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# TROPHIC CASCADES IN BOREAL LANDSCAPES: TOP PREDATOR PROTECTION ON TREE SEEDLINGS AND FOREST GROUSE

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## ABSTRACT

Changes in the abundance of top predators have brought about notable, cascading effects in ecosystems around the world. In this thesis, I examined several potential trophic cascades in boreal ecosystems, and their separate interspecific interactions. The main aim of the thesis was to investigate whether predators in the boreal forests have direct or indirect cascading effects on the lower trophic levels.

First, I compared the browsing effects of different mammalian herbivores by excluding varying combinations of voles, hares and cervids from accessing the seedlings of silver birch (*Betula pendula*), Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). Additionally, I studied the effect of simulated predation risk on vole browsing by using auditory cues of owls. Moving upwards on the trophic levels, I examined the intraguild interactions between the golden eagle (*Aquila chrysaetos*), and its mesopredator prey, the red fox (*Vulpes vulpes*) and the pine marten (*Martes martes*). To look at an entire potential trophic cascade, I further studied the combined impacts of eagles and mesopredators on the black grouse (*Tetrao tetrix*) and the hazel grouse (*Tetrastes bonasia*), predicting that the shared forest grouse prey would benefit from eagle presence.

From the tree species studied, birch appears to be the most palatable one for the mammalian herbivores. I observed growth reductions in the presences of cervids and low survival associated with hares and voles, which suggests that they all weaken regeneration in birch stands. Furthermore, the simulated owl predation risk appeared to reduce vole browsing on birches in late summer, although the preferred grass forage is then old and less palatable. Browsing by voles and hares had a negative effect on the condition and survival of Scots pine, but in contrast, the impact of mammalian herbivores on spruce was found to be small, at least when more preferred food is available.

I observed that the presence of golden eagles had a negative effect on the abundance of adult black grouse but a positive, protective effect on the proportion of juveniles in both black grouse and hazel grouse. Yet, this positive effect was not dependent on the abundance of foxes or martens, nor did eagles seem to effectively decrease the abundance of these mesopredators. Conversely, the protection effect on grouse could arise from fear effects and also be mediated by other mesopredators.

The results of this thesis provide important new information about trophic interactions in the boreal food webs. They highlight how different groups of mammalian herbivores vary in their effects on the growth and condition of different tree seedlings. Lowered cervid abundances could improve birch regeneration, which indirectly supports the idea that the key predators of cervids could cause cascading effects also in Fennoscandian forests. Owls seem to reduce vole browsing through an intimidation effect, which is a novel result of the cascading effects of owl vocalisation and could even have applications for protecting birch seedlings. In the third cascade examined in this thesis, I found the golden eagle to have a protective effect on the reproducing forest grouse, but it remains unclear through which smaller predators this effect is mediated. Overall, the results of this thesis further support the idea that there are cascading effects in the forests of Northern Europe, and that they are triggered by both direct and non-lethal effects of predation.

## TIIVISTELMÄ

Muutokset suurpetojen runsaudessa ovat aiheuttaneet huomattavia heijastevaikutuksia ekosysteemeissä eri puolilla maailmaa. Tässä väitöskirjassa tarkastelin useita mahdollisia ravintoverkkojen sisäisiä kaskadivaikutuksia sekä lajienvälisiä vuorovaikutussuhteita pohjoisella havumetsävyöhykkeellä. Työni päätavoitteena oli tutkia, onko pohjoisten havumetsien pedoilla suoraa tai epäsuoraa heijastevaikutuksia ravintoverkon alemmille trofiatasoille.

Ensiksi vertasin aitauskokeissa eri nisäkäs-kasvinsyöjien laidunnusvaikutuksia puiden taimiin siten, että estin myyrien, jänisten tai hirvieläinten pääsyn syömään rauduskoivuja (*Betula pendula*), mäntyjä (*Pinus sylvestris*) sekä kuusia (*Picea abies*). Lisäksi tutkin simuloitun saalistusuhkan vaikutusta myyrien laidunnukseen pöllöjen ääntelyä käyttämällä. Seuraavaksi selvitin ylemmillä trofiatasoilla petokillan sisäisiä vuorovaikutussuhteita käyttäen tutkimuslajeina maakotkaa (*Aquila chrysaetos*) sekä tämän saaliiksi toisinaan joutuvia kettua (*Vulpes vulpes*) ja näätä (*Martes martes*). Tutkiakseni kokonaista trofiakaskadia, selvitin lisäksi maakotkan ja mainittujen pienpetojen yhteisvaikutuksia teeren (*Tetrao tetrix*) sekä pyyn (*Tetrastes bonasia*) populaatioihin. Ennusteena oli, että kotkan läsnäolo voisi hyödyttää näitä metsäkanalintuja.

