EXPLORING CONNECTIONS IN SOCIAL-ECOLOGICAL SYSTEMS

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Exploring connections in social-ecological systems

The links between biodiversity, ecosystem services and human well-being in South Africa

Doctoral thesis in Sustainability Science

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To Omi.

Abstract

A key challenge of the Anthropocene is to advance human development without undermining critical ecosystem services. Central to this challenge is a better understanding of the interactions and feedbacks between biodiversity, ecosystem services and human well-being, which interact in dynamic and complex social-ecological systems. These relationships have been the focus of much work in the past decades, however more remains to be done to comprehensively identify and quantify them, especially at larger scales. In this thesis, a social-ecological systems approach is adopted to investigate connections between biodiversity, ecosystem services and human well-being in South Africa. The country's high levels of biological and socio-economic diversity, as well as its emerging economy make South Africa an interesting case for exploring these connections.

Using data from a variety of public sources, and at different sub-national scales, the thesis first identifies and analyses a variety of bundles of ecosystem service use. Based on these bundles, three social-ecological system archetypes were identified and mapped in South Africa, namely the green-loop (high overall use of local ecosystem services), transition, and red-loop (low overall use of local ecosystem services) systems. Further analysis explored the social and ecological drivers of these patterns, and found the distribution of systems mainly influenced by social factors including household income, gender of the household head, and land tenure.

Second, this thesis uses human well-being indicators to construct, analyse and map multi-dimensional human well-being bundles. These bundles were found to spatially cluster across the landscape, and were analysed for congruence with the ecosystem service use bundles. Discrepancies in the expected overlap of ecosystem service use and human well-being were highlighted and concur with findings elsewhere and the ongoing debate in the literature on the impacts of time-lags, indicator choice and scale of these interactions.

Third, biodiversity in South Africa was analysed by employing an indicator of biodiversity intactness (BII) at the population level. The BII was found to have declined by 18.3% since pre-industrial times. Biodiversity loss was linked to the potential supply of ecosystem services, as well as human well-being patterns. A

potential threshold at 40% biodiversity loss was detected, beyond which population abundances decline sharply.

Finally, the thesis examines multiple perspectives on ecosystem services in sustainability research, including the social-ecological systems perspective, and discusses the complementarity of the different perspectives in furthering a deeper understanding of the connections between people and ecosystems. The social-ecological systems perspective employed throughout the empirical work presented in this thesis contributed towards cross-cutting insights, the testing of new kinds of data and the development of new approaches, all of which represent important steps towards unravelling the connections between biodiversity, ecosystem services and human well-being, and contributing to the key Anthropocene challenge of sustainable development.

Keywords: complex adaptive systems, mapping, ecosystem service bundles, multidimensional human well-being, biodiversity loss, inequality, research frameworks, interdisciplinarity, natural resource management, sustainable development

Sammanfattning

En av tidsåldern Antropocens stora utmaningar är att främja mänsklig utveckling utan att underminera nödvändiga ekosystemtjänster. Centralt för denna utmaning är en bättre förståelse av interaktioner och återkopplingar mellan biologisk mångfald, ekosystemtjänster och mänskligt välbefinnande, vilka interagerar i dynamiska och komplexa social-ekologiska system. Dessa samband har varit i fokus för många studier under de senaste decennierna, men mycket återstår för att på ett heltäckande sätt identifiera och kvantifiera sambanden, i synnerhet i större skala. Denna avhandling använder social-ekologiska system som angreppssätt för att undersöka kopplingar mellan biologisk mångfald, ekosystemtjänster och mänskligt välbefinnande i Sydafrika. Landets höga nivåer av biologisk- och socio-ekonomisk mångfald, samt dess framväxande ekonomi gör att Sydafrika utgör en intressant fallstudie för att utforska dessa kopplingar.

I avhandlingen används data från olika offentliga källor, på olika subnationella skalor, för att först identifiera och analysera en rad olika knippen av ekosystemtjänstanvändning. Baserat på dessa knippen identifierades och kartlades tre arketyper av social-ekologiska system i Sydafrika, nämligen system med grönt kretslopp (generellt hög användning av lokala ekosystemtjänster), system i övergång, samt system med rött kretslopp (generellt låg användning av lokala ekosystemtjänster). Vidare analys undersökte vilka sociala och ekologiska drivkrafter som ligger bakom dessa mönster, och fann att fördelningen av de olika social-ekologiska systemen främst påverkas av sociala faktorer som hushållsinkomst, kön hos den som leder hushållet, samt besittningsrätt för mark.

För det andra använder denna avhandling indikatorer på mänskligt välbefinnande för att konstruera, analysera och kartlägga flerdimensionella knippen av mänskligt välbefinnande. Dessa knippen visade sig uppträda spatialt som kluster i landskapet, och analyserades för överensstämmelse med knippen av ekosystemtjänster. Skillnader i de förväntade överlappningarna mellan användning av ekosystemtjänster och mänskligt välbefinnande markerades, och dessa överensstämmer med resultat från andra platser, och med den pågående debatten i vetenskaplig litteratur om konsekvenser av fördröjda effekter, val av indikatorer samt interaktionernas skala.

För det tredje analyserades biodiversitet i Sydafrika genom användning av en indikator för hur intakt den biologiska mångfalden är (BII) på populationsnivå. BII visade sig ha minskat med 18.3 % sedan förindustriell tid. Förlust av biologisk mångfald var kopplad både till den potentiella försörjningen av ekosystemtjänster och till mönstret av indikatorer på mänskligt välbefinnande. Ett potentiellt tröskelvärde vid 40 % förlorad biologisk mångfald identifierades, efter vilket populationsnivåer abrupt minskar om den biologiska mångfalden minskar ytterligare.

Slutligen undersöker avhandlingen flera perspektiv på ekosystemtjänster inom hållbarhetsforskning, bland dem det social-ekologiska systemperspektivet, och diskuterar hur de olika perspektiven kan komplettera varandra för att fördjupa förståelsen för sambanden mellan människor och ekosystem. Det social-ekologiska systemperspektivet som använts i det empiriska arbetet presenterat i denna avhandling bidrar med övergripande insikter, test av nya typer av data och utveckling av nya angreppssätt, bidrag som alla representerar viktiga steg på väg mot att reda ut kopplingarna mellan biologisk mångfald, ekosystemtjänster och mänskligt välbefinnande, och till att lösa utmaningen om hållbar utveckling i Antropocen.

Thank You

When I first packed my bags to go "do a PhD" in Sweden, most people looked at me in confusion. "Sweden?! But it's so cold there!" Yes, yes it is, but it's also been a fantastic experience, not because of the chilly temperatures, but because of the warm people I met along the way. There are too many to mention everyone by name, but I'd like to single out a few, to say a special Thank You.

First and foremost, to my supervisors: Oonsie Biggs, for being patient, for listening and taking my opinion into account like few people I've ever met, and for pushing me to think better, write better and ask better questions; Belinda Reyers, for reminding me to always check my assumptions and think of the big picture, and for giving me so many opportunities to broaden my horizons; and Thomas Elmqvist for sage advice and holding my hand through the labyrinth of Swedish administration. I am so grateful to you all.

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Contents

List of papers

The following papers are included in this thesis:

I. **Hamann, M.**, Biggs, R., & Reyers, B. (2015) Mapping social–ecological systems: Identifying 'green-loop' and 'red-loop' dynamics based on characteristic bundles of ecosystem service use. *Global Environmental Change* 34: 218-226.

II. **Hamann, M.**, Biggs, R., & Reyers, B. An exploration of human well-being bundles as identifiers of ecosystem service use patterns. Revised manuscript to be resubmitted to *PLoS One*.

III. **Hamann, M.** & Biggs, R. Biodiversity change in South Africa: connections to ecosystem services and human well-being. Manuscript.

IV. **Hamann, M.**, Biggs, R., Reyers, B., Tengö, M., Daw, T., Hahn, T., Selomane, O., Polasky, S., Elmqvist. E. Four perspectives on ecosystem services. Manuscript to be submitted to *Ecology & Society*.

Contribution to papers:
The research in **Papers I – III** was conceived and designed together with the co-authors. I collected all data for **Papers I – III** from public sources, performed all the analyses, and wrote the text with input from the co-authors. For **Paper IV**, the original research idea was conceived in discussions about the social-ecological perspective on ecosystem services at the Stockholm Resilience Centre. The different perspectives were then identified by the co-author group at a number of workshops hosted by the Programme on Ecosystem Change and Society (PECS). I distilled the discussions into a paper, wrote the majority of the text and co-ordinated the co-authors' contributions.

