Functionality of Wet Grasslands as Green Infrastructure

Waders, Avian Predators and Land Covers in Northern Europe

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Wet grasslands as functional green infrastructure: waders, avian predators and land covers in Northern Europe

Abstract

Habitat loss is a global issue that affects land cover patterns, ecological processes and the distribution and abundance of species. As a result, many conservation approaches have appeared, such as the European Union's green infrastructure (GI) policy and UNESCO's Biosphere Reserve (BR) concept. Both are being applied in southern Sweden's Kristianstad Vattenrike Biosphere Reserve (KVBR). Despite concentrated conservation efforts at a local scale to conserve biodiversity, focal grasslands and waders have declined. This calls for the assessment of outputs within the KVBR in terms of both knowledge production and its dissemination, as well as the consequences of management on the ground (Paper I). Focusing on supporting the KVBRs' work and wader conservation in general, this thesis studied how anthropogenic factors affect the land cover patterns and processes of wet grasslands for waders. Over the past two centuries land use and land cover change have reduced the KVBR's area of functional grassland habitat by >98% (Paper II). Whilst loss and degradation of wet grassland habitats is considered a primary reason of wader decline in Europe, predator–prey relationships have been proposed as a secondary reason. Using several wet grassland landscapes across Northern Europe, predator-prey relationships were explored (Paper III, IV & V). Firstly, the distribution and abundance of avian predators is determined by resource diversity and anthropogenic factors of a landscape at multiple spatial scales. Secondly, predator abundance and predation pressure were positively correlated, and linked to different wet grassland developmental stages in Northern Europe. Thus, based on the studies contained in this thesis, changes to both land cover patterns and ecological processes play a vital role for the maintenance of wet grasslands as functional GI. Finally, the multiple landscape case study approach employed in this thesis is a novel macroecological tool that encourages knowledge production and learning for functional GI.

Keywords: Landscape approach initiatives, Kristianstad Vattenrike Biosphere Reserve, Macroecology, Pattern, Process, Ecological sustainability, Conservation.

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Dedication

To my family and friends.

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 Manton, M. and Angelstam P. How do landscape approach initiatives' learn for conservation and use of biodiversity? - a review of research portfolios in the Kristianstad Vattenrike Biosphere Reserve. Submitted.

II Manton, M. and Angelstam P. Two centuries of loss, alteration, and fragmentation of grasslands in Southern Sweden's Kristianstad Vattenrike landscapes. Submitted.

III Manton, M., Angelstam, P., Milberg, P. and Elbakidze, M. 2016. Wet grasslands as a green infrastructure for ecological sustainability: Wader conservation in Southern Sweden as a case study. Sustainability 2016, 8(4), 340; doi:10.3390/su8040340

IV Manton, M., Angelstam P. and Naumov, V. Green infrastructure is more than land cover: anthropogenic factors affecting the abundance of generalist and specialist avian predators. Submitted.

V Manton, M. and Angelstam P. Avian predator abundance and predation pressure on waders in European wet grasslands: a macroecological comparison. Submitted.

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The contribution of Michael Manton to the papers included in this thesis was as follows:

I 80%

II 75%

III 80%

IV 60%

V 60%

Abbreviations

BR	Biosphere Reserve
GI	Green Infrastructure
KVBR	Kristianstad Vattenrike Biosphere Reserve

1 Introduction

1.1 Background

Landscapes contain many different land cover types, forming different habitats for species with different habitat selection. To maintain viable populations of species, networks of different habitats need to be functional. Green Infrastructure (GI) is a policy concept and tool that aims at satisfying the functionality of green spaces, as well as to deliver a range of other ecosystem services (European Commission, 2013). Assessment of GI functionality is a critical component of implementing GI policy, and to determine the need for conservation areas, management and restoration of different land cover types.

Globally, wetlands are one of the most threatened and degraded ecosystems (Brinson & Malvárez, 2002; Joyce & Wade, 1998). Being biologically productive, naturally dynamic wet grasslands have been used and developed by human management throughout millennia (Bakker & Londo, 1998). Grazing and traditional hay-making on wet grasslands resulted in an expanding cultural landscape favouring wet grassland birds such as waders (Price, 2003; Antrop, 1993). However, over the past decades, the area extent of wet grasslands have been severely reduced (Benstead et al., 1999; Beintema, 1986) through a range of human-induced factors including intensification of agriculture (Schekkerman et al., 2008; Newton, 2004), hydrological changes (Beintema, 1986), eutrophication (Brinson & Malvárez, 2002; Alvarez-Cobelas et al., 2001), land abandonment (Illyés et al., 2008), forest expansion (Durant et al., 2008; Wretenberg et al., 2006), urbanization (Catry et al., 2011), climate change (Roodbergen et al., 2011) and land management shifts (Donald et al., 2006; Rönkä, 1996).

These management drivers and consequences of land use change have resulted in the alteration of both land cover patterns and ecological processes. This applies to species, their habitats of anthropogenic and natural origin, as well as important ecosystem processes at multiple spatial scales (Eriksson &

Cousins, 2014; Joyce & Wade, 1998). For example, the loss of habitat causes fragmentation that negatively affects species (Fahrig, 2003). As for processes, trophic interactions can be affected through changes in the abundance of predators, and thus also need to be considered when analysing the functionality of different land covers as GI for biodiversity conservation (Manton, 2014). To counteract the degradation and loss of compositional, structural and functional biodiversity elements a variety of policies at multiple levels have been proposed and implemented (Boitani et al., 2007).

1.2 Policy implementation

Implementation of policies about ecological sustainability towards successful conservation of species, habitats and processes as natural capital in social-ecological systems is a paramount contemporary challenge (Sabogal et al., 2015). The policy concepts "biodiversity" (Noss, 1990) and "ecosystem services" (Norgaard, 2010) are two good examples for both advocacy and systematic analysis (Lele et al., 2013). As a response to the difficulties of communicating these concepts to actors and stakeholders in Northern Europe, policy on GI has appeared (e.g., European Commission, 2013). According to the European Commission (2013) GI is:

"a strategically planned network of natural and semi-natural areas with other environmental features designed and managed to deliver a wide range of ecosystem services. It incorporates green spaces (or blue if aquatic ecosystems are concerned) and other physical features in terrestrial (including coastal) and marine areas. On land, GI is present in rural and urban settings".

To implement GI policy calls for the maintenance of sufficient amounts of representative terrestrial, freshwater and coastal ecosystems with functional connectivity among land cover patches (e.g., Tischendorf & Fahrig, 2000), and if necessary management of ecological processes that affect GI functionality.

