4). High levels of both FR and RD (top right part of Figure 4) imply the functions provided by the FEGs foster adaptive capacity while low levels of both FR and RD (bottom left part of Figure 4) suggesting lower adaptive capacity. The positive relationship between FR and RD suggests that the functional aspects in the streams that become vulnerable as functional redundancy decreases in FEGs 1 through 4 are unlikely to be preserved due to maintained levels of response diversity.

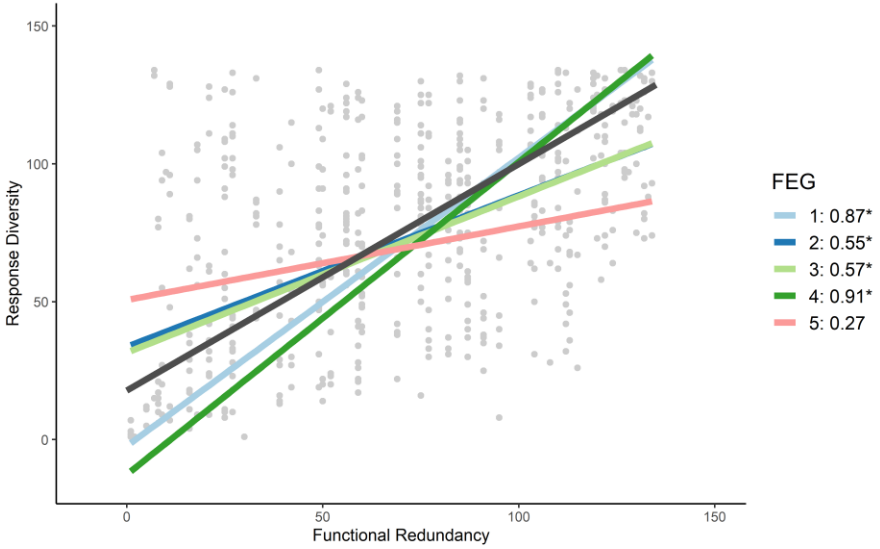


Figure 4. Correlations between ranked functional redundancy and response diversity across all functional effect groups (best-fit line across all FEGs in black, Pearson’s rank correlation r = 0.67, p < 0.001) and individually for each FEG (r correlations and significance at the 0.001 level * noted in legend). Figure from **Paper IV**.

4.4 Drivers of stability and adaptive capacity

Either implicit or explicit in the definitions of ecological resilience, adaptive capacity, and stability (Table 1) are the disturbances or perturbations, which the system can cope with (adaptive capacity) or not, potentially leading to a regime shift (ecological resilience). Throughout the research on ecosystem response to change are terms such as perturbation, pressure, stressor and disturbance, used to indicate events or conditions in the environment that affect ecosystems (Borics et al. 2013). In reality, ecosystems face many and various types of environmental disturbances simultaneously (Odum 1985). Additionally, the scale, frequency, and intensity of these disturbances are increasing (Turner 2010, Seidl et al. 2016). This undoubtedly impacts ecosystem structure, function, and composition and yet the consequences of long-term spatially extensive disturbances on metrics of ecological resilience, adaptive capacity, and stability are underexplored. In **Papers III and IV**, we examine how the indicators of stability and adaptive capacity based on taxonomic and functional metrics (section 4.3) are affected by environmental conditions.

4.4.1 Physiochemical drivers of lake stability

We examined broad scale, long-term patterns in invertebrate community stability using individual measures of lake stability across a spatially extensive area historically influenced by heterogeneous pressures. Regional level patterns in stability were that less alkaline, more species-rich northern lakes with lower mean total-phosphorus were more stable along DCA 1. Stability was also higher for smaller more species-rich lakes along DCA 2. Southern lakes with higher species-rich were more stable along DCA 1 as were smaller lakes along DCA 2.

