Managing Green Infrastructures

Trophic Interactions in Anthropogenic and Natural Ecosystems

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Licentiate Thesis
Swedish University of Agricultural Sciences
Skinnskatteberg 2014
Cover: Predation matters illustration by Mindaugas Ilčiukas.
Concept design by Michael Manton.
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Abstract
The term green infrastructure addresses the spatial structure of anthropogenic, seminatural and natural areas, as well as other environmental features which enable society to benefit from ecosystems’ multiple services. Focusing on two green infrastructures, anthropogenic wet meadows and natural forest successions, this thesis applies a macro-ecological approach based on comparisons of multiple landscapes as complex social-ecological systems. Firstly, the trophic interactions of avian predation in anthropogenic wet meadows under different management regimes in southern Sweden were explored (Paper I). This study tested the hypothesis that the abundance of avian predators and predation is higher in rapidly declining vs. relatively stable wader populations. Secondly, the trophic interactions of large mammals in Europe’s boreal forest biome were explored (paper II). This study tested the hypotheses that reduced numbers of large carnivores and increased numbers of large herbivores affect the recruitment of both ecologically and economically valuable trees, and that forest management intensity is correlated to a reduction in tree recruitment. The results show, firstly, that the abundance of avian predators and predation was higher in rapidly declining wader populations. Secondly, reduced numbers of large carnivores and abundant large herbivore populations were correlated to reduced recruitment of focal tree species. There was no relationship with the index of forest management intensity. To conclude, this thesis illustrates the consequences of disturbed tropic interactions on two different green infrastructures (anthropogenic wet meadows and boreal forests). The governance and management of green infrastructures is thus complex, because both the quantity and quality of land cover, and trophic interactions, need to be considered. This thesis confirms the importance of studying the consequences of altered trophic interactions in multiple landscapes rather than in a single landscape or region alone. Macro-ecological studies comparing countries and regions with different contexts, e.g., landscape history, traditions, governance and management systems, can support the development of more holistic views on the planning and management of green infrastructures.

Keywords: Green infrastructures, Land cover, Habitat, Trophic interactions, Predation, Macro-ecology

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Dedication

To my family and friends.
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., Angelstam, P., Milberg, M. and Elbakidze, M. Governance and management of green infrastructures for ecological sustainability: wader bird conservation in southern Sweden as a case study. (manuscript).

II  Angelstam, P., Manton, M., Pedersen, S., Shakun, V. and Elbakidze, M. Disrupted trophic interactions affect recruitment of key-stone boreal deciduous and coniferous trees in northern Europe. (manuscript).
The contribution of Michael Manton to the papers included in this thesis was as follows:

I  80%
II 45%
1 Introduction

Natural capital is the stock of natural ecosystems that yields a flow of valuable ecosystem goods or services into the future (Costanza & Daly, 1992). Natural resource management practices, such as forestry, agriculture and mineral extraction, generally result in a decline in natural capital at multiple scales (Gergle & Turner, 2001; Young, 2000; Antrop, 1993). A wide range of studies in Europe have indicated that intensified management and use of different land covers (forests, meadows, wetlands and etc.) can cause reductions in different components of biodiversity (Noss, 1990). This applies to species, anthropogenic and natural habitats as well as important ecosystem processes (Brumelis et al., 2011; Angelstam et al., 2004b; Shorohova & Tetioukhin, 2004; Siitonen, 2001; Mikusiński & Angelstam, 1999; Esseen et al., 1997). In conjunction with the continuing expansion of intensified land management, transport infrastructure and urban areas, important abiotic and biotic processes are directly and indirectly affected (Angelstam et al., 2004c) resulting in a reduction of species specialising on natural habitat dynamics (Mikusiński & Angelstam, 1998).

To counteract the degradation and loss of compositional, structural and functional biodiversity elements of green infrastructures, a variety of policies at multiple levels have been proposed and implemented (Tzoulas et al., 2007; Larsson et al., 2001; Raivio et al., 2001). The policy concept “Green Infrastructure” captures the need to secure natural capital, due to the wide range of services that ecosystems provide (European Commission, 2013). The ecosystem services concept considers the values of anthropogenic, semi-natural and natural ecosystems for both biodiversity and human well-being (European Commission, 2013). The importance of the ecosystem services concept has been widely accepted at both international and local levels (Kumar, 2010; TEEB, 2010). There are various definitions of the ecosystem services approach (Fisher et al., 2009). However, they all consider the various goods, services and values of ecosystems for humankind (Kumar, 2010; TEEB, 2010; de Groot
et al., 2002; Costanza et al., 1997; Daily et al., 1997). The ecosystem services are broadly classified into four main categories (1) Provisioning Services – as resources provided by nature, (2) Regulating Services – how nature regulates natural occurrences, (3) Cultural Services – intangible benefits based on peoples beliefs and the benefits they obtain, and (4) Supporting (or habitat, see TEEB, 2010) Services – strengthens the other services and provides habitat to support life (Kumar, 2010). These services are maintained in networks of natural and semi-natural areas, i.e. green infrastructures, which comprise of both blue (water) and green (land cover) components (Benedict & McMahon, 2002). Thus, the green infrastructure concept attempts to convey ecological, economic and social benefits of nature to humans (Andersson et al., 2014; Tzoulas et al., 2007). Conversely, policies such as the European Union’s (EU) green infrastructure policy, may aid in securing biodiversity and suitable habitats for species. However, this requires assessment as to whether or not ecosystems form functional representative land covers in terms of patch quality, size, and their connectivity in sufficient amounts to form functional habitat networks, i.e. green infrastructures (Angelstam & Andersson, 2001; Opdam et al., 1995).

To conserve anthropogenic and semi-natural land covers requires active ongoing management, whereas natural land covers may be conserved by networks of protected areas if natural processes are allowed, facilitated and enhanced (Angelstam, 2006). Forests and wet meadows are examples of land covers that can exist in both highly anthropogenic and natural systems. Nevertheless, the habitat of particular species may include factors other than just land cover. Composition, structure and function of green infrastructures can be influenced by individual species in different ways (Westman, 1990). Thus, in addition to the spatial structure of natural and semi-natural land covers, both anthropogenic and natural processes need to be understood at multiple spatial scales from patches and landscapes to regions and countries (European Commission, 2013). For example, species other than the target or focal species need to be considered, such as their predators, prey and competitors, as well as the ultimate reasons for their current and historic status and trends. Accordingly, green infrastructure is more than just land cover and requires a comprehensive understanding of social-ecological systems to aid in the protecting, conserving and enhancing of natural capital for both biodiversity and human society. Therefore, the management of landscapes and green infrastructures need to be integrated among owners, multiple sectors, levels of governance and land use.