Tutkituista puulajeista koivu vaikutti olevan alttein nisäkäskasvinsyöjien laidunnukselle. Havaitsin, että hirvieläinten läsnä ollessa koivujen kasvunopeus hidastui, kun taas jänikset ja myyrät alensivat näiden taimien selviytymistä. Tämän perusteella kaikki kolme nisäkäsryhmää heikentävät uusiutumista koivutaimikoissa. Lisäksi havaitsin, että simuloitu pöllön saalistusuhka vaikutti vähentävän koivujen laidunnuspainetta loppukesästä, vaikka tuolloin myyrien suosima ruoho on vanhaa ja vähemmän maittavaa. Myyrien ja jänisten laidunnuksella oli haitallinen vaikutus männyntaimien kasvuun ja kuntoon, mutta sen sijaan kuusentaimiin eivät nisäkäskasvinsyöjät juurikaan vaikuttaneet, ainakaan oloissa joissa vaihtoehtoista ravintoa on myös saatavilla.

Havaitsin että maakotkan läsnäolo vähensi teeren runsautta, mutta toisaalta lisäsi poikasten osuutta sekä teeren että pyyn populaatioissa. Tämä maakotkan suotuisa suojeleuvaikutus ei kuitenkaan ollut riippuvainen ketun tai näädän runsaudesta, eikä maakotka vähentänyt näiden pienpetojen lukumääriä. Sen sijaan kanalintuihin ulottuva suojeleuvaikutus voi johtua kotkan aiheuttamasta pelotteesta ja sen välittäjänä voivat toimia myös muut pienpedot.

Tämän väitöskirjan tulokset tarjoavat uutta, tärkeää tietoa pohjoisen havumetsävyöhykkeen ravintoverkoista. Ne korostavat sitä, miten eri nisäkäskasvinsyöjillä voi olla vaihtelevia vaikutuksia eri puulajien kasvuun ja kuntoon. Hirvieläinten vähentyminen voisi parantaa koivikoiden uudistumista, mikä epäsuorasti tukee ajatusta siitä, että hirvieläinten tärkeimmät pedot voisivat runsastuessaan aiheuttaa heijastevaikutuksia myös Fennoskandian metsissä. Pöllöt näyttävät vähentävän myyrien laidunnusta pelotevaikutuksen kautta, mikä on uusi löydös pöllöjen ääntelyn kaskadivaikutuksista, jota voidaan jopa soveltaa koivutaimikoiden suojaamisessa. Tarkastellessani väitöskirjani kolmatta trofiakaskadia havaitsin, että maakotkalla on suojeleuvaikutus metsäkanalintuihin, joskin epäselväksi jää, minkä petolajien kautta tämä vaikutus välittyy. Kaiken kaikkiaan tämän väitöskirjan tulokset antavat lisää tukea ajatukselle, että Pohjois-Euroopan metsissä esiintyy trofiakaskadeja, ja että ne lähtevät liikkeelle sekä petojen suorista saalistusvaikutuksista että epäsuorista pelotevaikutuksista.

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## LIST OF ORIGINAL PUBLICATIONS

This thesis consists of the following publications and manuscripts, which are referred to in the text by their Roman numerals:

- I Lyly M.S., Klemola T., Koivisto E., Huitu O., Oksanen L., Korpimäki E. (2014) Varying impacts of cervid, hare and vole browsing on growth and survival of boreal tree seedlings. *Oecologia* 174(1):271–281.
- II Lyly M.S., Koivisto E., Klemola T., Huitu O., Korpimäki E. Simulated predation risk on voles and varying herbivore densities modify tree seedling condition. *Submitted manuscript*.
- III Lyly M.S., Villers A., Koivisto E., Helle P., Ollila T., Korpimäki E. (2015) Avian top predator and the landscape of fear: responses of mammalian mesopredators to risk imposed by the golden eagle. *Ecology and Evolution* 5(2):503–514.
- IV Lyly M.S., Villers A., Koivisto E., Helle P., Ollila T., Korpimäki E. Guardian or threat: does golden eagle predation risk have cascading effects on forest grouse? *Submitted manuscript*.