Analyses of temporal patterns of biodiversity have found that more diverse communities show smaller compositional changes over time (Yodzis 1981, McCann et al. 1998), potentially indicating that high diversity is associated with greater temporal stability in species composition (Shurin 2007). The results from **Paper III** seem to support this. The “insurance effect” is often also used to explain this positive relationship between richness and stability; community level stability increases when there is functional redundancy of species with important stabilizing roles, and those species respond differently to varying conditions (McCann 2000). Disturbances may drive change in ecosystems by acting as a stressor for some species, while providing opportunity for others, depending on their life history (Paine et al. 1998). A major new insight gained from recent experimental work is that diversity may stabilize aggregate ecosystem or community properties while simultaneously destabilizing individual species abundances (Loreau and de Mazancourt 2013). While these mechanistic may be underpinning the community dynamics, we did not address their relevance in our study.

An additional result from **Paper III** was that northern lakes with higher mean total-phosphorus tended to be less stable. Total-phosphorus is declining overall across Swedish lakes and the largest relative declines are in northern Swedish lakes (Huser et al. 2018). These results suggest that stability of invertebrate communities may be related to mean levels of total-phosphorus, especially in the north.

There have been advances in theoretical insights into community stability at broader spatial scales, but a comprehensive framework has yet to be developed. The detected influence of ecoregion (north and south of the Limes Norrlandicus) on stability suggests that accounting explicitly for spatial and/or biogeographical characteristics (location, connectivity, dispersal) is important for understanding regional-scale patterns of stability, which need to be accounted for when developing management strategies. Given that ecoregions differed in their environmental conditions and the biotic responses, a one-size-fits-all management approach might not be appropriate across ecoregions.

4.4.2 Effects of two disturbance gradients on functional redundancy and response diversity

We examined the effects of an agricultural land-use gradient and a hydrological modification gradient on functional redundancy and response diversity overall (i.e. in all 670 measures), and individually for each FEG. Functional redundancy and response diversity were either unaffected (FR) or slightly positively affected (RD) overall by agricultural land-use intensification, but patterns within individual effect groups varied greatly. The effect of the agricultural land-use gradient on FR included positive (FEGs 1 and 4), negative (FEGs 2 and 3), and nonsignificant (FEG 5) relationships. The results were the same for RD, with the exception of FEG 5, which increased across the gradient (Figure 5).

Streams with higher levels of hydrological modifications had higher levels of functional redundancy but response diversity was unaffected. The individual FEGs were overall unaffected by the hydrological modification gradients, with the exception of increasing functional redundancy of FEG 5 and increasing response diversity of FEG 1 (Figure 5).

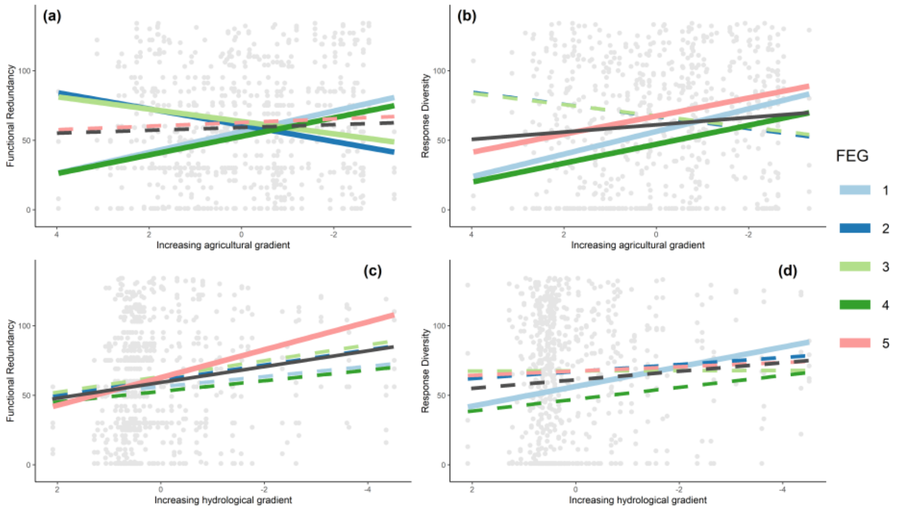


Figure 5. Response in ranked functional redundancy and response diversity overall (black lines) and of all 5 functional effect groups to an increasing agricultural land-use (a & b), and increasing hydrological modification gradient (c & d). Solid lines represent significant effects and dashed lines non-significant effects. Figure from **Paper IV**.