The aim of thesis is to explore the role of trophic interactions as factors affecting the functionality of anthropogenic and natural green infrastructures.
To fulfil this aim, macro-ecological research approaches were employed by investigating the trophic interactions linked to two conservation priorities in Europe. Firstly, the roles of avian predation on anthropogenic wet meadows under different management regimes in southern Sweden were explored (Paper I). This study tested predictions that the abundance of avian predators and predation should be higher in rapidly declining vs. relatively stable wader populations. Secondly, an investigation was undertaken among regional landscapes in Europe’s boreal forest biome to test the hypothesis that disrupted trophic interactions affect the recruitment of key-stone deciduous trees and the economically important Scots pine (Paper II). This study explored two predictions: (1) that reduced number of large carnivore species is correlated to increased large herbivore abundance and reduced recruitment of deciduous tree species and Scots pine reaching maturity; and (2) that forest management intensity is correlated to reduced recruitment of deciduous tree species.

1.1 Niches, trophic interactions and habitat

Niche, trophic interactions and habitat are three of the most common and important terms used in ecology, but at the same time easily and most often confused or misinterpreted (Kearney, 2006; Hall et al., 1997; Whittaker et al., 1973).

An ecological niche is defined as the position or functions of a given species within its ecosystem, and should apply solely to the intra community role of the species (Whittaker et al., 1973). Niches can be filled by competing species (Caro & Stoner, 2003). For example, wolves (*Canis lupus*), lynx (*Lynx lynx*) and bears (*Ursus arctos*) are top predators of northern Europe that share similar ecological niches (Mech & Boitani, 2010). By sharing the same ecological niches, these species compete directly with each other for resources (i.e. space, food supply, breeding locations). Although these top predators share an ecological niche they can co-exist as their trophic interactions differ (Pasanen Mortensen, 2014; Schmidt et al., 2009).

Trophic interactions relate to the food chain or food web and consist of multiple levels (i.e., the position an organism occupies in the food chain) (Elton, 1927). The levels and linkages of the food chains can have both one-way, two way or multiple connections. Ecosystems with higher biodiversity generally have more complex trophic interaction pathways (Paine, 1980). Ecosystems are organised by internal and cross species relationships, and abiotic and biotic factors (Nilsson & Ericson, 1997). Both bottom up and top down processes of ecosystems are important and changes in either may result in a cascade of effects (Pasanen Mortensen, 2014; Carpenter et al., 1985;
Oksanen et al., 1981). The relationship between predators, prey and associated cascading effects are known as trophic interactions, and may be influenced by human activity. Trophic cascades are defined as give-and-take predator-prey effects that may change the abundance, biomass or dynamics of a population or trophic level across multiple linkages in a food web (Carpenter et al., 1985). Trophic cascades may originate from any level of the food web but is most often related to large predators (Pace et al., 1999). Interspecific competition between predators is also an important consideration among trophic interactions and is a common occurrence in predators (Pasanen-Mortensen et al., 2013; Donadio & Buskirk, 2006). Therefore, trophic interaction and their cascading effects may play an important role in the management of habitats and species conservation.

Habitat is defined as resources and conditions present in an environment that produces occupancy, including survival and reproduction, by a particular species (Hall et al., 1997). Habitat is specific to a particular species, or populations within a species’ distribution range, and can consist of singular or multiple vegetation types and vary in configuration, structure and characteristics. Habitat is therefore about the combination of resources and climatic conditions, required by any given species and the interaction with competition and predators (Franklin et al., 2002). Also of importance is habitat quality, which is a continuous variable that can range from low to high based on the environmental conditions appropriate for both individual species and population persistence (Franklin et al., 2002; Hall et al., 1997; Van Horne, 1983). When considering habitat it is also important to understand the summer and winter migration ranges and to the degree in which these different habitats influence species and their mean relative fitness (Van Horne, 1983). Therefore, habitat is thus not only about patch quality and size linked to vegetation characteristics, but also involves trophic interactions, such as predation (Eglington et al., 2008; Van Horne, 1983). Just because a green infrastructure is suitable habitat for a variety of species at a particular time does not mean it will continue to remain suitable. For example, if a land manager decides to alter a land cover or its surrounding area and these modifications alter the structure and quality of the habitat and or the surrounding area, then the given species requirements may no longer be met. Thus niches, trophic interactions and habitats are interconnected and include many factors other than just land cover.
1.2 Predator-prey systems

Whilst there are arguments among stakeholders and actors both for and against the conservation of large carnivores, predator-prey-vegetation interactions are generally overlooked. Trophic interactions extend throughout all trophic levels and the loss of key-stone species (Estes et al., 2011; Simberloff, 1998), such as large terrestrial predators, in an ecosystem may cause cascading effects (Säterberg et al., 2013; Ripple & Beschta, 2004). This includes large herbivore densities due to improved survival (Edenius et al., 2002). In northern Europe the increased populations of moose (Alces alces), red deer (Cervus elaphus) and roe deer (Capreolus capreolus) (Côté et al., 2004) have considerably impacted field layer vegetation and structure (Putman et al., 2011; Gordon & Prins, 2008), tree recruitment and the composition of tree species in stands (Müller et al., 2008), and the natural dynamic processes of forest ecosystem (Speed et al., 2014). This may in turn affect the amount and quality of habitat for other species.

Thus, the loss of predators and increased densities of prey and the associated cascading effects are good examples of large-scale challenges for natural resource managers and conservationists. On the other hand increased populations of predators and losses in prey may also affect the trophic interactions of species at various levels. For example, species can inadvertently interfere with each other’s food source and may be driven into new environments in a bid to survive (Abrams & Ginzburg, 2000). Therefore, the consideration of trophic interactions at more than two levels is extremely important. Upon understanding the trophic interactions of such systems one should not only try to understand distribution and abundance of both predators and prey, but also the carrying capacity and impacts on habitat, vegetation and competition, as well as the cascading effects on species and ecosystems (Leopold, 1933).

1.3 Herbivore-plant systems

The interrelationships between herbivores and plant systems are complex involving flora, fauna, climate and soils as well as other factors (Augustine & McNaughton, 1998). Changes in any of these factors may influence plant community structure and function, animal foraging strategies and ecology, and ecosystem processes (Hodgson & Illius, 1996). In anthropogenic land covers, such as wet meadows, changes in species and grazing intensity often directly results in the transition of grass swards, composition and structure and alters soil composition (Durant et al., 2008; Briske, 1996; Belsky, 1992). In turn this may affect small invertebrates and their predators, such as waders.
The herbivore plant relationship in forest ecosystems are as equally important and most often involves the replacement of early successional species (e.g., aspen (*Populus tremula*), rowan (*Sorbus aucuparia*) and sallow (*Salix* spp.) with later successional species (e.g., spruce (*Picea abies*) (Hester *et al.*, 2006). As the primary affect is on the juvenile stages, many early successional trees do not reach maturity, and in turn implications may occur in mature tree species composition, species habitats and the nutrient cycle (Augustine & McNaughton, 1998). Conversely, should management practices of green infrastructures be reduced or intensified, changes in habitat and ecosystem process may lead to vulnerabilities in species survival (Ihse, 1995).