1.3 Landscape approach

Fulfilling GI policy requires a landscape approach (e.g., Sabogal et al., 2015; Sayer et al., 2013; Axelsson et al., 2011) that involves both social and ecological systems. This means place-based integration of (1) evidence-based knowledge about evidence-based performance targets, measures for sustainably managing and restoring habitats for wild species and human well-being , (e.g., Svancara et al., 2005; Angelstam et al., 2004), and (2) multi-level collaboration and learning among researchers, stakeholders and policy makers towards sustainable landscapes (e.g., Axelsson et al., 2013). To support the implementation of policies aiming at sustainable landscapes on the ground, and thus functional GI, place-based concepts such as Biosphere Reserve (BR), Model Forest, Ecomuseum, Ramsar Convention and other landscape approach concepts have been developed to enhance collaborative learning towards tangible results (Axelsson et al., 2013; Elbakidze et al., 2013). Undertaking multi-level learning by evaluating the policy implementation processes is difficult and should be applied at multiple scales from local initiatives (Borsdorf et al., 2014), as well as among their networks both nationally and internationally, and also among different concepts with similar ambitions (Axelsson et al., 2013; Reed & Egunyu, 2013; Price et al., 2010). However, the final step in the policy implementation process, i.e., understanding the extent to which a promising governance arrangement actually results in ecological sustainability as part of resilience of social-ecological systems (e.g., Tuvendal & Elmberg, 2015; Lundquist, 1987), is poorly studied.

1.4 Kristianstad conservation initiatives

The wet grassland ecosystem along the lowland part of the Helgeå River near Kristianstad is one of the last remaining fragments of this once wide-spread anthropogenic enhanced land cover in southern Sweden (Ekberg & Nilsson, 1994) (Figure 1). As such, it has been subject to a range of conservation, management and restoration measures towards becoming a functional GI. To conserve and protect its rich biological diversity the Kristianstad wet grasslands complex was nominated as a Ramsar area in 1974. Unfortunately, this nomination as a Ramsar wetland did not have the desired results (Walker & Salt, 2006). Subsequently, a bridging organisation, the Kristianstad Vattenrike ("Water kingdom" in Swedish) Ecomuseum was founded in 1989 as a local response of the community to deal with degradation and management issues of the wet grassland landscape (Folke et al., 2005). The creation of the Kristianstad Vattenrike Ecomuseum set the foundations to establish the Kristianstad Vattenrike BR (KVBR) in 2005. Following the Seville strategy (UNESCO, 1996) BRs are designed as 'living laboratories' for developing and demonstrating integrated governance and management for biodiversity conservation. Thus an effective BR should involve conservation and development groups, management authorities, local communities as well as integrated social and natural science research (Elbakidze et al., 2013). In 2016 the Kristianstad landscape joined another landscape approach concept aimed at creating partnerships for sustainability called the Model Forest (Besseau et al., 2002) (Jan Lannér, pers. comm.). The ultimate aims of the Ramsar, Ecomuseum, BR and Model Forest concepts are to contribute to the implementation of both social and ecological sustainability. One of the key tasks of the KVBR landscape approach initiative includes improving the conservation efforts for biodiversity of wet grasslands, as well as other land covers (Magnusson et al., 2004).

Indeed, since the late 1980s several wet grassland patches of today's KVBR have been actively managed with the aim to meet habitat requirements of waders (Magnusson et al., 2004). In response, the wader population initially increased by 59% over a seven-year period (Cronert, 2014). However, these efforts have neither been sufficient nor sustained long-term, and the breeding populations of red-listed wader species of the wet grasslands have subsequently declined with some species becoming locally extinct (Paper III).

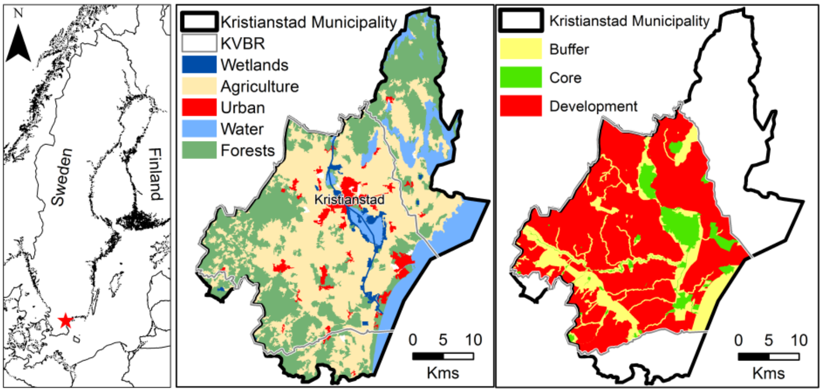


Figure 1. The Kristianstad case study in Northern Europe (left), including the distribution of key land covers (centre) and the zoning of Kristianstad Vattenrike Biosphere Reserve (right).

1.5 Pattern and process

Habitat loss for waders in anthropogenic wet grasslands in Northern Europe is not a new phenomenon (Nilsson, 1858). In general, wader decline has been linked to the intensification of land management leading to changes in both the patterns of land covers and ecological processes (Batáry et al., 2007; Wilson et al., 2004). This includes a loss of habitat in both terms of quantity and quality (Ottvall et al., 2009; Rönkä, 1996) as well as the effects of predation (Kentie et al., 2015; Roodbergen et al., 2011). There is clear evidence that the abundance and breeding success of birds are dependent on both the quality of the biophysical land cover patch (e.g., Angelstam et al., 2004), as well as on processes within the surrounding landscape's matrix (Laidlaw et al., 2015; Andrén et al., 1985). For example, avian predator abundance and predation rates of ground nesting birds have been shown to affect the composition and abundance of bird species (Manton et al., 2016; Kentie et al., 2015; Amar et al., 2008; Angelstam, 1986). Both the removal of predators (Kauhala et al., 2000; Marcström et al., 1989) and the provision of alternative food (Lindström et al., 1987) have been shown to positively affect the reproductive success of ground nesting birds. Consequently, assessments of GI functionality need to include land use and land cover change, as well as predator-prey relationships.

Wet grasslands and waders highlight that species' distribution, behaviour and abundance are affected by complex interactions at multiple scales, including both pattern and process. However, as policy and management of GI often result in similar outcomes within landscapes of a particular region or country, relationships between different land covers as habitats for species may be absent due to limited variation (e.g., Törnblom et al., 2011; Roberge et al., 2008). Stewardship and management towards functional GI requires that their composition, structure and function are understood in time and space. Thus, the effects of landscape pattern and process on avian predation can be enhanced by combining a multi-case study macroecological approach (e.g., Brown, 1995) with a traditional local case study approach (Flyvbjerg, 2011).