Overall, the results indicate that agricultural land-use intensification has more pronounced effects on individual FEGs and the functions they provide. This may have lead to the vulnerability of two FEGs (2 and 3) through decreases in functional redundancy. However, decreases in RD of these two groups were not significant, suggesting that response diversity can potentially be maintained with lower levels of species richness if the remaining species are widely dispersed in response trait space. Interestingly, FEGs 1 and 4 actually increased in both functional redundancy and response diversity along the agricultural land-use gradient. This may be because of changes that make the environment more suitable for certain organisms. Another possible explanation is a form of pollution-induced community tolerance, which relates to differences in sensitivity to toxicants between different species in communities (Blanck and Wangberg 1988). Traits are also not lost randomly with respect to disturbances (Srivastava and Vellend 2005, Ives and Carpenter 2007, Bracken et al. 2008, Zavaleta et al. 2009). Communities may first lose traits related to sensitive life histories. Functional composition shifts as these stress-sensitive species are replaced with stress-tolerant and opportunistic species. The remaining community can be dominated by 'survivor' stress-tolerant species, which may be as or more tolerant to subsequent disturbances (Darling and Côté 2013). Trait-based approaches have been mainly studied and validated at local scales, but many drivers of biodiversity change operate at much broader spatial scales, from the ecosystem level to the landscapes in which they are embedded (Allen et al. 2016). Thus, trait-based approaches used as indicators of adaptive capacity should be applied at the spatial scales most relevant for capturing the effects of a given disturbance (Hevia et al. 2017).

5. Conclusions, considerations and outlook

This thesis addresses concepts and quantification of ecological resilience, ecosystem stability and adaptive capacity through transdisciplinary conceptual and framework development (**Papers I and II**), and empirical metrics (**Papers III and IV**). The overarching organization of themes leads to complementary and interlinked approaches to better understand how ecosystems are shaped by, and respond to, changes in the environment. Ecological resilience acknowledges the possibility of multiple regimes, and focuses on dynamics within and between alternative regimes, as well as on understanding and predicting thresholds between regimes (Gunderson 2000, Angeler and Allen 2016). Ecosystem stability can be thought of as nested within ecological resilience, focusing on specific processes of change (or lack thereof) and recovery in measures of ecosystem functions and structure in response to disturbances (Donohue et al. 2016). Adaptive capacity links these two concepts, in that it includes stability metrics (resistance, persistence, variability, and engineering resilience) in addition to other components of adaptive capacity (memory, cross-scale interactions, ecological functioning) that allow the ecosystem to stay within a regime. I also contend that strengthening links between adaptive capacity and adaptive potential, a concept which is strongly underpinned by evolutionary models at the individual and population levels, may improve the overall theoretical framework through understanding of underlying mechanisms of adaptive capacity at the community and ecosystem level.

The empirical approaches in **Papers III and IV** of this thesis only addressed a small subset of the potential sources of adaptive capacity in ecosystems. Namely, we looked at 1) compositional stability and 2) functional redundancy and response diversity as components of adaptive capacity related to ecological functioning.

The main conclusions of this thesis are:

- Quantitative developments in ecological resilience must be better integrated into assessments of social-ecological resilience.
- The concepts of ecological resilience, ecological stability, and adaptive capacity are inextricably linked and complementary. Adaptive capacity bridges ecological resilience and ecological stability and is underpinned by many factors operating within and across levels of biological organization.
- One indicator of stability in invertebrate communities points to variation in the stability of community composition across time and space in Swedish lakes. Two interlinked metrics of adaptive capacity based on invertebrate functional traits (functional redundancy and response diversity) show positive correlations at a broad spatial scale in Swedish streams.
- These indicators are influenced by physiochemical characteristics of the waterbodies, as well as known pervasive anthropogenic disturbances in the landscape.