Many plants have evolved various resistance strategies to counteract the effects from herbivores (Kennedy & Barbour, 1992). Likewise, many herbivores have developed preference for specific types of vegetation, and have even evolved with the defence strategies of plants (Meijden *et al.*, 1988). The interactions of two or more herbivore species can potentially increase the pressure on plant species and communities at both patch and landscape scales (Latham, 1999; Briske, 1996). Herbivore browsing or grazing can result in both positive and negative changes in plant communities through various direct and indirect processes. However, the results on individual plants are most often negative resulting from biomass removal. There is increasing evidence that the abundance and breeding success of species, such as waders in wet meadows habitats and deciduous forest specialists, such as woodpeckers in forest habitats, are not only dependent on processes within their niche, but also on processes and quality of habitat within the surrounding landscape (Fahrig, 2003; Baillie *et al.*, 2000).

### 1.4 Two green infrastructures in focus

#### 1.4.1 Anthropogenic wet meadows

Historically, grazing and mowing of wet meadows has expanded at the expense of naturally dynamic land covers, resulting in a cultural landscape (Antrop, 1993). Wet meadows, traditionally managed to provide grazing and hay for domestic animals is a good example. Being biologically high in productivity, naturally dynamic wet meadows were thus expanded during the millennia. However, with the advent of modern agriculture based on effective crop production and economic profit, wet meadows have been severely reduced by draining, water regulation as well as the creation of dykes and polders (Beintema, 1986). Increased operating applications and land management shifts, from small scale to large scale operations, have contributed to
development outcomes where wetland biota has suffered from habitat degradation, fragmentation and loss. This means that wet meadows need to be subject to ongoing conservation management to maintain their biodiversity values. Mowing grass, removing encroaching shrubs and regulating water levels are three examples of efforts to maintain appropriate land covers for wader birds. However, recent studies have shown that not only land cover amount and quality is important for wader bird conservation, but also predation (Wilson et al., 2014; Pearce-Higgins & Grant, 2006; Ottvall, 2005; Dyrcz et al., 1981).

1.4.2 Natural boreal forests

Forest ecosystems in Scandinavia have undergone immense changes throughout the last two centuries in a drive to produce more timber, pulpwood and bioenergy (Ericsson et al., 2000). Conversely, during the same timeframe carnivore numbers, browsing pressure and hunting quotes have changed, which may also influence forest ecosystems. Northern European forests range from plantations of introduced species to protected area that host similar characteristics found in naturally occurring landscapes (Mikusiński & Angelstam, 2004; Angelstam et al., 1997). This intensified forest management is negatively affecting biodiversity, by reducing natural forest components (Larsson et al., 2001; McComb & Lindenmayer, 1999). At the stand scale, studies on northern European boreal forest history gradients have shown coniferous forest types have been promoted at the expense of deciduous stands resulting in an up to 90% decline in deciduous tree species (Shorohova & Tetioukhin, 2004; Mikusiński & Angelstam, 1999). At the landscape scale important abiotic and biotic processes have also been changed. As a consequence the amount of deciduous and old growth forests habitats suitable for specialised species has declined (Aakala, 2011; Angelstam et al., 2011a; Lõhmus & Lõhmus, 2011; Mikusiński & Angelstam, 1998; Esseen et al., 1997).

1.5 Case study research

Case study research is a strategy that focuses on understanding the dynamics present within a single settings (Eisenhardt, 1989). Even though case studies are often viewed as controversial and misleading (e.g., Flyvbjerg, 2006; Yin, 1981), 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 in multidisciplinary sciences (Angelstam et al., 2013a; Flyvbjerg, 2011; Flyvbjerg, 2006; Eisenhardt, 1989). Specifically, case
studies provide reliability, validity and a sound concept that can help scientists understand hypotheses on tangible circumstances (Stryamets, 2012; Flyvbjerg, 2006) and are used to develop theories, test hypotheses and provide descriptions of different settings. Collected qualitative or quantitative evidence may be obtained from fieldwork, desktop studies, verbal reports, observations, or any combination of these (Eisenhardt, 1989; Yin, 1981). Case studies can provide an opportunity to undertake research experiments in both historic and current situations. 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).

The use of entire landscapes as case studies to investigate, test hypotheses and compare results of species interactions and subsequent effects is an appropriate method to study trophic interactions in the context of green infrastructure governance and management. With both focal avian and large carnivore predators and herbivore species requiring large home ranges, the comparison of local habitat patches alone is insufficient. Therefore, sufficiently large areas with a variety of different green infrastructure, habitat quality and different species need to be compared to understand the trophic interactions of focal species, their competitors and predators. Thus, a landscape scale approach should be considered (e.g., Baillie et al., 2000), which is linked to species’ life history traits (Wiens, 1989). In an analysis of relationships between land cover and fragmentation versus occurrence of avian and mammalian predators using multiple landscapes, Angelstam et al. (2004b) and Mikusiński and Angelstam (2004) used sampling areas of ca. 100 km² and 2500 km², respectively and stress the need to continue studies at varying landscape scales.

It is important to appreciate the multitude of different landscapes under an array of landscape histories as well as governance arrangements in Europe. These differences have contributed to unique local ecological, economic and socio-cultural environments, which can be used as a ‘time machine’ (Angelstam, 2001) to help understand the effects humans have on the environment (Angelstam et al., 2011b; Angelstam & Elbakidze, 2006). This diversity in landscape history and governance settings provides a unique situation to learn from the consequences of the past and present to help develop knowledge for society and species conservation and thus better sustainability (Elbakidze et al., 2010).

With policy and management of wildlife and green infrastructure varying only slightly or being the same within landscapes and regions of a country, local relationships between predator, prey and competition, have limited
variation (Månsson et al., 2007). The policy and management outcomes in Scandinavia have led to relatively homogenous ecosystems with little differences in vegetation composition, structure and biodiversity (Danilov, 1987; Nygrén, 1987). As a consequence, many specialised species such as waders and large predators have become rare and endangered (Angelstam et al., 1997; Esseen et al., 1997). In comparison, eastern countries of northern Europe have less intensive land management histories (Angelstam & Dönz-Breuss, 2004; Puumalainen et al., 2003). As a result these countries still host a variety of species that are often locally extinct or critically declining in Scandinavia (Angelstam et al., 2004c). Hence, the diversity of contexts linked to landscape history and governance arrangements on the European continent provides ample opportunity for replicated case studies of both wetlands and forest landscapes as social-ecological systems. This context is appropriate for macro-ecological studies that trade off the precision of small-scale research with an appropriate spatial scale (Brown, 1995). Comparative studies of multiple landscapes with different governance contexts can deliver results and shortcuts to develop both knowledge and societal learning processes toward sustainability (Angelstam et al., 2013a; Angelstam et al., 2013b; Angelstam et al., 2011b). Moreover, Angelstam et al. (2004a) suggests international collaboration and networks of interdisciplinary professionals exploring landscape management may ensure green infrastructures are re-established in previous areas and preserved in areas where they occur. Thus, Europe’s SW - NE gradient should be used to compare local knowledge, experience and insights on landscape processes in different countries. However, studies that examine the effects of altered trophic interaction at landscape scales spanning across ecoregions are limited. Studying predator-prey relationships across a gradient of different landscapes may aid actors and stakeholders to develop a better understanding of disrupted trophic interactions, different management regimes and lead to mutual knowledge transfer.
2 Methodology

2.1 Study areas

To study the trophic interactions of predators and prey, as well as associated the cascading effects within anthropogenic and natural green infrastructures, a multitude of case studies were undertaken throughout northern Europe (Figure 1, Table 1).