Related work not included in the thesis

My thesis work was embedded in the global Programme on Ecosystem Change and Society (PECS), and its southern African research network (SAPECS). Being part of these programmes, as well as the Stockholm Resilience Centre, resulted in a number of collaborations that greatly enhanced my learning process and contributed indirectly to this thesis. The following are selected outcomes of these collaborations:

- Oteros-Rozas, E., Martín-López, B., Daw, T., Bohensky, E., Butler, J., Hill, R., Martin-Ortega, J., Quinlan, A., Ravera, F., Ruiz-Mallén, I., Thyresson, M., Mistry, J., Palomo, I., Peterson, G., Plieninger, T., Waylen, K., Beach, D., Bohnet, I., **Hamann, M.**, Hanspach, J., Hubacek, K., Lavorel, S., Vilardy, S. (2015) Participatory scenario planning in place-based social-ecological research: insights and experiences from 23 case studies. *Ecology and Society*, 20(4).

- Balvanera, P., Daw, T., Gardner, T., Martín-Lopez, B., Nörstrom, A., Ifejika Speranza, C., Spierenburg, M., Bennett, E., Farfan, M., **Hamann, M.**, Kittinger, J., Luthe, T., Maass, M., Peterson, G., Pérez-Verdin, G. Key features for successful place-based sustainability research on social-ecological systems. Manuscript in review for *Ecology & Society*.

- Kadin, M., **Hamann, M.**, Merrie, A., Anker-Nilssen, T., Olsson, O. (2014) Seabirds and changes in ecosystem services – from exploitation to stewardship. Chapter in doctoral thesis by M. Kadin, *Seabirds as food for thought: an integrative study on seabird ecology and ecosystem services in changing marine systems*, Stockholm University, Sweden.

- Haider, L.J., Hentati-Sundberg, J., Giusti, M., Goodness, J., **Hamann, M.**, Masterson, V., Meacham, M., Merrie, A., Ospina-Medina, D., Schill, C., Sinare, H. Building strong sustainability science: the young interdisciplinarian's journey. Manuscript to be submitted to *Sustainability Science*.

- **Hamann, M.** & Masterson, V., Biggs, R., Tengö, M., Reyers, B., Dziba, L., Spierenburg, M. (2012) Social-ecological scenarios for the Eastern Cape 2012 – 2050. Report. Southern African Programme on Ecosystem Change and Society (SAPECS). Available at www.sapecs.org.

- **Hamann, M.** & Tuinder (Masterson), V. (2012) Introducing the Eastern Cape: a quick guide to its history, diversity and future challenges. Report. Southern African Programme on Ecosystem Change and Society (SAPECS). Available at www.sapecs.org.

Introduction

Shortly after Rachel Carson kindled the modern environmental movement with the publication of her influential book "Silent Spring" in 1962, she was asked to testify before a U.S. Senate subcommittee on pesticides. She told them that "our heedless and destructive acts enter into the vast cycles of the earth and in time return to bring hazard to ourselves" (Griswold, 2012). Though she was speaking specifically of the use of pesticides and other chemical pollutants in the quest for enhanced agricultural productivity, and the adverse effects of these chemicals on people's health, the more general notion of vital connections and feedbacks between human society and natural systems is as relevant today as it was more than 50 years ago.

In fact, the need to understand the connections between the impact of people's activities on ecosystems, and how ecosystem change in turn affects human societies, has never been greater. We have entered the Anthropocene, an epoch where the scale of human activities rivals that of global geophysical processes (Steffen et al., 2011a; Waters et al., 2016). There has never been a time when more land has been transformed to feed us, when more species are being lost in the wake of our actions, or when we have come this close to potentially crossing critical Earth system boundaries (Barnosky et al., 2012; Butchart et al., 2010; Foley et al., 2005; Gibbs et al., 2010; MA, 2005; Steffen et al., 2015a; Steffen et al., 2015b). Crossing planetary boundaries in climate change or biogeochemical flows of phosphorus and nitrogen, for example, has the potential of setting in motion irreversible environmental changes that could leave the planet in a far less hospitable state for humanity by impacting the ability of ecosystems to provide vital ecosystem services (Steffen et al., 2011b; Steffen et al., 2015b).

Human societies depend deeply on ecosystem services such as food, water, protection from hazards, cultural fulfilment and many others for their well-being, but the majority of these services have been degraded over the past 50 years (MA, 2005). However, life expectancy has never been higher, proportionally fewer people now live in extreme poverty than ever before, and the world is more peaceful (GBD, 2015; Pinker, 2011; World Bank Group, 2015). This apparent contradiction of increasing human well-being despite ecological degradation has been termed the "environmentalist's paradox", and may in part be explained by time lags in the feedbacks between changes in ecosystems and their impacts on human well-being (Raudsepp-Hearne et al., 2010b).

There is growing recognition that the continued well-being of people on this planet requires a better and more comprehensive understanding of the coupled and reciprocal relationship between humans and ecosystems (Berkes et al., 2003; Carpenter et al., 2009; Costanza, 1996; Díaz et al., 2015; Folke et al., 2002; Future Earth, 2013; Liu et al., 2007). Particularly developing regions like sub-Saharan Africa face the challenge of enhancing the well-being of their people and reducing poverty, while at the same time ensuring the continued supply of vital ecosystem services that underpin their societies and economies (MA, 2005). This dual challenge has to be performed in the context of large-scale social-ecological changes like urbanization and climate change, which are putting ever-increasing pressure on southern Africa's already stressed agricultural systems and biodiversity (Müller et al., 2011; United Nations, 2015; Williams et al., 2007). These trends are particularly worrying because poor people tend to depend directly on ecosystem services for their livelihoods, health, and protection from the elements to a much larger degree than the wealthy, and are therefore much more vulnerable to negative impacts of environmental change (MA, 2005; Nadkarni, 2000; Vedeld et al., 2007; WRI, 2008). In this context, it is crucially important to understand the dynamics of social-ecological systems, and specifically the interdependent relationships between biodiversity, ecosystem services and human well-being, if these challenges are to be addressed and sustainable trajectories for development are to be nurtured.

Adopting a social-ecological systems perspective, this thesis investigates new approaches and new data sources for characterising and analysing biodiversity, ecosystem services and human wellbeing, and their interactions, at multiple scales in South Africa, a developing country with exceptionally high levels of biological and socio-economic diversity. In the following I begin by outlining the theory of social-ecological systems, and how biodiversity, ecosystem services and human well-being fit into the theoretical framework that forms the foundation for this thesis. I highlight the outstanding research gaps that this thesis aims to address, and introduce the research questions that guide each of the papers included in this thesis. I then describe the research approach and study area, followed by a summary of the results of the papers. Finally, I synthesize the findings, and reflect upon potential future research avenues.

Features of social-ecological systems

A social-ecological system can be defined as a set of social and ecological components that interact in a constantly evolving and interdependent manner (Berkes and Folke, 1998; Folke, 2006) (Fig. 1). Social-ecological systems are complex adaptive systems, in which interactions between components may give rise to emergent properties that cannot be predicted or explained by the properties of individual components on their own (Goldstein, 1999; Manson, 2001). Furthermore, interactions take place across multiple spatial and temporal scales, often resulting in feedbacks that may either amplify or stifle change (Gunderson and Holling, 2002; Levin et al., 2013). This means that small changes in one part of a social-ecological system may lead to non-linear responses in other parts of the system, or may indeed result in a complete reorganization of the system if critical thresholds in controlling variables are crossed (Scheffer et al., 2001). The ability to adapt to change and self-organize means that social-ecological systems may exist in multiple possible configurations or regimes, characterized by different system structures with different feedbacks and dynamics (Holling, 1973; May, 1977; Scheffer and Carpenter, 2003).