5.1 Considerations and outlook

As is probably the case with most people finishing their PhDs and reviewing what they have done, I have identified some things I would now do differently, and many ways I would like to follow up on what I have done. Such is the learning process! The following are broader considerations on the field, concerns, and possible future directions.

5.1.1 The organization of concepts

At the beginning of this thesis, I pointed out that the fields of stability and resilience research have diverged to the detriment of both. The two fields have largely progressed in parallel with limited intellectual overlap, slowing scientific progress in both. A recent review by Van Meerbeek et al. (2021) quantified this intellectual and conceptual schism using a bibliometric literature analysis of the stability and resilience literature. Their analysis revealed two distinct fields differing in their focus on equilibrium versus non-equilibrium dynamics of ecosystems. This difference in focus is similar to the basis of the conceptual hierarchy presented in this thesis. However, the authors of this paper advocate, based on a thorough review and with empirical developments in mind, for the nesting of resilience within ecological stability. Although their treatment of ecological resilience concepts is somewhat superficial, they argue convincingly that this is the most parsimonious path to a common lexicon and empirical framework. All of this is to say that this ambiguity between the fields is acknowledged, but clearly not resolved. Terminology matters, but when studying entities as complex as ecosystems, staking claims on jargon alone will hinder our understanding and the broader societal relevance of these concepts.

5.1.2 Functional ecology

Since the 1990s, functional diversity has been considered a key component of biodiversity. That is, understanding the diversity and distribution of functional traits, and not only species-identity based metrics became a widespread goal in ecology (Laureto et al. 2015). Functional traits are ‘morphological, biochemical, physiological, structural, phenological, or behavioral characteristics that are expressed in phenotypes of individual organisms and are considered relevant to the responses of such organisms to the environment and/or their effects on ecosystem properties’ (Violle et al. 2007, Díaz et al. 2013). Functional diversity is often examined as the most effective diversity measure for linking changes in communities to effects on ecosystem functioning and services (Díaz et al. 2006, Balvanera et al. 2006). This purported link has been used widely to argue that species diversity matters only for the traits and related interactions that help maintain the functioning of ecosystems and that this approach will yield a more predictive science (Loreau et al. 2001). A quick search shows that there is no clear definition of ‘ecosystem functioning’. ‘Ecosystem services’ were first defined by the Millennium Ecosystem Assessment (MEA 2005) as those processes occurring within an ecosystem that provide benefits to humanity. For one there is a lack of clarity and the other a clear anthropocentric viewpoint, yet management decisions are often made with the goal of increasing or preserving ecosystem functioning and services. Biodiversity has intrinsic value, or values that we have not or can not conceive, even if it is “useless” from the perspective of human needs or for ‘ecosystem functioning’. Others have pointed this out (e.g. Ghilarov 2000) and it shows that management recommendations from studies of functional ecology should be made with care.