Firstly two regional study areas were selected in southern Sweden (Paper I). These include (A) a specially managed inland wetlands system in Kristianstad municipality, and, (B) a series of three wetland systems in Östergötland County, i.e. Lake Tåkern, Lake Roxen and the inner Bråviken Bay in the Baltic Sea. The Kristianstad municipality which contains the acclaimed Kristianstad Vattenrike Biosphere Reserve is specifically managed for ecological, economic and social sustainable development. The wetlands of Östergötland County are governed and managed under normal Swedish regulations.

Secondly, ten case study areas located throughout the boreal forest zone were selected to cover the full gradient of species richness of large carnivores and herbivores (Paper II). The study areas ranged from Vestfold near Oslo in Norway, to the Komi Republic, Russia in the European boreal forest region. The chosen study areas also reflect a gradient of unique governance and management histories across countries, thus providing a broad range of past and present land management outcomes and settings.
<table>
<thead>
<tr>
<th>Country</th>
<th>Study area</th>
<th>Location (lat/long)</th>
<th>Forest % per (100 x 100 km²)</th>
<th>Altitude (m)²</th>
<th>Human population density (n/km²)³</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sweden</td>
<td>Kristianstad (Kr)</td>
<td>61 19 91 N, 13 77 65 E</td>
<td>31</td>
<td>0-203</td>
<td>70.2</td>
</tr>
<tr>
<td>Sweden</td>
<td>Östergötland (Ög)</td>
<td>64 86 64 N, 15 15 15 E</td>
<td>37</td>
<td>0-248</td>
<td>49.2</td>
</tr>
<tr>
<td>Norway</td>
<td>Vestfold (VE)</td>
<td>59 22 40 N, 10 07 10 E</td>
<td>46</td>
<td>0-1074</td>
<td>106.8</td>
</tr>
<tr>
<td>Norway</td>
<td>Østerdalen (ØS)</td>
<td>61 39 37 N, 10 39 48 E</td>
<td>27</td>
<td>160-2020</td>
<td>3.2</td>
</tr>
<tr>
<td>Sweden</td>
<td>Bergslagen (BE)</td>
<td>59 57 20 N, 14 30 20 E</td>
<td>65</td>
<td>200-400</td>
<td>12.6</td>
</tr>
<tr>
<td>Sweden</td>
<td>Asa (AS)</td>
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<td>61</td>
<td>133-368</td>
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<tr>
<td>Latvia</td>
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<td>51</td>
<td>42-276</td>
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<tr>
<td>Belarus</td>
<td>Ostrovets (OS)</td>
<td>54 33 58 N, 26 04 56 E</td>
<td>37</td>
<td>117-318</td>
<td>36.5</td>
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<tr>
<td>Belarus</td>
<td>Novogrudok (NO)</td>
<td>53 40 57 N, 26 18 20 E</td>
<td>31</td>
<td>116-311</td>
<td>29.6</td>
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<tr>
<td>Russian Federation</td>
<td>Pskov (PS)</td>
<td>58 22 01 N, 29 09 08 E</td>
<td>65</td>
<td>30-190</td>
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<td>Ilomantsi (IL)</td>
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<td>68-324</td>
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<tr>
<td>Russian Federation</td>
<td>Komi (KO)</td>
<td>61 53 22 N, 52 09 39 E</td>
<td>67</td>
<td>72-263</td>
<td>11.9</td>
</tr>
</tbody>
</table>

¹ Hansen et al. (2013)  
² Jarvis et al. (2008)  
³ Columbia University et al. (2011) and Balk et al. (2006)
2.2 Methods

To test the hypotheses the trophic interactions of predators and prey, and the associated cascading effects within anthropogenic and natural green infrastructures, two distinct studies were undertaken.

Firstly, a desktop study and three experiments on the trophic interactions of breeding waders (Charadrii) and avian predators (corvid birds and birds of prey) were explored on differently governed and managed anthropogenic wet meadows in southern Sweden.

1. A desktop study was undertaken on the population trends of breeding waders and the avian predator assemblages.

2. At the beginning of the wader breeding season in April 2013, observational counts of all waders, corvids and birds of prey was performed by undertaking a 30-minute 360 degree point sweep using binoculars and a spotting scope at the wet meadows of Kristianstad and Östergötland. The field observations were undertaken in succession over a two week period from dawn to mid-afternoon under favourable weather conditions. The wet meadows of Kristianstad were observed first with the wet meadows of Östergötland undertaken the following week. From the observational counts
an index of predation pressure, was calculated separately for corvids and birds of prey and expressed as the ratio of predators to the sum of predators and waders. Using the software Comprehensive Meta-Analysis 2.2 (www.meta-analysis.com), an overall average predation pressure index for Kristianstad and Östergötland using the random model was calculated.

3. During the latter part of the breeding period, 180 avian predator observational counts were conducted in each of the Kristianstad and Östergötland study areas (Total = 360). Using a Geographical Information System (GIS) (ESRI, 2012) and land cover data from the Swedish Land Surveying Authority six main land cover types were identified (1) wet meadows, (2) urban areas (>40% coverage), (3) agricultural fields (forest cover ~0%), (4) mixed field and forest (forest cover 5-20%), (5) mixed forest and field (forest cover 40-60%) and (6) forests (forest cover >80-95%). The forest land cover type intervals were chosen to reflect clearly fragmented areas (i.e. <20% forest cover), mixed forest and open areas, and contiguous forest (Fahrig, 2003). Using this landscape data and a 1-km grid overlay I randomly selected 30 observational locations for each land cover type per study area. At the centre of each selected grid cell a 5-minute, continuous 360 degree point sweep with binoculars was undertaken to count all corvid birds and birds of prey. The point counts were undertaken in succession during June 3-17, 2013. Field work was suspended in adverse weather conditions, such as when windy and rainy. Average counts per land cover type were calculated on ln(1+x)-transformed data, and then back-transformed for display purpose.

4. Following Pehlak and Lõhmus (2008), an experiment on the predation of artificial wader nests was undertaken June 3-17, 2013. In each of the study areas, I randomly selected five open wet meadows and five open agricultural fields with a vegetation height of 0-30 cm suitable for wader breeding (Smart et al., 2006). Within each of the selected wet meadows and open agricultural fields ten artificial wader nests were placed at night > 100 m apart, each nest contained two brown chicken eggs (cf., Angelstam, 1986). The aim was to simulate wader nests, which are simply eggs laid on the ground. Each nest was then inspected for predation during the night after 5 and 10 days, respectively (Wilson et al., 2007; Ottvall & Smith, 2006). To establish the perpetrator, signs such as peck holes, feathers, footprints, tyre tracks or farming operations (e.g., slashing and ploughing) were identified. Site-wise nest predation data were entered into a meta-analysis that then estimated the predation (event rate) in Kristianstad and Östergötland using the random model and the software Comprehensive Meta-Analysis.
Secondly, a two staged study on the trophic interactions of large mammals and herbivores, and their effects on tree recruitment for forest management and biodiversity across Europe’s boreal biome were explored.