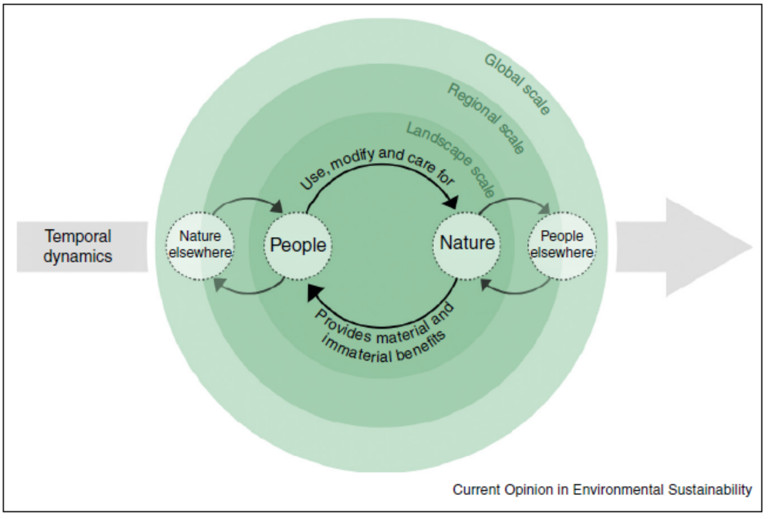

Fig. 1. Social-ecological systems are characterized by reciprocal interactions between people and nature, across various spatial and temporal scales.
(Source: Fischer et al. 2015, reprinted with permission from the publisher)

A key gap in social-ecological systems research is the identification and delineation of social-ecological systems in space. This is a difficult endeavour because the social and ecological components within a complex system often operate at very different scales, and interact across scales, so that assigning definitive spatial boundaries is not straightforward (Cilliers, 2001; Cumming et al., 2006; Folke et al., 2007). Yet knowing where different systems are located in a landscape can relay crucial information to management authorities on the specific dynamics at play in certain areas, like different natural resource use patterns, human well-being challenges or conservation issues (Alessa et al., 2008; Cumming et al., 2014; Su et al., 2012; Walker et al., 2002).

For example, Cumming et al. (2014) recently identified different theoretical system archetypes based on the strength of the direct feedbacks between ecosystems and societies, arguing that so-called "green-loop" systems occur when feedbacks between rural communities and their local ecosystems are strong and direct, but that these systems transition into "red-loop" systems as populations grow and societies are urbanized, leading to feedbacks becoming weaker and more indirect, ultimately resulting in a disconnect between people and nature. According to this review, green-loop systems run the risk of falling into a green trap, where people may begin to overexploit their local ecosystems to support themselves and a growing population, which can result in a cycle of environmental degradation and rural poverty unless the system reorganizes. Similarly, a red trap occurs when people in urbanized systems indulge in overconsumption of natural resources because of a failure to understand the impacts of their demands on far-away (and out-of-sight) ecosystems, which may then lead to a lack of environmental regulation and, once again, ecological decline.

It is clear from this example that knowledge of the spatial distribution of different system types could help environmental management authorities and policy makers target areas with specific interventions that are best suited to the areas' particular sustainability challenges, thus enhancing the likelihood of achieving sustainable future trajectories for these systems.

Ecosystem service bundles as emergent features of social-ecological systems

In 2000, recognizing the scale and impact of anthropogenic forces on the planet's natural environment, the United Nations commissioned the Millennium Ecosystem Assessment (MA), a global assessment of the conditions and trends of ecosystems and their services (MA, 2005). The MA was formative in many ways. It provided one of the most widely used definitions of ecosystem services as the "benefits that people obtain from ecosystems", and categorized them into provisioning services (such as food, fibre and fuel), regulating services (such as water purification and pollination), cultural services (such as places for recreation and religious practices), and supporting services (such as soil formation and production of atmospheric oxygen). While this definition of ecosystem services is by no means the only one (Nahlik et al., 2012), it has found broad appeal, and since the MA the interest in ecosystem services – in both the science and policy arenas – has increased exponentially (Abson et al., 2014; Carpenter et al., 2009; Díaz et al., 2015; Dick et al., 2011).

The great appeal of ecosystem services is that they intuitively represent a link between people and ecosystems, and have the potential to highlight the vital contribution of nature to society's well-being – a contribution which is often taken for granted or invisible (Daily, 1997). However, ecosystem services are not generated by ecosystems in isolation, without any input by humans. For instance, crops (a classic example of a provisioning service) are co-produced in a complicated interplay of biophysical processes and the application of human labour, skill and technology – not to mention the socio-economic drivers that may be acting at larger scales to create a demand for the crops in the first place. In fact, most ecosystem services represent integrated outcomes of interacting social and ecological factors, and as such may be seen as emergent features of social-ecological systems (Huntsinger and Oviedo, 2014; Palomo et al. 2016; Reyers et al., 2013).

Different social-ecological systems generate different ecosystem services, in different quantities and combinations. In other words, different systems can be linked to distinct "bundles" of ecosystem services (Bennett et al., 2009; Cumming and Peterson, 2005). The variety of bundles arises because of trade-offs and synergies between different services – no social-ecological system can produce maximal amounts of all services simultaneously (Kareiva et al., 2007).

Trade-offs between people's land use practices and resource priorities, combined with the biophysical characteristics of the landscape, thus determine the configuration of an area's ecosystem service bundle (Foley et al., 2005; Gordon et al., 2010; Raudsepp-Hearne et al., 2010a; Rodriguez et al., 2006) (Fig. 2). Putting this theory to practice, ecosystem service bundles have been used to identify different social-ecological dynamics in a mixed-use landscape near Montreal, Canada (Raudsepp-Hearne et al., 2010a), but it has not been tested whether these bundles can also be used to map social-ecological systems at larger scales, nor whether certain system archetypes (like green-loop or red-loop systems) can be identified with the help of ecosystem service bundles. The objective of **Paper I** in this thesis is to develop and test an approach to mapping social-ecological systems based on characteristic bundles of ecosystem service use at different scales within South Africa, and to identify key predictor variables that explain the distribution of the systems.

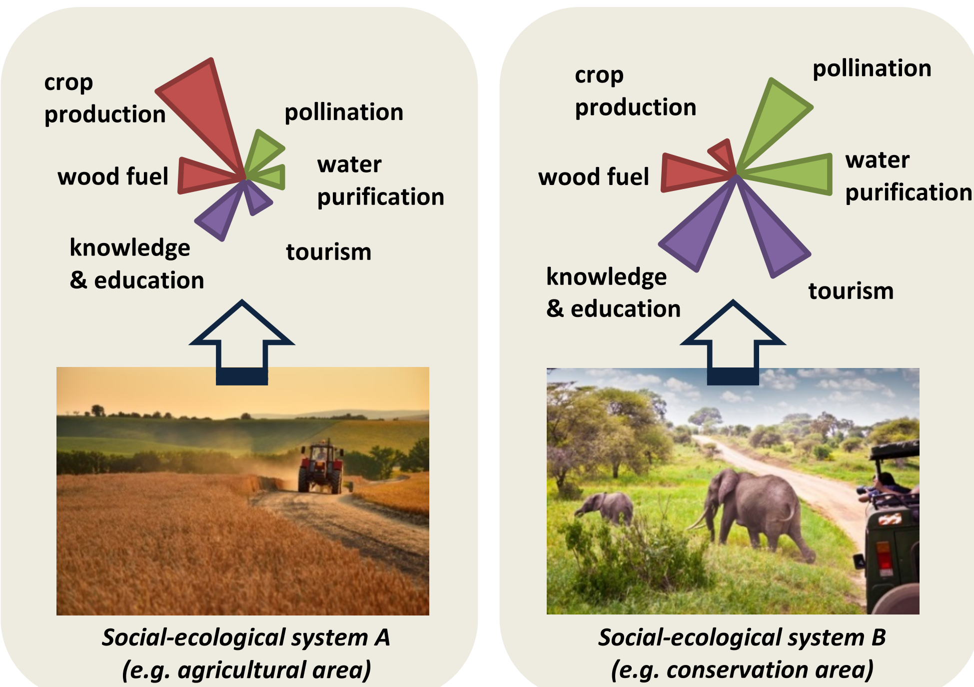

Fig. 2 Concept diagram of ecosystem service bundle types generated by two different social-ecological systems. Colours indicate ecosystem service categories: purple = cultural services; green = regulating services; red = provisioning services.

Links between ecosystem services and human well-being

The MA was not only instrumental in advancing the ecosystem services concept, it also pioneered a systematic synthesis of the links between ecosystem services and human well-being (Mooney et al., 2005). Provisioning, regulating and cultural ecosystem services were directly linked to four constituents of well-being, namely security, basic material for a good life, health and good social relations. These four constituents in turn support and enhance the fifth constituent of well-being: freedom of choice and action (MA, 2005). Of course, the constituents of well-being outlined by the MA are not the only way to define human well-being, which is a highly context-dependent and multi-faceted concept, and is influenced by many different factors (environmental and other) (Alkire, 2002; Summers et al., 2012). While the MA's assessment of the links between ecosystem services and human well-being was an important – though largely descriptive – contribution, much about the relationship remains to be understood and quantified (Balmford and Bond, 2005; Bennett et al., 2015; Carpenter et al., 2009).