5.1.3 Correlation between taxonomy and traits

Paper III of this thesis worked with compositional invertebrate data and **Paper IV** with functional data. The previous section highlighted that biodiversity is a multifaceted concept that includes genetic, taxonomic, phylogenetic, and functional components. Despite this complexity, studies of biodiversity and changes therein generally consider only a single facet at once. Richness has historically been the dominant measure but trait-based approaches continue to increase in the field. There have been studies focusing on both taxonomic measures and functional composition, which have been extremely fruitful to understand the extent to which variation in functioning can be inferred from taxonomic data vice versa (Gagic et al. 2015, Soininen et al. 2016). While some studies have found changes in species composition coupled to changes in functional trait composition (Soininen et al. 2016, Biswas et al. 2017), others have found that species and trait composition can show different trajectories (Fukami et al. 2005, Gallagher et al. 2013) due to functional redundancy, functional convergence or functional divergence. The monitoring data used for our empirical papers consists of routine taxonomic inventories but there are few functional studies as of yet. To that end, we have begun to look at the relationships between different taxonomic and functional turnover metrics (richness-based and abundance-based). Results so far indicate that taxonomic and functional turnover metrics are generally weakly correlated in these macroinvertebrate assemblages. Additionally, taxonomic turnover was consistently lower than functional turnover, both in space and time, and for richness- and abundance-based metrics. This suggests that turnover of one metric cannot necessarily be inferred from turnover in the other and highlights the importance of studying both taxonomic and functional turnover over space and time.

5.1.4 Future directions

This thesis highlighted the complexity of topics such as resilience, stability, and adaptive capacity. In some ways, increases in our understanding of the dynamics underpinning these concepts have led to more questions. I felt the same way about the progress of my PhD as I guess many do as they dive deeply into a field. One thing is certain though: the continued collection and exploration of long-term and spatially extensive data of biotic communities that experience dynamic environmental conditions is critical to research in this area. Strengthening empirical emphasis in the ecological resilience field may help to further resolve conceptual questions. The Swedish monitoring dataset is particularly suitable for further indicator development, particularly because of its spatial and temporal extent, and although it is open access, is still underexplored.

This thesis began by talking about divisions between the fields of resilience and stability. Another division that hinders progress is that between quantitative approaches developed by evolutionary ecologists for studying the dynamics of populations and the approaches in community ecology. Cross-fertilization between these two frameworks can lead to a better understanding of the adaptive capacity of communities and ecosystems. Using the Swedish monitoring dataset, one of my future plans is to test theories of stochastic population dynamics at the community level. Stochastic fluctuations in the environment are expected to result in fluctuations in population sizes, which increases extinction risk (Lande et al. 2003) especially when fluctuations are spatially autocorrelated. The framework to study this phenomena by evolutionary ecologists can be extended to community ecology in order to study how species are affected differently by environmental fluctuations. This will lead to changes in community composition, potentially affecting the interaction between species, ecological resilience, and adaptive capacity to climate change. This theoretical framework has been applied mostly to single populations so this project will help bridge the gap between stochastic population dynamics and community ecology, improving our ability to understand and predict how communities will be able to adapt to the increasing anthropogenic pressures changing our environment.

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Popular science summary

Before reading on much further, please take a moment to think about a few things. First, what does the word ‘resilience’ mean to you? What is the first thing that comes to mind? How do you think this word relates to ‘stability’ and ‘adaptive capacity’? Now think about if and how you could measure these things.

Different people probably thought about very different things depending on their frame of reference. Some might have thought about a person’s ability to cope with difficult events. Others about how quickly an organization can prepare for, respond to and recover from a disruption. To others these ideas made them think about an object springing back into shape after being bent, compressed, or stretched. These terms are everywhere, and often mean something a little different in each field. However, their widespread use in many fields suggests that they are describing something important, and are not just empty concepts. The idea of change, and the ability to cope with or adapt to it, is the common element.

In the field of ecology, we often talk about ‘ecological resilience’, which is the amount of disturbance that a particular ecosystem can handle while still maintaining its basic identity. Measuring ecological resilience is difficult because ecosystems are complex and they may be affected by different disturbances at the same time. There is still much uncertainty about how to best measure this property, but there has been extensive research focused on this, especially in the last 20 years. Since human society and ecosystems are so closely linked and dependent on each other, it is no surprise that there is great interest in how ecosystems respond to disturbances. One of the aims of my thesis was to summarize how some of these measurements of ecological resilience could be helpful for measuring the resilience of linked systems of humans and nature, or ‘social-ecological systems’.