1. A desk top study using GIS (ESRI, 2012) was undertaken to create coarse index maps (50 km x 50 km) on the occurrence of both large carnivores (Kaczensky et al., 2012) and large herbivores (IUCN, 2014), and forest management intensity using data on forest loss (Hansen et al., 2013) to provide a proxy of the broad scale forest management trends. Forest loss refers to an area of forest, harvested or loss by a natural event, such as a fire or windthrow that contributes to young browse.

2. To assess the cascading effects on four young boreal forest species, field work measuring tree recruitment was undertaken at 600 points within 10 study areas (10 study areas x 10 stands x 6 survey points). To assess the impact of trophic interactions affecting the recruitment of young trees into mature trees, the accumulated browsing damages on young aspen, rowan and sallow and young Scots pine (*Pinus sylvestris*) were measured. A statistical analysis of the collected data was undertaken to understand what factors affect browsing damages on young trees of species that are preferred by large herbivore, specifically moose, in the ten study areas. Analyses of the entire data set of 10 study area replicates were undertaken by firstly testing the hypotheses that large herbivore abundance and forest management intensity, respectively, is related to mean damage levels among the study area replicates, and secondly making an ordination using PCA.
3 Results

3.1 Predators, prey and anthropogenic wet meadows (Paper I)

3.1.1 Breeding wader and the avian predator trends

The breeding wader population trends were clearly negative in Kristianstad, while the trends for Östergötland were relatively stable to slightly decreasing (Table 2).

Table 2. Annual rate of change of waders at the wet meadow sites in Kristianstad, and the three areas in Östergötland. Data extracted from Cronert (2014) for Kristianstad and Bergner (2013) for Östergötland.

<table>
<thead>
<tr>
<th></th>
<th>Body mass (g/ha)</th>
<th>SE</th>
<th>Metabolic weight (g/ha)</th>
<th>SE</th>
<th>Nests (No./ha)</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kristianstad</td>
<td>-27.367</td>
<td>2.452</td>
<td>-4.808</td>
<td>0.488</td>
<td>-0.061</td>
<td>0.007</td>
</tr>
<tr>
<td>Ög Roxen</td>
<td>0.929</td>
<td>0.150</td>
<td>0.199</td>
<td>0.061</td>
<td>0.004</td>
<td>0.002</td>
</tr>
<tr>
<td>Ög Tåkern</td>
<td>-8.667</td>
<td>2.660</td>
<td>-1.723</td>
<td>0.499</td>
<td>-0.010</td>
<td>0.005</td>
</tr>
<tr>
<td>Ög Bråviken</td>
<td>1.930</td>
<td>-</td>
<td>0.368</td>
<td>-</td>
<td>0.005</td>
<td>-</td>
</tr>
</tbody>
</table>

The desktop study on avian predator assemblages and their population trends showed that the populations of both corvids and birds of prey have generally increased in numbers over the past 30 years (Table 3). During the winter months all corvids are resident with both areas providing important wintering grounds for a number of birds of prey.
Table 3. Summary of avian predator assemblages for Kristianstad (Kr) and Östergötland (Ög) and the 10 and 30 year population trends for southern Sweden. Trends, ↑ = Large increase, ↑ = Slight increase, ↔ = Stable, ↓ = Slight decline, ↓ = Large decline. ¹= (Ottvall et al., 2009), Waders in Diet A = Adults, E = Eggs and Y = Young. Status R = Resident, B = Breeding and M = Migrating. ²= (Cramp, 1980) ³ = (Cramp et al., 1980), ⁴= (Svensson et al., 2009).

<table>
<thead>
<tr>
<th>Species</th>
<th>Trends ¹</th>
<th>Waders in Diet²,³</th>
<th>Status², ³, ⁴</th>
</tr>
</thead>
<tbody>
<tr>
<td>Corvids</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Magpie (Pica pica)</td>
<td>↔</td>
<td>E, Y R R</td>
<td></td>
</tr>
<tr>
<td>Jay (Garrulus glandarius)</td>
<td>↑</td>
<td>E, Y R R</td>
<td></td>
</tr>
<tr>
<td>Jackdaw (Corvus monedula)</td>
<td>↑</td>
<td>E, Y R R</td>
<td></td>
</tr>
<tr>
<td>Rook (Corvus frugilegus)</td>
<td>↑+</td>
<td>A, E, Y R R</td>
<td></td>
</tr>
<tr>
<td>Hooded Crow (Corvus cornix)</td>
<td>↓</td>
<td>A, E, Y R R</td>
<td></td>
</tr>
<tr>
<td>Raven (Corvus corax)</td>
<td>↑+</td>
<td>A, E, Y R R</td>
<td></td>
</tr>
<tr>
<td>Birds of prey</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>White-tailed Eagle</td>
<td>↑+</td>
<td>A, E, Y R B</td>
<td></td>
</tr>
<tr>
<td>Osprey (Pandion haliaetus)</td>
<td>↔</td>
<td>Fish B B</td>
<td></td>
</tr>
<tr>
<td>Golden Eagle (Aquila chrysaetos)</td>
<td>↑</td>
<td>Adults R R</td>
<td></td>
</tr>
<tr>
<td>Red Kite (Milvus milvus)</td>
<td>↑+</td>
<td>A, E, Y B M</td>
<td></td>
</tr>
<tr>
<td>Marsh Harrier (Circus aeruginosus)</td>
<td>↔</td>
<td>A, E, Y B B</td>
<td></td>
</tr>
<tr>
<td>Hen Harrier (Circus cyaneus)</td>
<td>↓</td>
<td>A, E, Y M B</td>
<td></td>
</tr>
<tr>
<td>Montagu’s Harrier (Circus pygargus)</td>
<td>↓</td>
<td>A, E, Y B B</td>
<td></td>
</tr>
<tr>
<td>Rough-legged Buzzard (Buteo lagopus)</td>
<td>↓</td>
<td>A, Y M M</td>
<td></td>
</tr>
<tr>
<td>Buzzard (Buteo buteo)</td>
<td>↑</td>
<td>A, Y B B</td>
<td></td>
</tr>
<tr>
<td>Honey Buzzard (Pernis apivorus)</td>
<td>↔</td>
<td>Insects B B</td>
<td></td>
</tr>
<tr>
<td>Sparrowhawk (Accipiter nisus)</td>
<td>↑</td>
<td>A, Y R R</td>
<td></td>
</tr>
<tr>
<td>Goshawk (Accipiter gentilis)</td>
<td>↔</td>
<td>A, Y R R</td>
<td></td>
</tr>
<tr>
<td>Kestrel (Falco tinnunculus)</td>
<td>↑+</td>
<td>A, Y B B</td>
<td></td>
</tr>
<tr>
<td>Hobby (Falco subbuteo)</td>
<td>↑</td>
<td>A, Y B B</td>
<td></td>
</tr>
<tr>
<td>Peregrine (Falco peregrinus)</td>
<td>↑+</td>
<td>A, Y R R</td>
<td></td>
</tr>
<tr>
<td>Merlin (Falco columbarius)</td>
<td>↔</td>
<td>A, Y B M</td>
<td></td>
</tr>
</tbody>
</table>

3.1.2 Relative abundance of avian predators and waders

The corvid index of predation pressure was three times higher on the wet meadows in Kristianstad compared to Östergötland. However, the index of predation pressure for birds of prey was similar in each study area (Figure 2). During the relative abundance field work a total of 11 species among 517 wader individuals, 6 corvid species among 556 individuals, and 6 birds of prey species among 66 individuals, were observed.
3.1.3 Landscape avian predator counts

Mean corvid numbers were higher in Kristianstad compared to Östergötland for all land cover strata, and significantly higher for wet meadows and urban areas (Figure 3). Birds of prey also exhibited higher mean numbers in Kristianstad compared to Östergötland for all land covers except for the land class with >80% forest cover. However, the confidence intervals overlapped for the other land covers (Figure 3). In total 6 corvid species among 2695 individuals, and 7 birds of prey species among 88 individuals, were observed during the landscape avian predator counts.