One approach to analysing relationships between ecosystem services and human well-being is to relate individual indicators or indices to one another, like the Ecosystem Services Product (ESP) and Human Development Index (HDI) or the amount of urban greenspace and the reduction of environmentally-borne illnesses such as asthma (Smith et al., 2013; Vemuri and Costanza, 2006). A different approach could take a more integrated systems-perspective. One would expect different social-ecological systems to be characterized not only by distinct ecosystem service bundles, but also by different human well-being patterns. For example, Cumming et al.'s (2014) system models predict that a green- to red-loop transition (from strong direct feedbacks between local ecosystems and rural human communities to weak, indirect feedbacks and a disconnect between urbanized people and nature) brings with it fundamental shifts in the way that society is structured: economies scale up and become cash-based, infrastructure and technological development takes place, and education and health care are expanded. Consequently, human well-being changes. **Paper II** aims to explore a systems-perspective on human well-being, building on the bundles approach and systems identified in **Paper I**. Multi-dimensional human well-being bundles are constructed from indicators linked to the MA well-being constituents, and used to map human well-being systems. **Paper II** then compares the spatial relationship between ecosystem service use patterns and human well-being systems to assess whether human well-being bundles can act as a proxy for ecosystem service use bundles when identifying and mapping social-ecological systems in a landscape.

Connecting biodiversity with ecosystem services and human well-being

Biodiversity – the variety of life at genetic, species, community and landscape levels – is the foundation upon which the ecological processes that generate ecosystem services are built, and is therefore essential in the co-production processes that link the biophysical stocks in ecosystems to the benefits that humans can enjoy and which ultimately contribute to human well-being (Haines-Young and Potschin, 2010; Kumar Duraiappah and Naeem, 2005). Human actions – striving to maximise human well-being at individual and societal levels – influence both biodiversity and ecosystem services through governance and management, thereby closing the loop on the human-environment relationship (Reyers et al., 2013) (Fig. 3).

While it is generally acknowledged that biodiversity has a positive or underpinning influence on ecosystem service provision, the links between biodiversity and ecosystem services are not uniform across all services and circumstances (for example, and contrary to predictions, biodiversity does not always increase crop yields or carbon storage) (Cardinale et al., 2012). Much of the research on the relationship between biodiversity and ecosystem services is based on observational and correlative landscape-scale analyses, since most ecosystem services cannot be manipulated experimentally (Cardinale et al., 2012; Egoh et al., 2009; Turner et al., 2007). However, there is a paucity of studies that look at the entire production process from biodiversity via ecosystem services to human well-being, or take a social-ecological systems approach to untangling some of these relationships (Bennett et al., 2015). In **Paper III**, the level of biodiversity loss since pre-industrial times is assessed for South Africa and correlated with ecosystem service and human well-being indicators. The change in biodiversity is also compared across the different social-ecological system types identified in **Paper I** and **Paper II**.

Multiple perspectives on ecosystem services

While this thesis adopts a social-ecological perspective, the concept of ecosystem services is multi-faceted, and used in a variety of different academic disciplines and research approaches (Abson et al., 2014). As a result, there are multiple different perspectives on ecosystem services, and how they relate to biodiversity and human well-being. This plurality of views allows the ecosystem services concept to be broadly applicable, but may also lead to some confusion and ambiguity that can be counter-productive in advancing ecosystem service science and its uptake in the policy arena (Costanza, 2008; Nahlik et al., 2012; Seppelt et al., 2011). **Paper IV** aims to alleviate some of this confusion by identifying four broad perspectives on ecosystem services – including the social-ecological systems perspective – and discussing their disciplinary origins, underlying assumptions and main areas of application. This paper demonstrates the complementarity of the perspectives in developing a fuller understanding of ecosystem services and their links to human well-being, which can ultimately inform the grand challenge of navigating humanity towards a more sustainable and just development trajectory in the Anthropocene.

Key research questions

Based on the key gaps outlined in the previous section, this thesis addresses the following research questions:

1. Can ecosystem service bundles be used to identify and map different social-ecological systems, at scales that are broadly policy-relevant? If so, what characterizes the different systems beyond their ecosystem service bundles?

2. Can human well-being bundles act as a proxy for ecosystem services bundles when identifying and mapping social-ecological systems in a landscape?

3. Is biodiversity loss linked to ecosystem service or human well-being patterns at the sub-national scale?

4. How do different perspectives on ecosystem services compare, and what does the social-ecological systems perspective contribute to the study of ecosystem services and their links to biodiversity and human well-being?

These questions are dealt with in the four papers included here. The conceptual focus area of each paper is indicated in Fig. 3, within the general theoretical framework guiding this thesis.

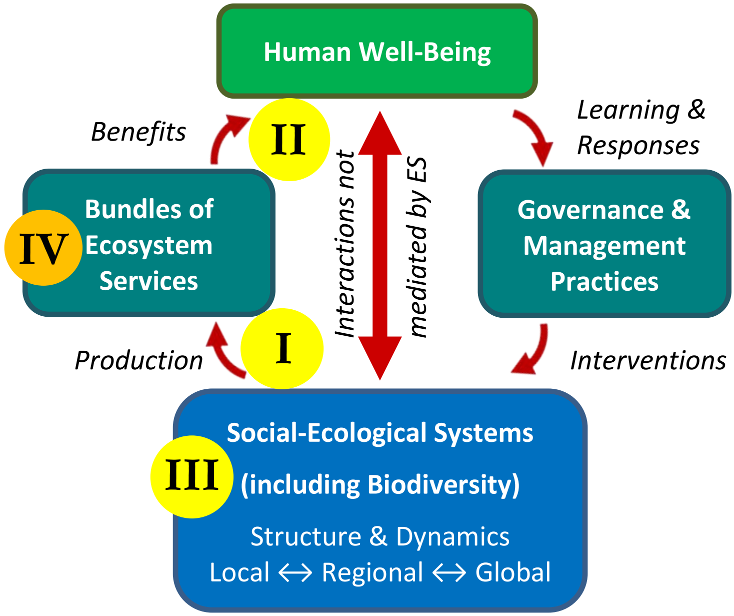

Fig. 3 Main focus areas of the four research papers included in this thesis. Papers I – III empirically deal with different aspects of the links between biodiversity, ecosystem services (ES) and human well-being, as well as the underlying social-ecological systems, while Paper IV is a theoretical exploration of diverse perspectives on ecosystem services in sustainability research. Framework has been adapted from the SAPECS framework (Biggs and Reyers, 2012).

Research approach

The research for this thesis was conducted under the auspices of the Southern African Programme on Ecosystem Change and Society (SAPECS, Box 1). This network of researchers interested in social-ecological dynamics in southern Africa provided much of the inspiration and guidance for the papers in this thesis, and supported my personal development as a social-ecological scientist. South Africa provides a fascinating case study for the exploration of key social-ecological connections. Due to its unique history and high levels of diversity – which are outlined in more detail below – we would expect many different social-ecological systems to co-exist side by side within the country, thus making it ideally suited to a systems-based approach to untangling the links between biodiversity, ecosystem services and human well-being

BOX 1 - SAPECS

The Southern African Programme on Ecosystem Change and Society (SAPECS) is an international, transdisciplinary research programme that aims to advance stewardship of social-ecological systems and ecosystem services in the southern African region (SAPECS, 2015). SAPECS is an official case study of the international Programme on Ecosystem Change and Society (PECS)(PECS, 2015). It is made up of a network of scientists and practitioners that are engaged in social-ecological systems research through empirical case studies, which are brought together in cross-cutting working groups to compare and synthesize across cases and develop new empirical insights or conceptual advances.

The main **objectives** of SAPECS are to:

1. Produce empirical evidence and develop practical theory and tools to improve understanding of social-ecological system dynamics;
2. Mainstream knowledge into policy and practice to have a tangible impact on governance and management of social-ecological systems;
3. Grow the community of practice, including researchers, students and practitioners engaged in social-ecological research and management in southern Africa.

Study area

The Republic of South Africa lies at the southernmost tip of the African continent (Fig. 4). It has a long history of human habitation, with some of the oldest human fossil sites in the world (UNESCO, 2015). South Africa's climate, topography and people have created a highly diverse country, full of extremes. It has a land surface area of 1.22 million km^2, making it more than twice the size of Sweden and the 9th largest nation in Africa. The vast interior plateau with altitudes between 1000 – 2100 m is covered by arid shrublands in the west, and the grasslands of the "highveld" in the east. Mountain ranges lie between the coast and the central plateau, including the Drakensberg Mountains with the country's highest peak, Mafadi (3 450m), on the border of KwaZulu-Natal and Lesotho. Conditions in the coastal belt range from Mediterranean in the southwest and temperate along the southern coast, to subtropical in the east. Due to this large variety of landscapes and climate, South Africa boasts extremely high levels of biodiversity, with a total of over 20 000 plant species and three internationally recognized biodiversity hotspots: the Cape Floristic Region, Maputaland-Pondoland-Albany and the Succulent Karoo (Conservation International, 2013; Driver et al., 2012).