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*Vole enclosure in study site NE, Lapua, in August 2010.*

# 1 INTRODUCTION

Ecosystems can be examined by grouping species together based on what they consume and who consumes them. This topological presentation describes how biomass flows in the ecosystem and it is typically referred to as a food web (Elton 1927; Paine 1966). On the lowest trophic level of the food web there are autotrophs, such as plants of the terrestrial ecosystems (producers), which provide the system with the input of biomass. On the next level, the terrestrial biomass is utilized by herbivores (primary consumers) and further on by predators (secondary and tertiary consumers).

Given the diversity of species and the complexity of interactions within ecosystems, food webs are necessarily a simplification of the systems they represent. Still, studying food webs and their individual parts, food chains, gives us valuable information about how species interact with each other and what factors define the structure of ecosystems. For example, interspecific interactions are not always direct and apparent, but rather they can be inconspicuous when mediated by third party species.

## 1.1 Bottom-up and top-down regulation – concurrent forcing

Food webs have traditionally been considered essentially bottom-up controlled, i.e. the higher levels of the webs are controlled by the producers and the productivity of the system. Yet, since the “green world hypothesis” (Hairston, Smith & Slobodkin 1960), the primacy of bottom-up effects and abiotic factors has given way to the important role of top-down effects (e.g. predation), either on their own or concurrently with the bottom-up effects (Oksanen *et al.* 1981; Hunter & Price 1992).

Indeed, recent studies have provided increasing evidence to support the importance of species on the top of the food chains in shaping communities (Crooks & Soulé 1999; Pace *et al.* 1999; Hebblewhite *et al.* 2005; Borrvall & Ebenman 2006; Johnson, Isaac & Fisher 2007; Beschta & Ripple 2009; Terborgh & Estes 2010). Interestingly, the magnitude of top-down effects is not constant but seems to vary distinctly from one ecosystem to another, depending on e.g. productivity of the system (Fretwell 1977; Shurin *et al.* 2002; Elmhagen & Rushton 2007; Ritchie & Johnson 2009). Currently, there is increasing consensus for acknowledging both the bottom-up (physical surroundings, productivity of the system) and the top-down effects (predation, herbivory) when examining the interactions within food webs.

## 1.2 Trophic cascades

The phenomenon, where a predator regulates species on several lower trophic levels, has been named a trophic cascade (Paine 1980; Carpenter, Kitchell & Hodgson 1985). Trophic cascades are essentially top-down effects, as the upper levels of the food web (such as top predators) cause cascading effects on the subsequent trophic levels (e.g. on plants via herbivores) (Polis *et al.* 2000; Terborgh & Estes 2010).

The strength of trophic cascades usually alters if the surrounding ecosystem undergoes changes (Pace *et al.* 1999). One key perturbation has been the loss of top predators from many parts of the world (Myers & Worm 2003; Ripple *et al.* 2014), which has caused extensive effects in ecosystems and revealed trophic cascades through altered ecosystem states (Terborgh & Estes 2010; Estes *et al.* 2011; Ripple & Beschta 2012a; Ritchie *et al.* 2012). For example, the strong decline of top predators has in many cases caused a rapid increase in the numbers of smaller predators, often called mesopredators (Soulé *et al.* 1988; Courchamp, Langlais & Sugihara 1999; Prugh *et al.* 2009), and also induced secondary extinctions (Borrvall & Ebenman 2006). Furthermore, these changes can alter the dynamics of entire ecosystems and lead to trophic downgrading, e.g. through reduced diversity or increased invadability by alien species (Estes *et al.* 2011).

Earlier, the main focus of trophic cascade studies has been in aquatic and marine ecosystems and in invertebrate interactions (Pace *et al.* 1999; Borer *et al.* 2005). More recently, notable observational data has been gathered also from terrestrial ecosystems, but there still has remained a debate on whether terrestrial cascades are potent or not (Strong 1992; Polis *et al.* 2000; Schmitz, Hambäck & Beckerman 2000; Halaj & Wise 2001; Borer *et al.* 2005). Ideally, trophic cascades can be examined as a whole to understand their functioning. However, in many cases studying adjacent trophic levels separately is far more feasible. With large-scale experimental testing of terrestrial ecosystems, a more holistic view of their trophic cascades could be formed. Particularly, there is need for more long-term food web studies regarding the changes in predator communities to examine both the transition phases and the resulting new states of ecosystems (Ritchie *et al.* 2012).