1.6 Macroecological approach

The variety of landscapes spanning across Northern Europe provides good examples of steep gradients in landscape history, land covers and the viability of bird populations (e.g., Žalakevičius, 1999). Generally, the intensity of natural resource use is higher in the west than in the east (Angelstam et al., 2011; Gunst, 1989). With avian predators having large home range sizes, the comparison of local habitat patches alone is insufficient. Therefore, sufficiently large areas with a variety of different land covers and habitat quality and different predator species assemblages need to be compared. Thus, a landscape scale perspective should be considered (e.g., Baillie et al., 2000), which is linked to species' life history traits (Wiens, 1989). Additionally, the use of different spatial scales should be studied to ensure a sufficiently wide gradient to explore the effects of resource density on species at various scales (Wiens, 1995).

The scale dependency of species-habitat relationships (e.g., Hall et al., 1997; Wiens, 1989) highlights the need to include at least three spatial scales: (1) points within local land covers (Forman, 1995), (2) the patterns and processes at the spatial scale of focal species' land covers (Dunning et al., 1992), and (3) at coarser scales, such as landscapes in different regions (Poiani et al., 2000). A macroecological approach thus satisfies the need to include the trade-off between the precision of small-scale research in patches of habitat (Beck et al., 2012), the spatial scale of the local social-ecological system (Plieninger et al., 2015), as well as different regional context linked to different governance legacies and landscape histories (Angelstam et al., 2011; Brown, 1995). Therefore, the use of landscapes as replicated case studies (Flyvbjerg, 2011; Yin, 1981) to test hypotheses is an appropriate method to contribute to the maintenance of functional GI, including the influence of avian predators on wet grassland bird species. However, macroecological studies that explore anthropogenic factors affecting the abundance of avian predators within and among landscapes with different landscape histories and governance legacies are limited.

1.7 Landscapes as case studies

Case study research is a strategy that focuses on understanding the dynamics present within a given context (Eisenhardt, 1989). Even though case studies are often viewed as controversial and misleading (e.g., Flyvbjerg, 2006), case study research is an appropriate and essential method to undertake important scientific research to understand the dynamics within both singular and multiple settings and across multidisciplinary sciences (Angelstam et al., 2013; Flyvbjerg, 2011; Eisenhardt, 1989). Specifically, case studies provide reliability, validity and a sound concept that can help scientists understand hypotheses on tangible circumstances (Flyvbjerg, 2006) and can be used to develop theories, test hypotheses and provide descriptions of different settings. Qualitative or quantitative evidence may be obtained from fieldwork, desktop studies, historical information, verbal reports, observations, or any combination of these (Eisenhardt, 1989; Yin, 1981). The distinguishing aspect of a case study is that it foresees the examination of a contemporary phenomenon in its actual context, especially when the limitations between phenomenon and context are not visible (Yin, 1981). Therefore, the use of entire landscapes as case studies of individual social-ecological systems to investigate, test hypotheses and compare results of similar and differently managed land covers and the subsequent outcomes is an appropriate macroecological method to study the complexity of waders, avian predators and different land covers.

1.8 Thesis rationale and aims

The rationale for this thesis was to implement a research program to support wader conservation by identifying knowledge gaps and generating new knowledge on the anthropogenic factors affecting the land cover patterns of wet grasslands and predation as a process (Figure 2). The

The starting point of this thesis was thus to assess the contribution of social system, ecological system and integrated research to gain an understanding of the reasons for the limited success of wet grassland and wader conservation in Southern Sweden's Kristianstad Municipality (Paper I, III). The Kristianstad Municipality contains the acclaimed KVBR, which is specifically managed for ecological, economic and social sustainable development (Paper I). To study the functionality of wet grassland land cover as one type of GI, the history of semi-natural grasslands during the past two centuries was studied in Kristianstad (Paper II). Field data on wader and avian predator absolute and relative abundance, as well as estimates of predation pressure using artificial nests were collected in multiple case study landscapes in Northern Europe (Figure 3). A total of six case study landscapes located throughout Northern Europe were selected to cover the full gradient from disappearing (Sweden) to sustained in the long term (Lithuania and Belarus) and emerging (Iceland) wet grassland ecosystems (Paper IV and V). The chosen case study landscapes thus reflect a gradient of unique landscape histories, thus providing a broad range of past and present land management outcomes and settings as a base for generating improved knowledge on wet grassland conservation.

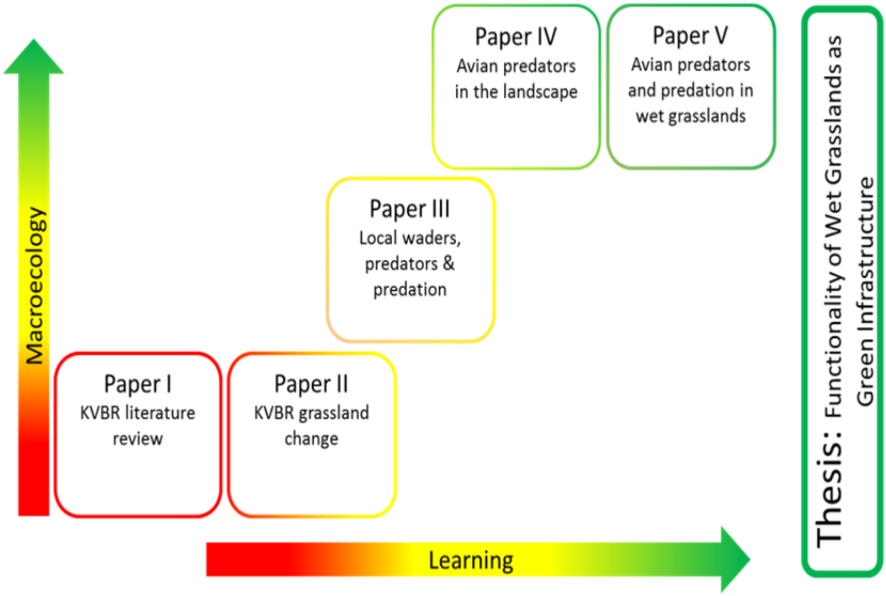
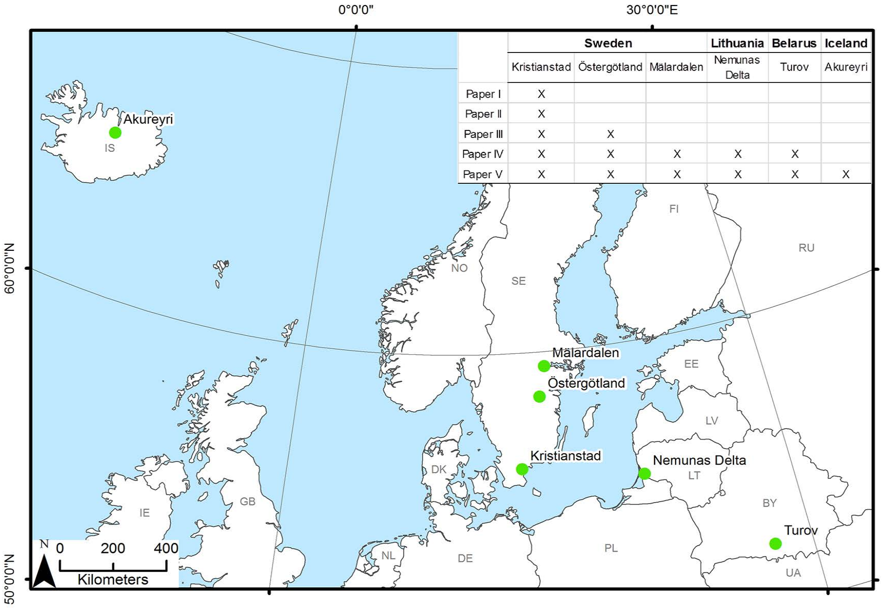