In terms of its people, South Africa has a total population of 51.8 million with a current growth rate of 1.58% (Stats SA, 2015b). There are eleven official languages, with most people speaking IsiZulu (22.7%), followed by IsiXhosa (16.0%) and Afrikaans (13.5%). South Africa has the second-largest economy on the African continent (behind Nigeria), built largely upon its extensive mineral resources, yet unemployment is at 25% and almost 22% of the population live in extreme poverty (defined as not being able to pay for basic food requirements) (Stats SA, 2015a). This situation results in a highly unequal society, illustrated by the country's Gini coefficient on disposable income, which is one of the highest in the world at 0.69 (World Bank, 2014). According to Oxfam, the two richest people in South Africa have the same wealth as the bottom 50% of the population (Oxfam, 2014).

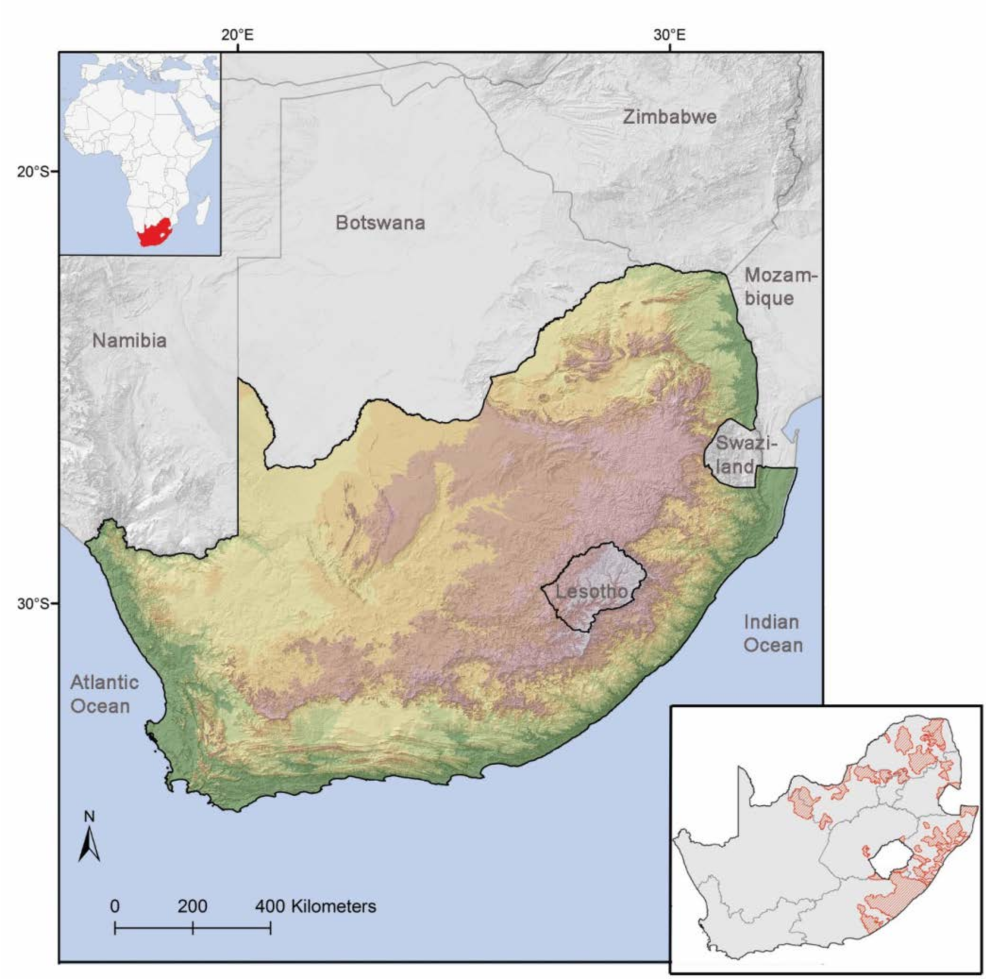

Fig. 4 Topographical map of South Africa, showing its high-altitude interior plateau and the lower-altitude coastal belt and north-eastern "lowveld". The inset on the bottom right corner shows the former homelands in red, as well as provincial borders.

South Africa became a democracy in 1994, after almost five decades of Apartheid characterized by systematic racism, Afrikaner minority rule, and significant restrictions of the rights of black South Africans (Clark and Worger, 2004). Racial segregation had already begun during colonial times, but was adopted as official policy following the general election of 1948. As part of this policy, non-white inhabitants were forced to live in separate neighbourhoods in urban areas, and in self-governing "homelands" in the rural areas. Very little economic and infrastructure development took place in the homelands, and to this day these areas still exhibit some of the highest unemployment and poverty rates in the country (Aliber, 2003; Stats SA, 2012). Apartheid started to crumble in the 1980s amid mounting domestic resistance and international pressure, culminating in the first multi-racial and free elections in 1994 which were won by the African National Congress (ANC) under the leadership of Nelson Mandela. Since then the ANC has governed with majority rule, and South Africa has become an increasingly important role player in Africa, as well as globally with its inclusion in the BRICS emerging economies collective (Alexandroff, 2015). Apart from the national government, South Africa has three main tiers of government, from largest to smallest: provinces, district municipalities (here referred to as districts), and local/metropolitan municipalities (here referred to as municipalities). There are a total of 234 municipalities (average size = 5217 km^2), 52 districts (average size = 23,477 km^2), and nine provinces. In this thesis, municipalities are the focal unit of analysis because they represent the most important spatial planning and decision-making units for government in South Africa.

Methods

The work presented in this thesis is largely based on publicly available census data. The benefits of using this kind of data were two-fold: For one, it allowed an exploration of social-ecological patterns at different scales, across the whole of South Africa. Secondly, this kind of data is becoming more readily available in other parts of the world as nations aim to track and report on progress towards the Sustainable Development Goals (IEAG, 2014; UN, 2016), and methods for applying such data in social-ecological analyses need to be developed and tested.

The South African census of 2011 provided a wealth of information (Stats SA, 2012). Beyond standard demographic questions, the census also asked households about their access to government services and use of natural resources. For example, households were required to state their main source of water, whether it came from a municipal supply, or whether they got water from a river or spring. Furthermore, the census collected socio-economic data related to indicators such as average household income and employment status of household members.

Based on the census questions about use of locally available natural resources, the percentage of households that made use of six provisioning ecosystem services was determined for each municipality and district in South Africa (**Paper I**). These services were: freshwater from a natural source; firewood for cooking; firewood for heating; natural building materials; animal production; and crop production. The municipalities and districts were then subjected to a cluster analysis to identify distinct types of ecosystem service use bundles, which were mapped using a geographical information system (GIS). Multinomial regression was then performed on the different bundle types to identify social and ecological predictor variables that explain the distribution of the bundle types in the South Africa landscape.

In **Paper II**, the census data was used to identify five human well-being indicators that correspond to the MA's five well-being constituents (MA, 2005). These indicators were income, life span, property ownership, unemployment, and education. Based on these five indicators, a human well-being bundle was constructed for each municipality. The municipalities were then subjected to a cluster analysis, followed by a spatial overlap analysis of the resulting human well-being bundles and the ecosystem service use bundles identified in **Paper I**.

In **Paper III**, the first goal was to assess biodiversity change in South Africa. This was done using the Biodiversity Intactness Index (BII), which represents the change in abundance of terrestrial animal and plant species since pre-industrial times. The BII is based on land use data, species richness, and expert estimates of the impact of various anthropogenic land use activities on population abundances (Scholes and Biggs, 2005). Land use and species richness data is publicly available for South Africa, and the expert impact estimates were provided by the authors of the original study. Once the BII was calculated and mapped, the goal was to assess the relationships between biodiversity, ecosystem services and human well-being. The BII was therefore compared to the wide range of human well-being and ecosystem service (use and supply) indicators that had been previously determined for **Papers I and II,** using correlation analyses. To examine the relationship between biodiversity loss and inequality, the Gini coefficient was calculated for each municipality and included in BII regression models.

In contrast to the other three papers, **Paper IV** is a theoretical contribution to the study of social-ecological systems, based on discussions that began among a group of researchers at the Stockholm Resilience Centre (SRC) in 2012. The discussions had been sparked by mounting critiques against the ecosystem services concept (e.g. (Norgaard, 2010), and a feeling among SRC scholars that the social-ecological perspective on ecosystem services, and how they relate to human well-being, had not been sufficiently explored and presented in the literature. Over the following years, the ideas for this paper were discussed and debated in numerous workshops and meetings hosted by the Programme on Ecosystem Change and Society (PECS) (PECS, 2015), and synthesized into **Paper IV** in a collaborative effort by a group of co-authors.