So what did you think about the terms ‘stability’ and ‘adaptive capacity’? Do they sound like synonyms of resilience? Another goal of this thesis was to explore this complicated topic of ‘adaptive capacity’ and summarize what contributes to it and ways to measure it more successfully. We argue that stability and adaptive capacity form part of the ecological resilience of an ecosystem. They describe things about the ecosystem in its current state, like how resistant it is to change when disturbed, or the specific mechanisms that allow it to buffer a disturbance.

I also studied stability and adaptive capacity in specific ecosystems. To do this, I used data from invertebrate communities in lakes and streams in Sweden. For the lake communities, I looked at how much the invertebrate species changed across 23 years and 105 lakes all over Sweden. I also looked into some reasons why these communities might be more or less stable. Some lakes were much more stable than others, and the stability was affected by species richness, the size of the lake, alkalinity and total phosphorus.

In the Swedish streams, we examined how the traits of the invertebrates, as indicators of adaptive capacity, were affected by two disturbances: increasing levels of agriculture surrounding the streams, and changes that affect the movement and flow of water in the streams. Traits in this case means characteristics of the invertebrates, like their body size or what they eat, as opposed to their identities. It can be helpful to look at how disturbances affect traits because this can tell you something about the functions in the ecosystem that are affected. We found interesting results about how increasing levels of agriculture can affect indicators of adaptive capacity that are based on invertebrate traits in these streams.

In summary, my thesis shows how complicated ecosystems are and how important it is to collect lots of information about them! It took a coordinated effort by many people to get just a couple measures of stability and adaptive capacity. There are many more groups of plants and animals, and many disturbances that can be studied to learn more about resilience, stability, and adaptive capacity in ecosystems.

Populärvetenskaplig sammanfattning

Innan du läser vidare, stanna upp och fundera på några saker. Först, vad betyder ordet ‘motståndskraft’ för dig? Vad är det första du kommer att tänka på? Hur tänker du att det ordet relaterar till ‘stabilitet’ och ‘anpassningsförmåga’? Fundera nu på om och hur du kan mäta de här sakerna.

Olika människor tänkte nog på väldigt olika saker beroende på sina referensramar. Vissa kanske tänkte på en människas förmåga att hantera svåra händelser. Andra på hur snabbt en organisation kan förbereda sig, svara på och återhämta sig efter en störning. För andra fick begreppen dem att tänka på ett föremål som återfår sin form efter att ha böjts, komprimerats eller sträckts ut. De här termerna finns överallt och betyder ofta något lite annorlunda inom varje område, men deras utbredda användning inom många områden tyder på att de beskriver något viktigt och inte bara är tomma begrepp. Den gemensamma nämnaren inom alla områden är idén om förändring, förmågan att hantera förändringar och att kunna anpassa sig.

Inom ekologin talar vi ofta om ‘ekologisk motståndskraft’, vilket är den mängd störningar som ett visst ekosystem kan hantera utan att förlora sin grundläggande identitet. Att mäta ekologisk motståndskraft är svårt eftersom ekosystem är komplexa och de kan påverkas av olika störningar samtidigt. Det finns fortfarande mycket osäkerhet om hur man bäst mäter den här förmågan, och det finns omfattande forskning på området, speciellt från de senaste 20 åren. Eftersom det mänskliga samhället och ekosystemen är så sammankopplade och beroende av varandra är det ingen överraskning att det finns ett stort intresse för hur ekosystem reagerar på störningar. Ett av syftena med min avhandling var att sammanfatta hur några av dessa mått på ekologisk motståndskraft kan hjälpa till att mäta motståndskraften hos länkade system av människor och natur, eller ‘socioekologisk system’.

Så vad var dina tankar om termerna ‘stabilitet’ och ‘anpassningsförmåga’? Kan de vara synonymer till motståndskraft? Ett annat mål med den här avhandling var att utforska det komplicerade ämnet ‘anpassningsförmåga’ och sammanfatta vad som bidrar till den och effektiva metoder att mäta den på. Vi hävdar att stabilitet och anpassningsförmåga ingår i ett ekosystems ekologiska motståndskraft. De beskriver saker om ekosystemet i dess nuvarande tillstånd, som hur resistent det är mot att förändras när det störs, eller de specifika mekanismer som gör det möjligt att buffra en störning.