Figure 3. Number of corvid observations per survey plot (left) and probability of observing birds of prey (right) by land cover classes in Kristianstad and Östergötland. Error bars indicate CI_{95%}.
3.1.4 Artificial nest predation

The predation rates on artificial nests over the 10-day period were on average 95% in the Kristianstad vs. 36% in Östergötland. This applied both to wet meadows and agricultural fields (Figure 4).

![Figure 4. Proportion of predated artificial nests on wet meadows and agricultural fields in Kristianstad (Kr) and Östergötland (Ög). Error bars indicate CI_{95%}. Numbers to the right indicate estimates with CI_{95%} to allow inclusion in future meta-analyses.](image)

The cause of predation/destruction of artificial nests was often visible. Avian predators, mammals, livestock and human farming practices contributed to the demise of the artificial nests (Figure 5). Nevertheless, a high proportion of the preyed upon eggs were unknown. Even though the majority of the eggs were gone with no obvious signs we assume that the eggs were preyed upon by either avian predators or small mammals. During the field work, observations of crows traversing the sky carrying unknown eggs and foxes frolicking in the vicinity of some egg predation experiments were noted.
3.2 Predators, prey and boreal forest (Paper II)

3.2.1 Carnivores, herbivores and forest management intensity

There was a clear gradient from SW to NE Europe in the current species richness of large carnivores (Figure 6). NW Russia, most of Finland and Estonia share a contiguous area with brown bear, wolf and lynx. Central Sweden and Norway share isolated populations of the same species.

The number of large herbivore species decreased from SW to NE in northern Europe (Figure 7), and was thus opposite to the trend for large carnivore species. The herbivore index decreased from west to east (F = 9.06, df = 9, p < 0.001, Table 4). Moose was the dominant contributor to this index, and the number of moose pellet piles was heterogeneous among the 10 study areas measured ($\chi^2 = 74.06$, df = 9, p < 0.001), except for Vestfold in Norway, with an overall decrease from west to east (Table 4).
Table 4. Properties of the 10 study areas (for abbreviations, see Table 1). (1) Large herbivore index (**LH index**) and the percentage contribution of the surveyed cervid species to this index (**Moose %**, **Red deer %** and **Roe deer %**). (2) mean (± 95% CI) number of pellet piles of moose (**Moose pellets**), field layer food (**Field layer**) (dm³ per 100 m²) and tree layer food (**Tree layer**) (m³ per 100 m²)(3) the average number of carnivore (**Carn sp**) and herbivore (**Herb sp**) species in the local landscape based on data from Figure 6 and 7. (4) forest management intensity (**Formanint**) from Figure 8. (mean forest loss yr⁻¹).

<table>
<thead>
<tr>
<th>Study Area</th>
<th>LH index</th>
<th>Moose</th>
<th>Red deer</th>
<th>Roe deer</th>
<th>Moose pellets</th>
<th>Field layer</th>
<th>Tree layer</th>
<th>Carn sp</th>
<th>Herb sp</th>
<th>Formanint</th>
</tr>
</thead>
<tbody>
<tr>
<td>VE</td>
<td>0.07 (0.07)</td>
<td>100</td>
<td>0</td>
<td>0</td>
<td>0.20 (0.19)</td>
<td>9.4 (5.0)</td>
<td>13.93 (3.42)</td>
<td>1.6</td>
<td>3.0</td>
<td>0.27</td>
</tr>
<tr>
<td>ØS</td>
<td>0.56 (0.18)</td>
<td>100</td>
<td>0</td>
<td>0</td>
<td>1.62 (0.53)</td>
<td>60.5 (15.0)</td>
<td>0.81 (0.18)</td>
<td>3.0</td>
<td>3.0</td>
<td>0.22</td>
</tr>
<tr>
<td>BE</td>
<td>0.42 (0.12)</td>
<td>99.2</td>
<td>0.01</td>
<td>1.20</td>
<td>68.1 (23.7)</td>
<td>0.81 (0.18)</td>
<td>2.9</td>
<td>3.0</td>
<td>0.74</td>
<td></td>
</tr>
<tr>
<td>AS</td>
<td>0.16 (0.11)</td>
<td>81.6</td>
<td>0</td>
<td>18.3</td>
<td>12.8 (8.8)</td>
<td>4.00 (1.12)</td>
<td>1.0</td>
<td>3.0</td>
<td>0.89</td>
<td></td>
</tr>
<tr>
<td>SM</td>
<td>0.05 (0.04)</td>
<td>72.1</td>
<td>0.01</td>
<td>18.8</td>
<td>22.7 (8.5)</td>
<td>4.42 (1.54)</td>
<td>2.6</td>
<td>3.0</td>
<td>0.60</td>
<td></td>
</tr>
<tr>
<td>OS</td>
<td>0.21 (0.15)</td>
<td>96.7</td>
<td>0.01</td>
<td>3.3</td>
<td>0.7 (0.6)</td>
<td>1.90 (0.45)</td>
<td>1.6</td>
<td>3.0</td>
<td>0.23</td>
<td></td>
</tr>
<tr>
<td>NO</td>
<td>0.13 (0.10)</td>
<td>88.1</td>
<td>0.01</td>
<td>2.5</td>
<td>30.3 (14.5)</td>
<td>5.71 (1.57)</td>
<td>1.1</td>
<td>3.0</td>
<td>0.18</td>
<td></td>
</tr>
<tr>
<td>PS</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0</td>
<td>191.8 (110.3)</td>
<td>19.17 (6.23)</td>
<td>3.0</td>
<td>2.2</td>
<td>0.25</td>
</tr>
<tr>
<td>IL</td>
<td>0.01 (0.01)</td>
<td>100</td>
<td>0</td>
<td>0.02</td>
<td>84.5 (20.6)</td>
<td>6.68 (1.74)</td>
<td>3.0</td>
<td>1.9</td>
<td>0.44</td>
<td></td>
</tr>
<tr>
<td>KO</td>
<td>0.02 (0.02)</td>
<td>100</td>
<td>0</td>
<td>0.05</td>
<td>2.9 (3.0)</td>
<td>16.65 (4.7)</td>
<td>3.0</td>
<td>1.0</td>
<td>0.28</td>
<td></td>
</tr>
</tbody>
</table>
Figure 6. Map showing the presence of large resident carnivore species, represented as 50x50 km grid cells, in northern Europe.