Figure 2. The rationale for this thesis was to implement a research program containing five papers that would identify gaps and generate knowledge on the anthropogenic factors affecting the land cover patterns and processes of wet grasslands for wader conservation.



	Sweden			Lithuania	Belarus	Iceland
	Kristianstad	Östergötland	Mälardalen	Nemunas Delta	Turov	Akureyri
Paper I	X					
Paper II	X					
Paper III	X	X				
Paper IV	X	X	X	X	X	
Paper V	X	X	X	X	X	X

Figure 3. Map of Northern Europe showing the case study landscapes and their presence in the five Papers forming this thesis. Kristianstad, Sweden forms the primary case study landscape of this thesis and is supported by the five other case study landscapes (Östergötland and Mälardalen in Sweden, Nemunas Delta in Lithuania and Turov in Belarus). These landscapes combined form gradients in land use history, wader and predator species assemblages.

2 Methods

2.1 Landscape initiatives for conservation (Paper I)

The KVBR has been a member of some kind of international concept for conservation and development for more than 40 years. As such concepts explicitly and implicitly call for integrative knowledge production locally, and sharing of this among local initiatives with their international networks, Paper I focused on the logistic function with respect to conservation and development of the BR concept. Multi-level learning requires the dissemination of knowledge as well as international access to knowledge.

Therefore, Paper I reviewed and analysed published international peer review research articles in English on the KVBR since its inauguration in 2005 using three dimensions. The first dimension describes the KVBR's portfolio of knowledge production with respect to (1) ecological systems, (2) social systems and (3) integrative research. The second dimension focuses on different steps in policy implementation (viz.: process, outcomes and consequences on the ground) (Rauschmayer et al., 2009), and the third dimension divided the articles into global, social and human systems (Komiyama & Takeuchi, 2006). Paper I also discusses whether or not research has improved the KVBR's ability to maintain and improve the priority land covers as functional GI, and how knowledge gaps can be bridged by systematic integrative knowledge production and sharing of knowledge not only within but also among BRs and other landscape approach concepts.

2.2 Land cover change in the KVBR (Paper II)

Research on land-use history resulting in vegetation change provides a background for understanding the development of the current ecosystems (Christensen, 1989). The responses of species, communities and ecosystem processes resulting from vegetation change caused by humans provide critically important perspectives into current and future outcomes of landscape management and can thus deliver insight into the protection, management and restoration of cultural and natural landscapes (Birks, 1988). Conclusive studies linking human activity and ecosystem change require analyses of not only land-use history, but also effects on vegetation and wildlife and their cascading effects (Foster, 1992). Long term land use and land cover change is related to species' habitats, occurrence, richness, and population trends (Eriksson & Cousins, 2014). Therefore, changes in land management can directly and indirectly result in both negative and positive outcomes on habitat quantity and quality for different species. A wide range of studies in Europe have indicated that intensified management and use of different land covers (e.g., forests, grasslands and wetlands) can cause population declines in species using these land covers as habitat (e.g., Angelstam et al., 2004). To produce knowledge requires systematic studies about the effects of habitat loss on GI functionality and ecosystem functions.

Using the KVBR as a representative case study of the Swedish field-forest landscape gradient, Paper II analysed the changes of semi-natural grasslands during the past 200 years, prior to and after major shifts in agricultural intensification. This paper tested the hypothesis that temporal changes have reduced the functionality of grasslands as GI with respect to three factors, viz. (1) habitat loss, (2) habitat alteration and (3) habitat fragmentation. This hypothesis was explored by analysing land cover change using two different types of land cover data: (1) land cover maps from three different time periods during two centuries (1812-1820, 1926-1934 and 2004) and (2) official Swedish agricultural statistics from 1927-1981.

2.3 Avian predators and predation (Paper III, IV and V)

The hypothesis that predation on eggs and chicks limit wader populations (Kentie et al., 2015; Pehlak & Lõhmus, 2008; Teunissen et al., 2008) stresses the need for comparisons of predator assemblages and predation among entire wet grassland landscapes that represent various condition from degraded ecosystems through to intact ecosystems that are functional and thus host stable species populations. Therefore, an initial study was designed to test three predictions in two southern Swedish landscapes, (1) the KVBR with a rapidly declining wader population and (2) Östergötland with a relatively stable population (Paper III). The predictions were: (1) the relative abundance of avian predators and waders; (2) the abundance of avian predators, and (3) the predation rate on artificial nests, should all be higher in rapidly declining wader populations. This study used the combination of field surveys to count the number of avian predator and waders; both within the wet grassland patches and also the number of avian predators within 5 key land covers surrounding the wet grasslands. In addition, an artificial egg predation experiment was used to estimate the potential impacts of predation on an avian assemblage (e.g., Martin, 1988). Paper IV and V expanded on this study.