Jag studerade också stabilitet och anpassningsförmåga i specifika ekosystem. För att göra det använde jag data från evertebratsamhällen (ryggradslösa djur) i sjöar och vattendrag i Sverige. För sjösamhällen tittade jag på hur mycket arterna förändrades över 23 år i 105 sjöar över hela Sverige. Jag tittade också på några av orsakerna till varför dessa samhällen var mer eller mindre stabila. Vissa sjöar var mycket stabilare än andra, och stabiliteten påverkades av artrikedom, storleken på sjön, alkalinitet och koncentrationen av totalfosfor.

I svenska vattendrag undersökte vi hur djurens egenskaper, som indikatorer på anpassningsförmåga, påverkades av två störningar: ökande mängd jordbruk som omger vattendragen och förändringar som påverkar rörelsen och flödet av vatten i vattendragen. Egenskaper i detta fall betyder egenskaper hos djuren, som deras kroppsstorlek eller vad de äter, istället för deras taxonomiska identitet. Det kan vara bra att titta på hur störningar påverkar egenskaper eftersom det kan berätta något om de funktioner i ekosystemet som påverkas. Vi hittade intressanta resultat om hur ökande nivåer av jordbruk kan påverka indikatorer för anpassningsförmåga, som baserades på djurens egenskaper, i de här vattendragen.

Sammanfattningsvis visar min avhandling hur komplicerade ekosystem är och hur viktigt det är att samla in mycket information om dem! Det krävdes en samordnad insats av många människor för att få bara ett par mått på stabilitet och anpassningsförmåga. Det finns många fler grupper av växter och djur och många störningar att studera för att lära oss mer om ekosystems motståndskraft, stabilitet och anpassningsförmåga.

Acknowledgements

Thank you…

To everyone at the Department of Aquatic Sciences and Assessment for making it such a pleasant place to work. From friendly hallway chats, to competitive Frisbee games, I have really enjoyed my time at MVM.

To the many people who collected, identified, and analysed samples for the freshwater monitoring program, over many years! You have provided a great resource to society.

To my family for your humour, for instilling a love of nature, and for unwittingly being the first to show me how to sample invertebrates in the streams near Thurmont. I love you!

To my supervisors: David, Brendan, Richard, Stina, and Martyn!

ACTA UNIVERSITATIS AGRICULTURAE SUECIAE

DOCTORAL THESIS NO. 2021:38

Understanding ecosystem response to environmental change is one of the biggest challenges in ecology. This thesis addresses change from the perspectives of ecological and social-ecological resilience, stability, and adaptive capacity. Relationships between the concepts are clarified. Functional and compositional indicators of adaptive capacity were measured using invertebrate communities in Swedish waterbodies. These indicators were influenced by physiochemical variables, and pervasive anthropogenic disturbances in the landscape. The results highlight the importance of studying long-term and spatially extensive changes in biotic communities.

Hannah Fried-Petersen received her doctoral education at the Department of Aquatic Sciences and Assessment at the Swedish University of Agricultural Sciences. She received her MSc in Ecology, Evolution and Systematics from the University of Munich and her bachelor's degree from the University of Pittsburgh.

Acta Universitatis Agriculturae Sueciae presents doctoral theses from the Swedish University of Agricultural Sciences (SLU).

SLU generates knowledge for the sustainable use of biological natural resources. Research, education, extension, as well as environmental monitoring and assessment are used to achieve this goal.

Online publication of thesis summary: http://pub.epsilon.slu.se/

ISSN 1652-6880
ISBN (print version) 978-91-7760-754-0
ISBN (electronic version) 978-91-7760-755-7