Figure 7. Map showing the presence of large resident herbivore species, represented as 50x50 km grid cells, in northern Europe.
The analysis of the mean forest loss per year as a proxy of forest management intensity showed a distinct west-east gradient in the boreal biome. This ranged from homogenously high values (>1% per year) in Sweden, Finland and Latvia to low and variable values in NW Russia (Figure 8).

![Figure 8. Map showing forest management intensity using forest loss per year, represented by 50x50 km grid cells, in northern Europe.](image)

### 3.2.2 Browsing damage analyses

A significant decrease in mean browsing damage from west to east across the boreal biome for aspen (F9,58= 10.01, df=9, p< 0.001), rowan (F9,67= 12.06, p< 0.001), sallow (F9,71= 13.87, p< 0.001) and Scots pine (F9,78= 17.47, p< 0.001) (Figure 9a, 9b, 9c & 9d respectively).
Figure 9. Estimates of mean damage level (± 95% CI) for the four young tree species. On a scale from 0 (unbrowsed) to 4 (dead by browsing) per stand, in the 10 boreal landscapes (for abbreviations, see Table 1).

Positive correlations (p<0.05) were observed for LH index vs. Tree damage and Herb sp vs. Tree damage, and negative correlations for tree browse (Tree layer) vs. LH index, Tree layer vs. Tree damage, and Herb sp vs. Tree layer, and Herb sp vs. Carn sp (Table 5).

The mean damage level on the four tree species at the landscape level increased as the large herbivore index increased (t=3.99, df=7, p=0.005, r²=0.59). However, there was no relationship between the mean damage level and forest management intensity (t=1.73, df=7, p=0.127, r²=0.06) (Figure 10).
Table 5. Correlation matrix for key variables in this study (data from Table 4, except tree damage, which was estimated as the mean of tree damage levels for the data presented in Figures 9 a, b, c, d). * indicates that p<0.005.

<table>
<thead>
<tr>
<th>Key variables</th>
<th>Formanint</th>
<th>LH index</th>
<th>Tree damage</th>
<th>Field layer</th>
<th>Tree layer</th>
<th>Carn sp</th>
<th>Herb sp</th>
</tr>
</thead>
<tbody>
<tr>
<td>Formanint</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LH index</td>
<td>0.09</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree damage</td>
<td>0.40</td>
<td>0.80*</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Field layer</td>
<td>-0.13</td>
<td>-0.08</td>
<td>-0.34</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree layer</td>
<td>-0.38</td>
<td>-0.69*</td>
<td>-0.83*</td>
<td>0.36</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carn sp</td>
<td>-0.10</td>
<td>0.11</td>
<td>-0.33</td>
<td>0.53</td>
<td>0.20</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Herb sp</td>
<td>0.23</td>
<td>0.50</td>
<td>0.74*</td>
<td>-0.17</td>
<td>-0.64*</td>
<td>-0.53*</td>
<td>1</td>
</tr>
</tbody>
</table>

Figure 10. Relationship between the large herbivore index (left) and forest management intensity (right), versus average damage levels of aspen, rowan, sallow, and Scots pine, among the 10 study areas in the European boreal biome.

The PCA axis 1 and 2 explained 74% of the variation in the dataset. The number of herbivore species, large herbivore index, damage of the four focal tree species, and forest management intensity index were all related to negative values of PC1. On the other hand, the number of large carnivore species, field, and tree layer food were related to positive values of PC1 (Figure 11). Note, however, field layer food was not correlated to any other variable (Table 5). Field layer food and number of large carnivore species were related to the negative values of PC2. Thus PC1 can be viewed as herbivore/young tree
damage versus young tree browse gradient, while PC2 can be viewed as a carnivore gradient.

The 10 study areas were grouped depending on similarity with regard to the variables in the PCA, with Novogrudok, Ostrovs, Vestfold and possibly Asa being one group, Østerdalen and Bergslagen another group and Komi, Ilomantsi and Pskov being a third group. Smiltene displayed intermediate values of most variables, and thus did not belong to any particular group.

*Figure 11. PCA of the 10 boreal landscapes (for abbreviations, see Table 1), and the means for each landscape of the respective main variables of this study: forest management intensity (Formanint), number of herbivore species (Herb sp), number of carnivore species (Carn sp), large herbivore index (LH index), field layer food (Field food), tree layer food (Tree food), as well as mean damage for the focal tree species aspen, rowan, sallow and pine.*
4 Discussion

4.1 Predators, prey and anthropogenic wet meadows (Paper I)

The predictions that the abundance of avian predators and predation rates should be higher in rapidly declining vs. relatively stable wader populations were supported (Paper I). The results thus indicate that the predation of wader eggs is a factor that contributes to explaining differences in population trends among waders. Firstly, the rapid assessment of wet meadows testing the relative abundance of avian predators and waders was three times higher in Kristianstad compared to Östergötland. Secondly, field observations showed that corvids, and to a slight extent birds of prey, were higher in the wet meadows and urban areas of Kristianstad compared to the Östergötland. Thirdly, the predation rates on artificial nests were much higher in Kristianstad compared to Östergötland. Therefore, 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 wader birds.

4.2 Predators, prey and boreal forests (Paper II)

The first prediction exploring the hypothesis that altered proportions of large carnivores and herbivores is correlated to reduced recruitment of deciduous tree species and Scots pine reaching maturity was supported. Thus, the macro-ecological design of the study showed a negative relationship between the number of large carnivore and herbivore species as this relationship formed a clear SW to NE European gradient. In general, higher levels of tree damages, more available tree layer browse, and a decreasing large herbivore index was evident in this gradient. However, the western-most study landscape, Vestfold in Norway, deviated from this general pattern. A likely reason for this deviation is that the region has had a long history of high browsing pressure by moose resulting in dramatic management actions to reduce the moose
population (Solberg et al., 2006). Thus, the results suggest the Vestfold landscape is similar to the landscapes found further east such as Ostrovets or Novogrudok in Belarus. This argumentation is supported by both the observed clear overall relationship between mean browsing damage levels on the four tree species, and the large herbivore index. The second prediction that forest management intensity is correlated to browsing damage on the recruitment of deciduous tree species was not supported.

4.3 Trophic interaction in space and time

As shown in this thesis, understanding and managing the trophic interactions and associated cascading effects on the functionality of green infrastructures for biodiversity conservation is of the utmost importance. Both papers I & II show that trophic interaction’s among predators, prey and different land covers need to be taken into account in both the governance and management of green infrastructures.

Using multiple landscapes spanning across regions and countries with unique past and current situations, such as this thesis, provides a broader perspective on what needs to be taken into account to maintain functional green infrastructures through governance and management of habitat in its complete and broad sense. Paper I shows that predator-prey relationships can result in undesirable outcomes for breeding wader populations on the anthropogenic wet meadows and that management decisions may impact conservation efforts.