The specific methods employed in **Papers I – IV** are described in detail within the papers, but an overview is provided here in Table 1.

Table 1. Analytical and statistical methods used in **Papers I – IV**

Paper	Methods
I	GIS analyses, cluster analysis, anthrome mapping and overlap analysis, correlation analysis, multinomial logistic regression, principal component analysis
II	GIS analyses, cluster analysis, overlap analysis, correlation analysis, multinomial logistic regression, t-tests, Mann-Whitney U tests, multidimensional scaling
III	BII calculation, GIS analyses, cluster and outlier analysis, Gini coefficient calculation, correlation analysis, linear regression, t-tests
IV	Focus group discussions, literature review

Key results

The main results of each paper are briefly outlined in the following sections.

Paper I

This paper identified three distinct bundle types, characterised by overall low, medium and high levels of direct ecosystem service use among households (Fig. 5). When the ecosystem service bundles were mapped, they formed coherent spatial units across the South African landscape, indicating that the dynamics driving their distribution are not random. Low ecosystem service use areas were found mainly in urban areas and the commercial farming areas in the interior of the country. Medium and high ecosystem service use was concentrated in former homeland areas in the east and north-east of the country. In the case of municipalities, low, medium and high ecosystem service use areas corresponded to 75.8%, 18.2%, and 6.0% of the total land surface area of the country, respectively.

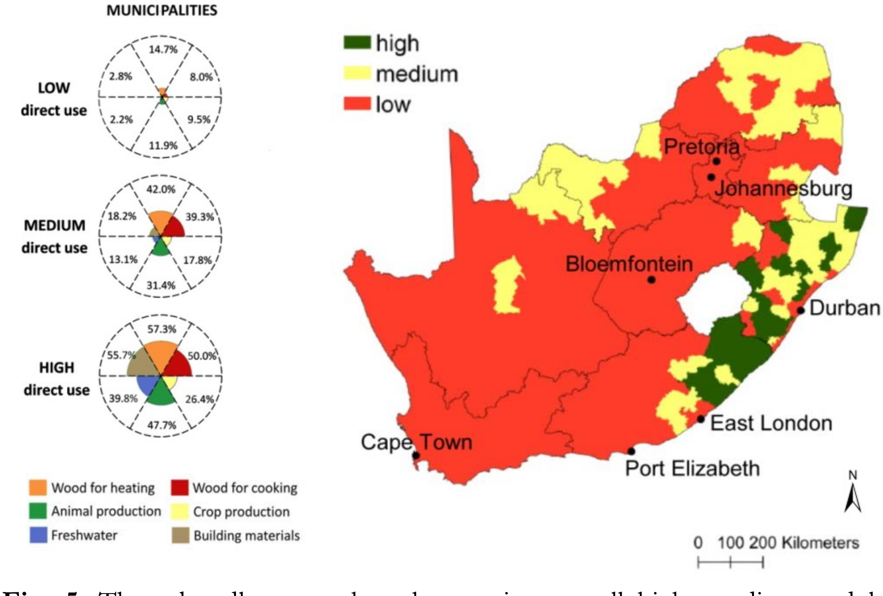

Fig. 5. Three bundle types that characterize overall high, medium and low direct use of locally available ecosystem services among households. Petal length indicates the average percentage of households using each ecosystem service (maximum 100%) within each use category. When mapped, these bundle types represent spatially coherent systems in the South African landscape.

The different bundle types can be taken to represent different social-ecological systems, where the connection between people and their local ecosystems ranges from weak to strong. We argue that the low, medium and high ecosystem service use bundles represent "red-loop", "transition" and "green-loop" systems as defined by Cumming et al. (2014). However, in our analysis, red-loop (low direct use) systems are not exclusively urban but also include relatively wealthy rural communities.

A predictor analysis revealed that the location of the different social-ecological systems was heavily influenced by social factors like household income, gender of the household head and land tenure. The green-loop system in which households rely most heavily on resources they garner from their local environment is characterized by low average household income, as well as high proportions of female headship and land under communal tenure. Interestingly, the use of ecosystem services was only partly determined by their supply in the landscape, again underscoring that socio-economic or cultural factors play an important role in determining the level of ecosystem service use by households, and that mere availability of the services in the landscape cannot necessarily be assumed to correlate to their levels of use.

Paper II

This paper identified three human well-being bundle types (Fig. 6). The first bundle was characterised by high levels of income and education, but unemployment was also high (hereafter called the "high income bundle"). The second bundle type exhibited medium income levels, the highest age of death and lowest unemployment rate (the "medium income bundle"). The third bundle type showed overall low levels of well-being compared to the other bundles, with the highest unemployment rate, and the lowest household income, age of death, and education levels (the "low income bundle"). However, the percentage of property ownership was very high, due to historical and cultural tenure arrangements in the former homeland areas of South Africa.

When these three well-being bundle types were mapped, and their distribution was compared to the distribution of the social-ecological systems identified in **Paper I** (based on ecosystem service use bundles), we found that the vast majority of medium and high income bundle areas overlapped with low ecosystem service use areas. In contrast, 59% of low income bundle areas overlapped with medium and high ecosystem service use areas. The distribution of human well-being bundles therefore only partly corresponded to the green-loop, transition, and red-loop systems identified by ecosystem service use bundles. As such we conclude that human well-being bundles can only partly serve as a proxy for identifying social-ecological systems defined by ecosystem service use.

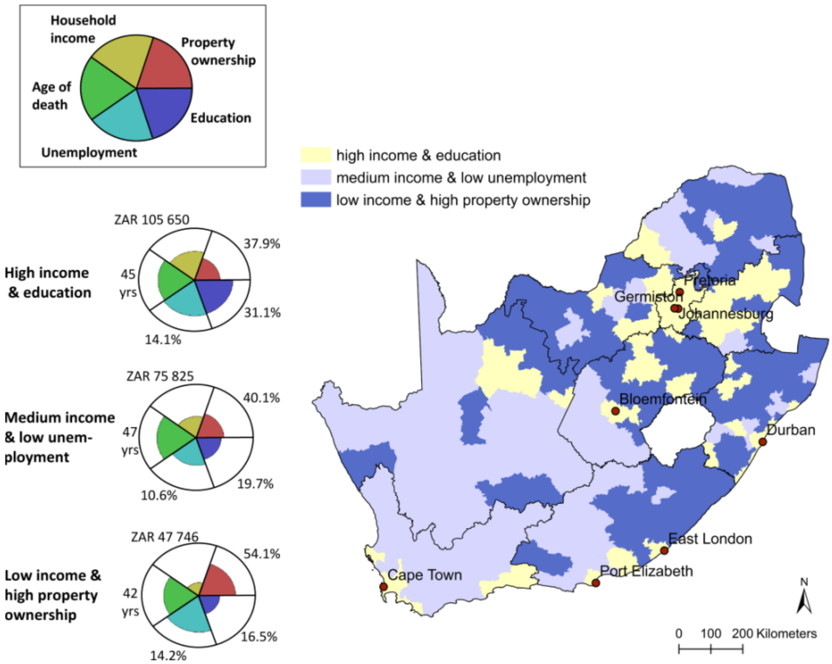

Fig. 6 Human well-being bundle types in South Africa, mapped at the municipal level.

Paper III

This paper found that biodiversity loss as measured by the BII in South Africa was 81.7%, meaning that the population abundances of terrestrial animals and plants have declined by an average of 18.3% since pre-industrial times.

Overall, biodiversity loss has been highest in areas where the potential supply of ecosystem services is high (i.e. areas with high levels of arable land, grazing potential, wood supply and water runoff). This indicates that biodiversity loss has been associated mainly with agricultural expansion and urban development in South Africa. This finding is supported by the analysis of biodiversity loss in different systems types. The greatest biodiversity loss was, on average, found in the high income bundle, as identified in **Paper II**. However, there was no detectable difference in the BII between ecosystem service use bundles (as identified in **Paper I**), suggesting no discernible link between long-term biodiversity loss and current ecosystem service use patterns at the household level.

We found a potential threshold in the BII of 60%, below which there is a precipitous decline in BII values (Fig.7). This raises concerns about the ability of ecosystems to supply ecosystem services at adequate levels. In addition, once the BII drops below 60%, we found that inequality becomes a significant predictor of biodiversity loss.