Building on the methodology used in Paper III, a macroecological approach using five case study landscapes, Paper IV explored anthropogenic versus natural factors at different spatial scales that correlate with the distribution and abundance of generalist (*Corvidae*) and specialist (*Accipitriformes*) avian predators. In particular, Paper IV tested the prediction that the abundance of generalist avian predators should be higher in regions, landscapes and land cover patches with higher land management diversity and stronger agricultural anthropogenic impacts.

Paper V expanded the macroecological approach by expanding from five case study areas to six different wet grassland landscapes representing a gradient in wet grassland emergence to degradation in Northern Europe to examine the relationships between avian predators and the predation effects on waders. This study tested the hypothesis that predator abundance and predation pressure is positively correlated. This was undertaken by (1) estimating the predation pressure on artificial wader nests (2) counting avian generalist and specialist predators, and (3) tested if there was a relationship between (1) and (2). This study employed both the observational field survey methods (Paper III and IV) and the artificial egg experiment (Paper III).

3 Results and Discussion

3.1 Landscape initiatives for conservation (Paper I)

The literature review of KVBR (Paper I) revealed that since its establishment in 2005 the number of international peer-reviewed publications about the ecological system (n=25) and the social system (n=20) were similar. However, only one third of the ecological studies acknowledged the KVBR. In contrast all studies of the social system studies acknowledged the KVBR. The ecological system studies focused on a variety of aspects of the KVBR, and did not reflect the priority land covers or species of the KVBR (Magnusson et al., 2004:85), except for the xeric sand steppe. Integrative research publications (n=3) containing both ecological and social research dimensions were rare with one study on brownification and two studies on greylag goose. These results call for a transition from isolated ecological or social system studies (n=45) to integrative knowledge production of a social-ecological system ((n=3), Figure 4) (see also Popescu et al., 2014). Ideally, the entire process of governance and its “outputs” in terms of management actions, and their consequences on the ground (see Rauschmayer et al., 2009) should be covered.

Paper I highlights several knowledge gaps regarding the prioritized terrestrial land covers of the KVBR. For instance, internationally published peer-review research on wet grasslands was very limited. The results thus show that there are gaps in knowledge regarding the ecological patterns and processes for the conservation of biodiversity within KVBR. However, there is a considerable body of grey literature (e.g., county reports) in Swedish demonstrating that the KVBR’s prioritized wet grasslands have not been sustained as a functional GI (Paper III). Unfortunately, peer reviewed research on generating knowledge and bridging barriers for stakeholder collaboration to assist conservation is limited.

On the contrary, social system research has convincingly demonstrated the potential for innovative governance arrangements and processes that could support biodiversity conservation in the KVBR. This applies to aquatic systems (Schultz et al., 2007) and focal species such as geese (Tuvendal & Elmberg, 2015; Hake et al., 2010). Thus the social system studies have improved the understanding of the sustainable development processes, i.e. the societal steering (Baker, 2006) and social learning about social systems (Johannessen & Hahn, 2013), both locally in the KVBR and also partly in the entire catchment of the Helge å River (Tuvendal, 2012). In fact, the social system research has been disseminated as a success story of societal innovation for adaptive co-management within the KVBR (Schultz et al., 2015; Walker & Salt, 2006; Millennium Ecosystem Assessment, 2005).

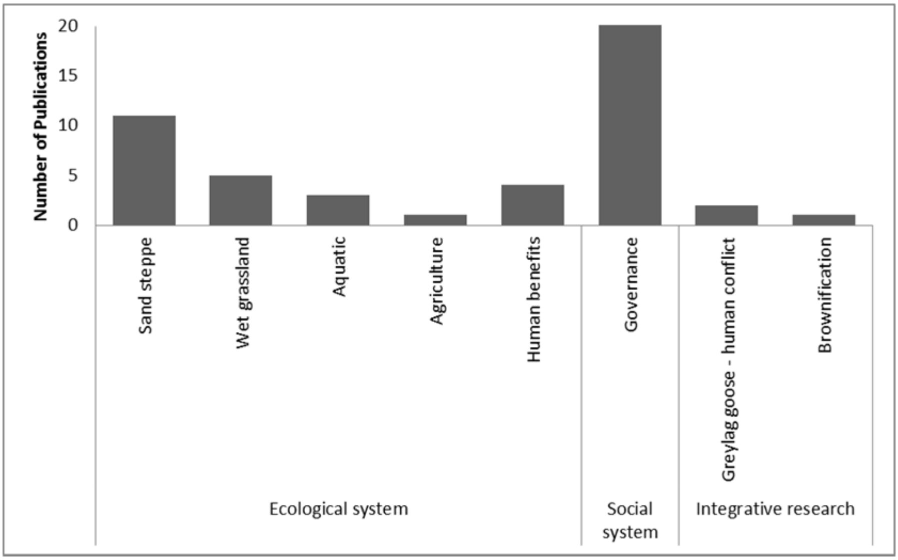


Figure 4. Break-down of the 48 international peer-reviewed publications on the KVBR divided into three groups of research, viz. about the ecological system, the social system and integrative research.

Studies on the benefits stakeholders' gain from different land covers, and the attitudes and values of what the priority habitats and species are in the context of biodiversity conservation have been conducted within the KVBR. The local community prioritized deciduous forest, the aquatic system and the wet grasslands as the most important land covers with birds being the most important wildlife species. Indeed, several of the priority land covers and focal species as set by the KVBR (Magnusson et al., 2004) align well with the attitudes of the local community as the most important areas for conservation (Johansson & Henningsson, 2011; Lindström et al., 2006).

However, Paper I shows that in spite of extensive high-level international praise, the KVBR's innovative multi-level governance arrangements have so far not fulfilled its logistic function aimed at multi-level learning by evaluation of the conservation and development functions. Knowledge regarding the status of species, habitats and processes among the different land covers of the KVBR has limited access for an international audience, or is inadequate. Paper I stresses the need to assess the consequences of new modes of governance on the patterns and processes of ecosystems. A key task is to improve the understanding of complex long-term changes in land management that affects habitat and land cover processes at multiple scales from patches to entire landscapes. Additionally, different approaches to landscape governance need to be examined to understand if and how natural capital can be sustained in the long term. A multiple case study approach that includes multiple landscapes, as applied in this thesis, would contribute to this.

3.2 Land cover change in the KVBR (Paper II)

Maps covering two centuries of land use and land cover change indicated a 75, 81 and 80% decline in grasslands for the forest, transitional and lowland plains landscape strata, respectively. Statistics for the latter part of that period (1927-76) showed that while the agricultural landscape lost 20% of its grasslands, the forest and transitional landscapes had declined by 54 and 50%, respectively. The area of semi-natural grasslands reported in the Swedish Agricultural Statistics of 1937 and the spatial data extracted from the state economic map of 1926-1934 showed a good correlation among the landscape strata ($r= 0.78$, $n=31$).