The decision to conserve both avian predators (birds of prey) and their prey (waders) may lead to a mixture of human-human, human-wildlife and wildlife-wildlife induced conflicts (Graham et al., 2005), as paper I identifies. These decisions can have a chain reaction effect throughout society and ecosystems and thus may actually end up placing more pressure on the focal species and natural disturbance regimes. This appears to be the case in Kristianstad.

The macro-ecological approach of paper II indicates that homogenous natural resources policy and management regimes within individual countries in northern Europe has led to small differences in landscape characteristics and tree damage levels within countries. In comparison, the landscape characteristics and trophic interactions among different countries within the European boreal biome differ immensely based on their past and present land use histories (Danilov, 1987; Nygrén, 1987). However, it should be noted that also special management strategies at a local level within a country may cause variations as illustrated by the study in paper I and the two Norwegian landscapes in paper II. Such disturbances and changes to trophic interactions
do pose multiple threats to ecosystem services benefiting human well-being, as well as green infrastructure as habitats for species (Treves et al., 2006; Treves & Karanth, 2003). Therefore, it is critical that studies such as this further investigate all levels of trophic interactions of predator, prey and vegetation, including both spatial and temporal scales. Thus there is a need to focus on the governance and management of entire ecosystems at appropriate scales.

Predator-prey relationships are an important feature of the European landscape, and can be viewed as a competition over space where predators try to maximise their spatial overlap with prey, and prey try to avoid the spatial overlap with predators (Sih, 2005). This thesis indicates that the trophic interactions among species (e.g., avian predators and waders, as well as large carnivores and herbivores and vegetation) need to be considered when managing for functional green infrastructures.

The hotly contested large carnivore debate in Scandinavia (e.g., Sjölander-Lindqvist, 2007) is a perfect example where direct and indirect disturbances have to a certain extent occurred, as highlighted in paper II of this thesis. As human policy has shaped the historic and current distribution and abundance of predator and prey, it is critically important to consider the predator prey relationships in context with human development (Muhly et al., 2011). This study supports Strandgaard (1982) and Cederlund and Bergström (1996) notions that reductions of large predators can lead to large increase in the herbivore population, and thus have a cascading effect on both deciduous trees species biodiversity and Scots pine. In addition, other studies have linked increases in herbivores to increases in lower level predator densities (especially corvid birds (cf. Tomialojc, 1990)) thus increasing the predation pressure on other smaller species at the landscape scale (Storaas, 1988). Paper II also support the assumption of Angelstam (1997) that a release of large herbivores through a lack of large carnivores may yield profoundly elevated browsing pressure. Therefore, it is important to consider how the outcomes of human decision making processes impact the interactions between predators, prey and competition. Thus, the governance and management of predators, prey and landscapes need be integrated with the maintenance of functional green infrastructures for biodiversity, and human well-being.

4.4 Green infrastructures in space and time

Green infrastructures are dynamic and do change in both time and space. This thesis shows that landscape history, governance and management can change ecosystems, and as a response alter trophic interactions and processes. While paper II suggests that forest management intensity does not correlate to the
browsing damage on recruitment of ecologically important deciduous trees, and the economically important Scots pine, it is important to consider the effects that land use intensification places on ecosystems. Europe’s various land use histories have shaped both anthropogenic and semi-natural green infrastructures (Angelstam, 1997). For instance, southern Sweden has long been considered a cultural landscape with small scale agriculture first introduced around 4000-5000 BP (Berglund, 1991). More recently the changes from tradition low production farming and forestry for survival to intensive farming and forestry for economic growth has seen further rapid complex alterations to green infrastructures and important ecosystem processes. As a result important wet meadow systems, such as Kristianstad, have undergone rapid change resulting in the loss of species and important ecosystem processes. Although wet meadows are anthropogenic landscapes, these land use changes have altered the once stable landscape that was maintained manually by people for agricultural purposes and thus created favourable habitats for many ground nesting birds such as waders. In comparison vast expanses of the boreal forest zone in Russia have only been exploited within the last two centuries (Naumov, 2014). Thus changes in land cover disturbance regimes may often affect species occurrence, abundance and the composition and structure of habitats, thus modifying the landscape mosaic in both time and space (Angelstam & Kuuluvainen, 2004).

4.5 Diagnosis of ecosystem as a base for learning

Functional green infrastructures provide a multitude of goods, services and values that benefit both biodiversity and human well-being (Norgaard, 2010). Anthropogenic wet meadows and natural forests are two green infrastructures along with many others that are facing the continued pressure of human development. A macro-ecological approach is a suitable tool to enhance learning about trophic interactions and their cascading effects. Combined with human sciences, comparative studies of different governance arrangements (e.g., Elbakidze et al., 2010) could further aid the restoration, maintenance and development of green infrastructures for future generations.

For instance, within the last decade changes in societal awareness and the need to secure different green infrastructure has come to the fro resulting in new policy and modified management regimes (e.g., European Commission, 2013). To support implementation of such policies aiming at sustainable landscapes on the ground, Biosphere Reserve, Ecomuseum, Model Forest and other concepts have been developed as tools to support collaborative learning towards tangible results (Elbakidze et al., 2013; Axelsson et al., 2011). Forest
management in Sweden is no exception with the Swedish State Forest Company Sveaskog establishing a network of Ecoparks to preserve and restore natural landscapes, including mixed aged deciduous forests, and creating public recreation and educational areas. These approaches and concepts can be interpreted as integrating green infrastructure for both biodiversity and human health.
5 Conclusions

To conclude, in addition to understanding the role of land cover patches’ size, quality, juxtaposition and matrix, trophic interaction are crucial to consider when addressing the maintenance of green infrastructures. Furthermore, it is important to understand the outcome of policies, governance and management decisions and their impacts on the trophic interactions of species at multiple scales. Using multiple landscapes as case studies that represent viable, declining and exterminated focal species populations is a valid approach to produce knowledge and encourage learning about what functional green infrastructures require. Additionally, different approaches to landscape governance need to be examined to understand if and how species populations can be managed and sustained in the long term. Finally, the combination of both local and regional studies to research predator-prey relationships and their effects may help to portray and easily disseminate digestible information to stakeholders and actors working with green infrastructures.
References


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Acknowledgements

Financial support for this thesis has been provided by the project “Green infrastructures” funded by FORMAS. I would also like to recognise the partnership agreement between the SLU’s School for Forest Management and Aleksandras Stulginskis University in Lithuania for facilitating my education.

Special thanks to my supervisor Per Anglestam for your passion, inspiration, ideas, wealth of knowledge and good friendship. A big thank you to Gediminas Brazaitis for providing the Lithuanian support, supervision, demanding conversations and the ground work to host me in Lithuania. Gratitude to Robert Axelsson and his family for helping me find my feet at the start of my Licentiate and all their great advice. I would also like to the entire Forest-Landscape-Society Research Network, including Marine Elbakidze, Pablo Garrido, Vladimir Naumov and Mikel Angelstam for many deep discussions and your support. Especially I would like to acknowledge the late Kjell Andersson, for his help, passion, knowledge and contribution to GIS and the team over the years. Others that have contributed and helped me over the short journey are Torgny Söderman for your patience, Annette Byrén for all your admin help, and all the many people who have contributed along the way. Finally I would like to deeply thank my family for their encouragement and support.