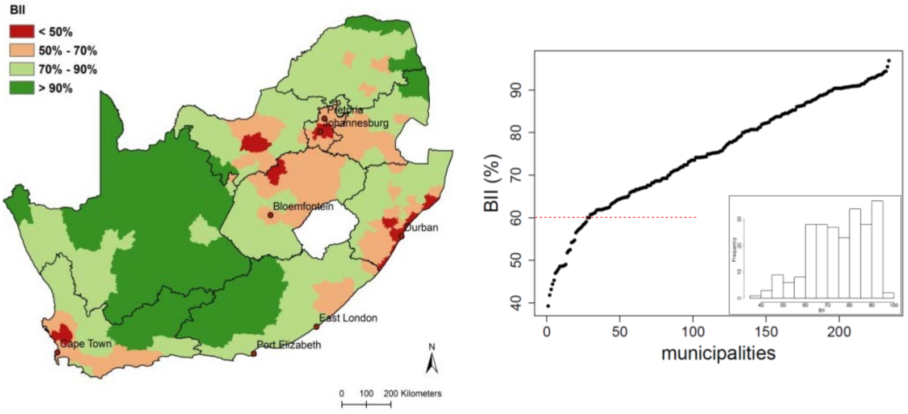

Fig. 7 The BII mapped at municipal level in South Africa (left). Plot of ranked BII values, showing a sharp decline at 60% (right).

Paper IV

This paper identifies four main perspectives on ecosystem services that are characterized by different disciplinary origins, assumptions, research foci and key areas of application, and are termed the "ecological", "ecological economics", "development" and "social-ecological systems" perspective. Each of these perspectives has a certain "centre of gravity" along a simplified ecosystem services production chain, where most of the empirical research within the perspective is focused (Fig. 8).

The ecological perspective emphasizes the relationship between biodiversity and ecosystem processes and services, as well as trade-offs between services and the impact of these trade-offs on human well-being. The ecological economics perspective focuses on the value (non-monetary and monetary) of ecosystem services, and the institutions that govern them, while the development perspective considers ecosystem services as one of many resources that people draw upon to support their livelihoods and well-being. Finally, the social-ecological perspective emphasizes the interactions and emergent relationships between all the components in the production chain, at various scales.

We argue that the different perspectives complement each other, specifically with regard to measuring and valuing ecosystem services, the social-ecological co-production of services, as well as analysing drivers of change and cross-scale connections that may influence the resilience of ecosystem service supply. Each perspective is necessary to develop a fuller understanding of ecosystem services and their links to human well-being, and ultimately contribute to the grand challenge of setting society on a more sustainable and just development trajectory.

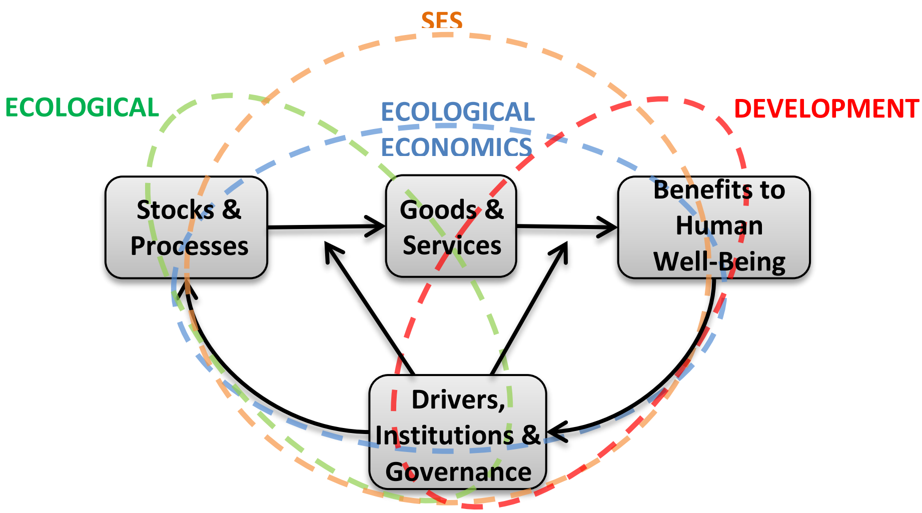

Fig. 8 Four perspectives on ecosystem services and their "centres of gravity" along a simplified ecosystem services production chain.

Discussion: key contributions

Overall, this thesis explores the links between biodiversity, ecosystem services and human well-being within the framework of social-ecological systems. The key contributions from each paper can be summarized as follows:

1. Presenting an approach for mapping social-ecological systems at multiple scales, based on an integrated social-ecological measure of ecosystem service use

2. Constructing human well-being bundles as an alternative form of assessing well-being, and investigating connections to ecosystem service use

3. Exploring the relationship between biodiversity loss, ecosystem services, human well-being and inequality at sub-national scales

4. Relating the social-ecological systems perspective on ecosystem services and putting it into context with other dominant perspectives, highlighting complementarities between the different perspectives

In the next section I briefly discuss each of these contributions, as well as several cross-cutting insights and reflections.

Mapping social-ecological systems based on bundles of ecosystem service use

Previous social-ecological mapping exercises have used combinations of separate social and ecological data (Alessa et al., 2008; Ellis and Ramankutty, 2008; Letourneau et al., 2012; Su et al., 2012), or a mix of different ecosystem service indicators to map social-ecological dynamics (Raudsepp-Hearne et al., 2010a). Many of these studies were conducted at a local scale, but others have mapped different land use systems (which are arguably also social-ecological systems) across the globe. **Paper I** advances on these studies by using a consistent type of indicator (use of provisioning ecosystem services) to map spatially coherent systems that reflect people's direct use of ecosystem services. These systems are argued to be indicative of green-loop, transition and red-loop systems identified in the literature (Cumming et al., 2014). Identifying such different social-ecological systems may assist in tailoring specific strategies to address the different kinds of sustainability challenges in different areas, where there may be a risk of ecological degradation either due to overconsumption (red-loop systems) or poverty (green-loop systems).

Mapping human well-being bundles

Based on the assumption that transitions from green-loop to red-loop systems bring with them a complete reorganization of society and potentially an improvement in traditional well-being measures such as income, health and education (Cumming et al., 2014), **Paper II** was aimed at investigating whether such a shift in well-being could be detected in the social-ecological systems identified in **Paper I**. To answer this question, **Paper II** constructed multi-dimensional human well-being bundles, and tested for congruence in the distribution of ecosystem service use bundles and human well-being bundles. Human well-being measures are usually either a single indicator of something like income (e.g. per capita gross domestic product or GDP) that represents social welfare and thus (arguably) human well-being (van den Bergh, 2009), or they are a collection of multiple facets of well-being that are combined into a composite indicator or index, like the United Nations Human Development Index (UNDP, 2013). Human well-being bundles were therefore an innovation in the context of well-being measures, and proved an insightful way of assessing different "well-being systems" in South Africa. For example, the relatively high level of property ownership in the low income bundle was an intriguing finding, and suggests that the security of having a rural homestead to fall back on constitutes an important source of resilience in poor people's lives.

Human well-being bundles were, however, only of limited use as a proxy for ecosystem service use bundles. To some extent, the overlap was as predicted, with overall high levels of well-being matching perfectly with low levels of direct ecosystem service use (the red-loop system). However, the low income bundle included not only the high ecosystem service use areas (green-loop system), but also the medium and low use areas. This indicates that just because households have stopped making use of local ecosystem services in an area – perhaps in response to improved access to government-provided substitutes like electricity and sanitation – it does not mean that their well-being is improving in-step. Well-being indicators like education, life span and unemployment are much slower to change than ecosystem service use, and the time lags between fast- and slow-changing variables may explain part of the discrepancies between the green-loop/red-loop systems and well-being systems that were identified in South Africa. Time lags have also been proposed as one of the possible explanations of the environmentalist's paradox, where global data have shown that environmental degradation does not lead to a decline in human well-being (Raudsepp-Hearne et al., 2010b). The argument is that time lags are masking the trend, and in the case of South Africa, human well-being may be similarly slow to respond to changes in ecosystem service use patterns.

Linking biodiversity, ecosystem services and human well-being

Overall, the findings of **Paper III** showed that the links between biodiversity, ecosystem services and human well-being are highly varied across South Africa. Biodiversity loss was most strongly associated with areas in which the potential supply of ecosystem services is high. Since biodiversity loss can be both cause and consequence of changes in productivity (Worm and Duffy, 2003), a concern is that reinforcing feedbacks may push these areas into more unproductive states and further biodiversity loss until the ecosystems no longer supply essential services (Barnosky et al., 2012).