However, treating all grassland patches as equal contributors to a functional GI ignores the fact that species require different grasslands as habitats for species. Thus, to understand how the functionality of GI has developed, the effects of grassland alteration need to be considered for representative grassland types.

Natural and semi-natural grasslands can be classified into many categories. This makes it easy to overestimate the amount of grasslands that form different types of representative GIs. The results of alteration from Paper II demonstrated a strong simplification in terminology used to describe grassland systems over time for both the map data (from five terms to three terms) spanning two centuries, and the Swedish Agricultural Statistic ((1927 to 1981) from five terms to one term). Likewise, Ihse and Lindahl (2000) highlighted that there were much more detailed classifications for natural grasslands in the past. Similarly, Sjöbeck (1973) quoted literature from 1650, which defined five grassland categories in the field-forest gradient.

The alteration of grassland structure from mainly semi-natural grassland to improved grassland was prominent. The proportion of natural and semi-natural grasslands declined 41-59% for the three different landscape strata. This result is similar to a study by Cousins and Eriksson (2008), were semi-natural grassland (permanent unfertilised pastures or meadows formed by traditional agricultural methods) had declined from 60% 150 years ago to 5% today. Ihse and Lindahl (2000) reported that historically the area of semi-natural grassland was at least ten-fold that of arable fields in southern Sweden. Focusing on wooded grasslands, Axelsson et al. (2007) showed that about 80% of the cultural wooded grassland area has been lost through conversion into spruce forests aimed at maximum sustain yield forestry. In addition, the reduced quantity and quality of low intensity farming has been shown to negatively affect many animal and plant species dependent on semi-natural grasslands (Öckinger et al., 2012; Schneider & Fry, 2005).

Finally, as fragmentation reduces the range of grassland patch sizes, the proportion of semi-natural grassland types that forms suitable habitat patches will be reduced. Spatial analyses of the semi-natural grasslands from 1812-1820, 1926-1934 and in 2004 showed the mean patch size distribution declined considerable over time. The area proportions of the grasslands in Kristianstad deemed sufficiently large enough to support specialised focal species (>100 ha) declined 89-100% in the three strata. These findings are consistent with previous studies made by Lindborg et al. (2008) and Cousins et al. (2007), that during the last century semi-natural grasslands have become highly fragmented and can only be found in small isolated patches scattered throughout the southern Swedish landscape. The large reductions in patch size, as well as increased fragmentation have led to losses of functionality for semi-natural grasslands as GI. These declines have been directly linked to a loss in species richness (Ekroos et al., 2013; Cousins & Eriksson, 2008; Cousins et al., 2007).

By combining the effects of loss, alteration and fragmentation the results of Paper II estimate that in Kristianstad the functionality of grasslands as GI has been reduced by at least 98-100% in the three landscape strata over the past two centuries (Table 1). The important change is the severe decline of large grassland patches. Divulging further back in time would most likely exacerbate the changes to the grassland habitat network. As a consequence, the area of wet grassland habitat for waders has severely declined and no longer forms a functional GI. Reduced connectivity (Eglington et al., 2009), altered hydrology (Brennan et al., 2005; Brinson & Malvárez, 2002) and edge effects in terms of increased predation (Manton et al., 2016; Andrén, 1992) are three additional negative factors.

Although this study shows that grasslands in Kristianstad have undergone considerable changes throughout the past two centuries, land cover change also took place earlier. Three good example of changes that took place >200 years ago (prior to the time period presented in this study) are (1) agricultural intensification, (2) the planting of vegetation to stop erosion and the shifting of the sand dunes, and (3) the lowering of the surface water table of the Helge å River to the Baltic Sea in 1774 (Sjöbeck, 1973). Therefore, the historic range of variability increases with the time period considered. For example, Christensen (1886-91) reported that about 1000 years ago 1/5 to 1/6 of the area was under plough compared to in the 1880s. Thus, the historical ecology approach shows that the benchmark depends on the baseline used as a reference point.

Table 1. Estimated cumulative effect of 200 years of grassland alteration and fragmentation on habitat loss affecting the functionality of grasslands as green infrastructure.

Landscape type in the forest upland to lowland plain gradient	Remaining proportion of grasslands 1812-20 to 1926-1934 (A)	Remaining proportion of grasslands 1926-1934 to 2004 (B)	Remaining proportion of semi-natural grassland 1926-1934 to 1976 (C)	Remaining Proportion of large patches >100 ha 1812-20 to 2004 (D)	Remaining proportion semi-natural grasslands, (A*B*C*D)
Forest	0.22	1.15	0.59	0.00	**0.0000**
Transition	0.28	0.67	0.42	0.06	**0.0047**
Lowland plains	0.21	0.97	0.41	0.11	**0.0091**

3.3 Avian predators and predation in Southern Sweden (Paper III)

The predictions that the abundance of avian predators and predation rates should be higher in rapidly declining vs. relatively stable wader populations in southern Sweden were all supported (Paper III). Firstly, the assessment of the wet grasslands testing the relative abundance of avian predators and waders was three times higher in Kristianstad (0.66) compared to Östergötland (0.23). Secondly, field observations showed that corvids, and to a slight extent birds of prey, were higher in the wet grasslands of Kristianstad compared to the wet grasslands of Östergötland (Table 2). Thirdly, the predation rates on artificial nests were much higher in Kristianstad (0.13) compared to Östergötland (0.04). Therefore, Paper III showed that predation contributes to wader decline in the Kristianstad landscape, and this is a factor that should be considered when planning and implementing conservation strategies for functional wet grasslands.

Paper III indicates that the number of predators both in the wet grassland and the surrounding landscape could be one factor that influences the breeding success of waders in southern Sweden. Thus, increased numbers of avian predators may lead to higher nest predation rates, and subsequently cause local extirpation, or drive waders to seek alternate breeding areas (see also, Norrdahl et al., 1995; Loman & Göransson, 1978). Paper III, supports the finding of Bell and Merton (2002) and Stien et al. (2010), that generalist predators, such as corvids, may act to accelerate the decline in wader populations, and consequently contribute to increasing the risks of local population extinction. Hence, predator behaviour and composition need to be considered at the landscape scale as applied in this study.