In terms of well-being, high rates of biodiversity loss occurred both in the high income bundle areas (i.e. overall high well-being), and the low income bundle areas (i.e. overall low well-being). This indicates that the environmentalist's paradox holds true for some areas in South Africa, where ecological degradation is high and well-being is high, but it does not apply to other areas where ecological degradation and low well-being go hand in hand. In addition, there is evidence of a threshold in BII values at around 60% beyond which degradation increases sharply. This raises further concerns about the decline of biodiversity and well-being, especially since inequality becomes a significant predictor of biodiversity loss in municipalities that have crossed the threshold. Such high levels of biodiversity loss, coupled with inequality, potentially exacerbate an already difficult situation for poor people living in those areas, who may depend heavily on local biodiversity and ecosystem services for their livelihoods.

In considering the findings of **Paper III**, it is important to remember that the effects of biodiversity loss on ecosystem services are varied, and depend not only on the quantitative loss of population abundances (as measured by the BII), but also on the loss of key functional groups and traits (Cardinale et al., 2012; Díaz et al., 2007; Elmqvist et al., 2003; Hooper et al., 2005). While this is acknowledged, the BII presents a unique opportunity to study the relationship between a robust, yet sensitive index of biodiversity change and ecosystem services at sub-national scales (Mace, 2005).

The value of a social-ecological systems perspective

The main point made by the description of different perspectives on ecosystem services in **Paper IV** is the complementarity between the perspectives in building a fuller understanding of the links between ecosystem services and human well-being. The social-ecological perspective complements the ecological, ecological economics and development perspectives in broadening the scope of interactions, contributing factors and values considered in ecosystem service assessments. More specifically, the social-ecological systems perspective explicitly considers the co-production of ecosystem services, drivers of change acting at and across multiple scales, and the diversity of values that capture the importance of ecosystem services (with a focus on cultural values). **Paper IV** shows that bringing the different perspectives together can contribute to successful interdisciplinary synergies, which play a crucial part in addressing real-world sustainability challenges (Carpenter et al., 2012; Fischer et al., 2015; Folke et al., 2011).

Beyond the contributions discussed in **Paper IV**, taking a social-ecological systems approach in this thesis to explore the patterns and relationships of biodiversity, ecosystem services and human well-being has yielded a number of insights. For one, the direct use of local ecosystem services can be considered one measure of social-ecological co-production of ecosystem services (Reyers et al., 2013). This is because the use of an ecosystem service by households requires the service to be supplied by the biophysical and ecological processes of the local ecosystem, *and* it requires the application of knowledge and skill by the users to harvest and manage the resource. All this takes place in a changing cultural context that encourages or discourages certain resource use practices, like the keeping of livestock or the use of thatch as rood material. The use of ecosystem services therefore represents an interaction between social and ecological factors, and proved useful in assessing the distribution of social-ecological systems in South Africa. This insight contributes to the growing research on co-production, in which there is a need for studies that give an indication of how to incorporate co-production in quantitative measures and analyses of ecosystem services (Bennett et al., 2015).

Furthermore, an understanding of systems as different configurations of multiple variables and feedbacks inspired the use of bundles to quantify and map ecosystem services and human well-being in **Papers I and II**, rather than using single indicators or composite indices. The bundles approach led to the discovery of patterns that may otherwise have been missed, such as the identification of green-loop/red-loop system archetypes (Cumming et al., 2014), or the varied and nuanced picture of human well-being in South Africa. Similarly, in **Paper III**, relationships between individual human well-being indicators and the BII did not show a clear pattern. Only when the BII was compared across multi-dimensional well-being systems did it emerge that biodiversity loss has been highest in the high income bundle areas, and lowest in medium income bundle areas. Finally, the detection of a potential BII threshold, and the emergence of a relationship between biodiversity loss and inequality at low BII levels was facilitated through complex systems thinking and explicitly considering non-linearities in data.

Reflections on the research approach

Taking an approach that relies on public data invariably places limits on the kinds of questions that can be answered and the analyses that can be done. In the case of this thesis, South Africa's census data provided a wealth of information on the use of provisioning ecosystem services, for example, but there was no information on regulating or cultural services. Similarly, the human well-being indicators that were derived from the census data provided information on a number of traditional, objective well-being indicators like household income, education and unemployment, but there was no information on subjective well-being indicators like quality of life or happiness. These limitations in the data mean that parts of the dynamics between ecosystem services and human well-being – like the role of cultural ecosystem services in enhancing subjective well-being, for example – remain undiscovered. In addition, the data was only available for socially-constructed units of analysis (municipalities and districts), rather than biophysical units or uniform grid cells that are commonly used in spatial GIS analyses. Fine-scale dynamics at levels below the municipality are therefore averaged and aggregated in the analyses presented here, which affects the conclusions that can be drawn. The kind of large-scale, quantitative analyses that characterize this thesis should ideally be complemented by place-based, local-scale cases studies that take a qualitative approach to understanding the links between ecosystem services and well-being. Through SAPECS, these kinds of collaborations will be possible going forward.

The explorative nature of the research conducted as part of this thesis is also emphasized. This is perhaps most clearly illustrated by the choice of cluster analysis as a method to identify distinct bundle types in **Papers I and II**. While cluster analysis is widely used to identify specific combinations of human-environment interactions (Ellis and Ramankutty, 2008; Letourneau et al., 2012; Raudsepp-Hearne et al., 2010a; Su et al., 2012), it is an inherently exploratory data mining technique, and different clusters may emerge from the same data if different clustering algorithms are applied (Kaufman and Rousseeuw, 2005). In this case, it was an appropriate method to use because the aim of the analyses was to find inherent patterns in the landscape, and not to impose an a priori understanding of South African dynamics on the data. Nevertheless, a different approach based on participatory mapping or social-ecological inventories (Klain and Chan, 2012; Schultz et al., 2007), for example, may have yielded different results. The challenge for future research is to combine multiple methods and approaches to arrive at a more comprehensive and holistic picture of social-ecological dynamics in South Africa.

Future research avenues

The work presented in this thesis focuses on exploring spatial patterns and covariance of biodiversity, ecosystem services and human well-being. Relationships and feedbacks between specific aspects of these concepts at local scales, e.g. the reciprocal relationship between cultural ecosystem services and the protection of certain species or landscapes, is not the focus of this study. However, emerging approaches on investigating the co-production of ecosystem services (Bennett et al., 2015; Palomo et al., 2016), or the development of methods to assess subjective human well-being at larger scales [using mobile phones, for example (Palmer et al., 2013)] offer interesting avenues to delve deeper into these relationships at the policy-relevant scales investigated here.

Time lags between changes in biodiversity or ecosystem services and the impacts of these changes on human well-being present another opportunity for further research. As the environmentalist's paradox and **Papers I - III** point out, time lags can result in confounding patterns in the data, especially if only snapshots of the condition of ecosystem services, well-being and biodiversity are available. One way to explore these potential time lags would be with the use of time series data that allows an investigation beyond static patterns, and another way could be the use of models that specifically take time lags into account (Schlüter et al., 2012). In the case of the work presented here, the next iterations of the South African census may offer opportunities to construct time series data for ecosystem service use and human well-being indicators, potentially providing insights into time lags and other long-term dynamics within social-ecological systems.

Finally, further research is needed on system changes or shifts, specifically the transition between green- and red-loop systems. How can systems thinking assist in managing such transitions in support of sustainable development, i.e. avoiding green or red traps? This could entail exploring system archetypes more broadly, asking whether there are other system types, characterized by particular ecosystem service bundles, that are mirrored in different places all over the world. Research into system archetypes is an exciting frontier since it could potentially be applied in the development of tailored management and policy strategies that address system-specific sustainability challenges, providing an entry point for more effective, spatially-explicit decision-making.

Conclusions

This thesis has contributed towards building a better understanding of the spatial patterns and covariance of biodiversity, ecosystem services and human well-being in complex social-ecological systems. This kind of knowledge is important in informing management and policy options that meet the key challenge of the Anthropocene: to ensure an adequate supply of essential ecosystem services while enhancing human well-being for all.

Exploring the connections between society and ecosystems requires an approach that incorporates multiple perspectives. The final paper presented in this thesis has shown how different perspectives can complement each other in the study of ecosystem services, while the empirical work in the first three papers has demonstrated some of the contributions that a social-ecological systems perspective can make in exploring the links between biodiversity, ecosystem services and human well-being – including the use of new kinds of social-ecological data and approaches, and insights into cross-scale dynamics and thresholds.

It is my hope that this work advances social-ecological systems science and encourages further collaboration and learning among the different research perspectives, as well as new perspectives that are yet to emerge. It is through this continual process of broadening research perspectives and considering more and different facets of biodiversity, ecosystem services and human well-being – and how they interact – that we have been able to build and expand upon the foundational work laid by Rachel Carson and her colleagues all those years ago, and will continue to advance the research frontier into the future.

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