The combination of Papers I, II and III highlight that the complex long-term changes in land management affecting both land cover patterns and ecological processes at multiple scales from patches to entire landscapes requires further research. Therefore, these three papers (I, II and III) set the foundations to use multiple landscapes as case studies that represent both the developmental stages of wet grassland from emerging to deteriorated as well as viable, declining and extirpated wader populations (Papers IV and V). In addition, Paper III supported the need to further examine predation, as well as the different histories of landscape governance to understand if and how wader populations of wet grasslands can be sustained in the long term.

3.4 Avian predators at the landscape scale (Paper IV)

The abundances of corvids and birds of prey varied independently from each other among the five case study landscapes (Figure 5). The overall abundance of corvids was higher in Sweden compared to the case study landscape of the Nemunas Delta in Lithuania and Turov in Belarus. The higher abundance of generalists at the landscape scale was linked to higher resource availability in Sweden compared to the two east European country case study landscapes. This is consistent with the level of economic development in the three countries (Jepsen et al., 2015; Jorgenson et al., 2014).

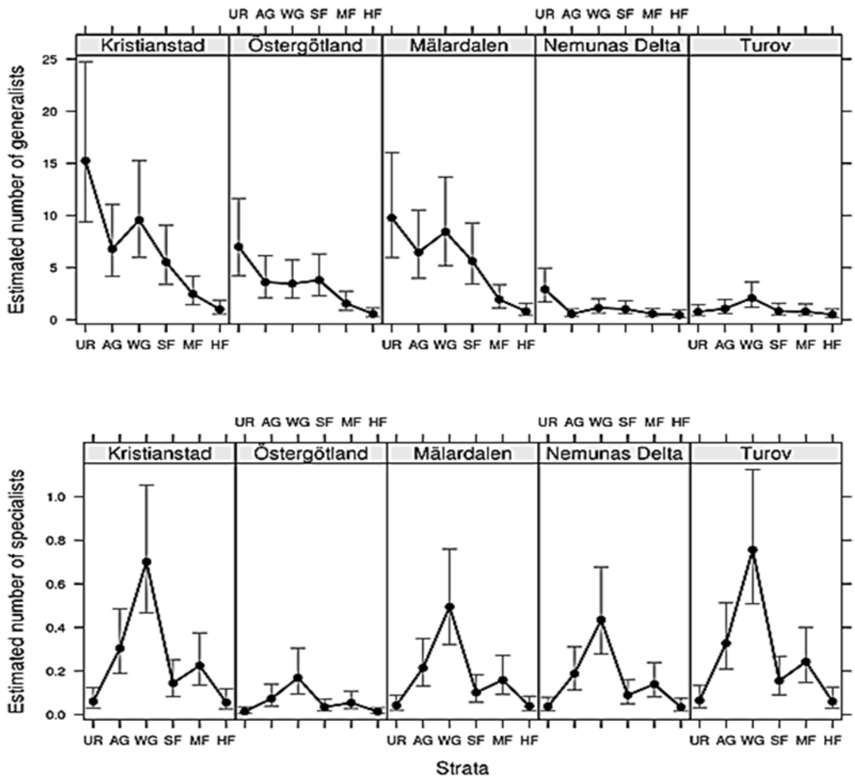


Figure 5. Effects of landscape strata for generalist avian predators (top) and specialist avian predators (bottom) with 95% confidence intervals among the 6 strata urban area (UR) (>40% coverage), agricultural land (AG) (forest cover ~0%), wet grassland, (WG) sparse forest (SF) (cover 5-20%), mixed forest and agricultural land (MF) (forest cover 40-60%) and high forest cover (HF) (>80-95%) in the five case study landscapes; Kristianstad, Östergötland, Mälardalen (Sweden), Nemunas Delta (Lithuania) and Turov (Belarus) (see Paper IV).

At the point scale factors related to resource diversity and availability to generalist predators, i.e., farms, piles of manure and abundance of livestock, were significant for generalist avian predators. However, further analysis revealed that different species of domestic herbivores (e.g., cows, horses and sheep) had different effects; the relationship between generalists and cows and horses respectively were both significant, but generalists and sheep were not. In the Kristianstad landscape, horses were particularly abundant. Here the use of horses has been transformed from a traditional work purpose on a traditional low nutrient diet, to cherished pets on a readily available high diet (e.g., Cunha, 2012), thus resulting in nutrient rich manure. In contrast, no relationship was found between these anthropogenic factors and birds of prey. Instead, the abundance of specialised avian predators was linked to natural differences affecting the distribution and abundance of their prey species. Mixed ecosystems support a high number of species and individuals; the carrying capacity of small mammal communities is one example (Bowman et al., 2001; Churchfield et al., 1997). This is consistent with the observations of Panzacchi et al. (2010) that grasslands may host the highest abundance of small mammals suitable as prey for specialist avian predators. Indeed the species assemblages of birds of prey varied between the monoculture landscapes in Sweden with 8 species recorded compared to the heterogeneous Turov landscape in Belarus with 12 species.

To conclude, Paper IV showed that the abundance of corvids, but not birds of prey varied due to of the availability of anthropogenic food among the land cover strata. The abundance of generalist avian predators depends on availability of anthropogenic food resources. This is indeed also highlighted in other studies on corvids (Marzluff & Neatherlin, 2006; Atkinson et al., 2005; Andrén, 1992). Corvids have been nominated as the main culprits of predation in a fragmented landscape and their abundance increases in mixed mosaic landscape of agriculture and forest (Andrén, 1992). Corvid species have indeed increased in abundance in southern Sweden over the past few decades (Ottvall et al., 2009). However, this study showed that birds of prey preferred wet grasslands.

3.5 Predators and predation on wet grasslands (Paper V)

Applying a macroecological approach to explore the role of predation for sustaining viable populations of waders indicates a clear difference among the predator abundances and predator-prey ratios and nest predation of the six wet grassland landscapes studied across Northern Europe. First, the probability of daily egg predation ranged from 0.036 on Iceland (Laidlaw et al., 2015) to 0.13 in Kristianstad. Second, the wader and avian predator ratios per patch were considerably higher in the more intensively manged landscapes of Sweden compared to the case study landscapes of Lithuania, Belarus and Iceland. However, among the Swedish case study landscapes, there was also a difference with Kristianstad (0.66) exhibiting much higher ratios than the case study landscapes of Östergötland (0.23) and Mälardalen (0.26). This is consistent with previous studies suggesting increasing predator density and predation pressure from north to south in Sweden (Andrén, 1992; Andrén et al., 1985). Third, the relative predation pressure ratio was correlated to the predation rates for generalist (corvid birds) but not for specialists (birds of prey) predators (Table 2).

Table 2. The Relative abundance of avian predators and waders from the six wet grassland landscapes in Northern Europe (see Paper V).

	Kristianstad	**Östergötland**	**Mälardalen**	**Nemunas Delta**	**Turov**	**Akureyri**	**Spearman rank test**
No. of wet grassland patches Total area (ha) Mean patch size (ha) SD Range of patch size	21 Total 1288 Mean 61.34 SD 36.40 Range 15.35 – 167.61	22 Total 726 Mean 33.00 SD 32.83 Range 6.08 – 152.77	27 Total 1486 Mean 55.03 SD 32.38 Range 17.52 – 134.33	37 Total 2698 Mean 72.91 SD 29.39 Range 24.24 – 132.53	30 Total 2135 Mean 71.15 SD 42.62 Range 22.61 – 219.16	31 Total 1196 Mean 38.59 SD 33.69 Range 7.00 – 174.20	r value, p value (one-tailed)
Mean number of waders per patch (biomass Kg)	14.33 (3.96)	23.95 (4.56)	27.04 (6.13)	28.08 (11.29)	62.80 (10.35)	35.6 (6.2)	-0.54, 0.13 (-0.54, 0.27)
Mean number of generalists per patch (biomass Kg)	25.00 (12.22)	5.77 (2.49)	9.00 (3.18)	0.97 (0.66)	1.30 (0.94)	0.35 (0.42)	0.77, 0.036 (0.77, 0.036)
Mean number of specialists per patch (biomass Kg)	2.48 (2.44)	1.18 (1.13)	0.67 (0.66)	0.41 (1.37)	0.30 (0.49)	0.0 (0.0)	0.66, 0.078 (0.77, 0.055)
Mean number of predators per patch (biomass Kg)	27.48 (14.67)	6.95 (3.62)	9.67 (3.85)	1.38 (2.03)	1.60 (1.43)	0.35 (0.42)	0.77, 0.036 (0.66, 0.078)
Relative predation pressure ratio (biomass Kg)	0.66 (0.79)	0.23 (0.44)	0.26 (0.39)	0.047 (0.15)	0.025 (0.12)	0.010 (0.06)	0.83, 0.021 (0.66 0.078)

These results are indeed supported by other studies. For instance, Groen et al. (2012) and Kentie et al. (2015) showed similar wader nest predation results, with an estimated daily predation probability of 0.025 on the semi-natural grasslands versus 0.045 on the grassland monocultures in Friesland, Netherlands. Chicks that hatched on semi-natural grasslands vs. monoculture grasslands had apparent survival rates of 0.14 vs. 0.06, respectively (Kentie, 2015:65). In addition, daily nest survival was higher on semi-natural grasslands, than on monocultures (Kentie, 2015:44). Our own unpublished avian predator and wader counts from within the same wet grasslands and monocultures in the Netherlands parallel this pattern. Counts in May 2015 showed that the mean number of predators per wader individual was 1/379 = 0.003 on semi-natural grasslands and 355/120 = 3.0 on the monocultures.

Summarising, these results does not contradict the hypothesis that predator abundance and nest predation should be positively related. This stresses the importance of understanding predator-prey relationships at the landscape scale when managing wet grasslands as functional GI. This study suggests that this can be linked to the developmental stages of habitats from natural via anthropogenic induced wet grasslands to degraded ones, followed by unsuccessful attempts towards restoration (Figure 6). This is consistent with the results of Paper IV that showed the gradient of anthropogenic transformation is paralleled by the abundance of corvid birds as generalist avian predators.

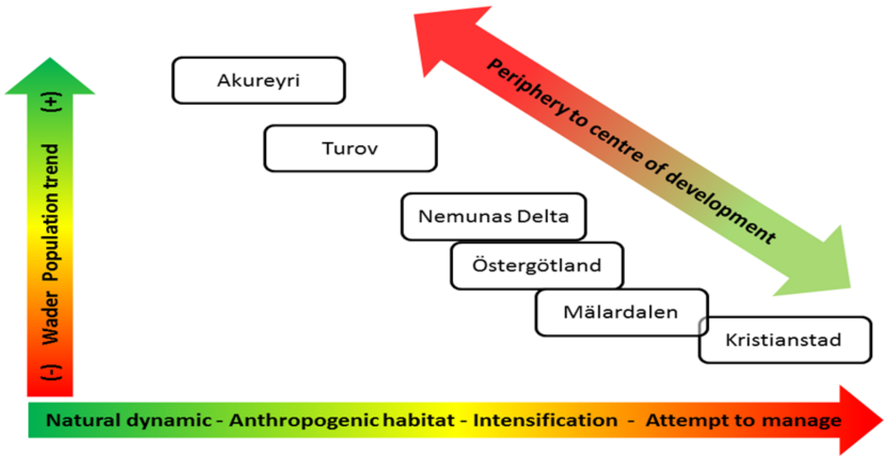


Figure 6. Tentative illustration of the population trends of wader birds in relation to the development of habitats from natural via anthropogenic induced to degraded, followed by attempts towards restoration (see Paper V).

4 Conclusion

Functional habitat networks are not only about patch quality and size linked to land cover characteristics, but also involve ecological processes, such as predation, conversion of farming practices, hydrology and climate change. As shown in this thesis, problem solving research requires a two-pronged approach. Firstly, a comprehensive understanding of the social-ecological systems that created the current land covers is needed to support knowledge production about protection, conservation and restoration for both biodiversity conservation and human well-being. This includes integrating management activities undertaken by multiple stakeholders and actors locally, regionally, nationally and internationally. Secondly, both anthropogenic and natural ecological processes from individual land cover patches through to landscape and regions need to be understood. Hence, the conservation of semi-natural grasslands as functional GI is complex and requires continuous knowledge production and learning, as well as the development of ongoing maintenance and monitoring programs. This thesis highlights gaps in knowledge, and the complexity of governing and managing wet grasslands as functional GI using the KVBR as a case study. There are two key parallel tasks. One is to improve the understanding of complex long-term changes in land use that affects land cover patterns as well as ecological processes at multiple scales from patches to entire landscapes in different regions and countries. The second is to facilitate learning by integration of researchers', stakeholders' and actors' perspectives in governance and management.

The multiple landscape case study approach employed in this thesis is a novel macroecological tool that helped identify barriers and encourage knowledge production as a base for learning towards securing functional GI. Extending across multiple landscapes and countries with unique landscape histories provided an essential broader perspective on what needs to be considered to maintain wet grasslands as functional GI. In closing, maintaining and restoring functional GI involves more than just land covers.

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