## 1.3 Effects of herbivory on plants

Large-sized herbivores have typically been considered the most relevant group to affect the biomass and diversity in plant communities. Studies from the boreal and temperate forests of the northern hemisphere have clearly demonstrated how ungulates, unchecked by the absent top predators, can have a strong impact on ecosystems by browsing selectively in young forest stands and affecting tree recruitment rates (Edenius



*et al.* 2002; Côté *et al.* 2004; Beschta & Ripple 2009; Kuijper *et al.* 2010). On the other hand, also smaller herbivores can impact the terrestrial ecosystems. What they lack in consumption rates per individual, they make up in rapid reproduction and large population sizes. For example, small-sized voles are considered keystone herbivores in many systems. In North American grasslands, voles exhaust their preferred forage and form plant communities of unpalatable herbs (Howe *et al.* 2006). In the boreal regions, voles can cause notable damage on tree seedlings during the peak phase of their population fluctuations (Hanski *et al.* 2001; Korpimäki *et al.* 2005; Huitu *et al.* 2009), and in North Europe, *Microtus* and *Myodes* voles together with *Lepus* hares are the most important smaller-sized mammalian herbivores (Gill 1992b; Hjältén, Danell & Ericson 2004; Vehviläinen & Koricheva 2006). Although the browsing effects of different-sized mammalian herbivores have been widely studied (e.g., Gill 1992a; b; c), they have still rarely been examined simultaneously.

## 1.4 Predation

### 1.4.1 Direct and non-lethal effects of predation

Predators are typically thought to affect their prey directly through killing that obviously reduces the numbers of the prey. Yet, predators may in fact cause even stronger effects indirectly than through direct consumption (Preisser, Bolnick & Benard 2005; reviewed in Cresswell 2008). A predator can form a “landscape of fear”, in which its prey experience differing levels of predation risk (Laundré, Hernández & Altendorf 2001; Ritchie & Johnson 2009; Swanson *et al.* 2014). The prey use multiple cues, often simultaneously, to observe predators and to assess the level of predation risk (Caro 2005), such as in the case of predator-naïve ungulates observing the olfactory and auditory cues of reintroduced predators (Berger, Swenson & Persson 2001; Chamaillé-Jammes *et al.* 2014). A perceived predation risk usually induces behavioural anti-predator strategies in the prey, as well as a physiological stress response, as they try to reduce the risk of being killed (Lima 1998; Werner & Peacor 2003; Caro 2005).

The combined costs of stress and altered behaviour, i.e. non-lethal effects, may lead to a reduction in prey fecundity or survival (Caro 2005; Preisser, Bolnick & Benard 2005; Zanette *et al.* 2011). For example, the non-lethal predation effects can reduce foraging behaviour of the prey (Brown & Kotler 2004; Verdolin 2006), lower the quantity and quality of offspring produced (Creel *et al.* 2007; Sheriff, Krebs & Boonstra 2009) and induce habitat shifts (Creel *et al.* 2005). This is the case also for those species that are only occasionally killed by the predator. For mesopredators, the risk-sensitive habitat selection in the presence of a top predator can reduce their breeding success and survival (Mitchell & Banks 2005; Sergio & Hiraldo 2008; Mukherjee, Zelcer & Kotler

2009). Importantly, the non-lethal effects can further reflect on the food species of the prey, e.g. via reducing the browsing pressure of herbivores (Schmitz, Krivan & Ovadia 2004; Preisser, Bolnick & Benard 2005).

### **1.4.2 Intraguild predation and mesopredator release**

One pathway for top-down effects is intraguild predation (IGP), where predators of the same ecosystem compete over shared prey but also prey on each other (Polis, Myers & Holt 1989; reviewed in Lourenço *et al.* 2014). Typically, the intraguild predator is a larger species that preys on its smaller competitor, the intraguild prey (Palomares & Caro 1999; Sergio & Hiraldo 2008). IGP is relatively common in ecosystems (Arim & Marquet 2004), and its effects are likely to cascade on lower trophic levels due to changes in the predation pressure experienced by the shared prey (Preisser & Bolnick 2008), although it is possible that IGP also dampens trophic cascades (Finke & Denno 2005). For example, in Europe the lynx (*Lynx lynx*) reduces the abundance of a competing mesopredator, the red fox (*Vulpes vulpes*) (Pasanen-Mortensen, Pyykönen & Elmhagen 2013). Moreover, studies in Finland have shown that this is further reflected on their shared prey, the mountain hare (*Lepus timidus*), by increase in abundance (Elmhagen *et al.* 2010).

If top predator populations decline (or their hunting behaviour is less effective), the populations of their intraguild prey, the mesopredators, will benefit from the lowered predation risk and the reduced competition, as is suggested by the mesopredator release hypothesis (Soulé *et al.* 1988; Crooks & Soulé 1999; Prugh *et al.* 2009). Examples of these effects are ample (reviewed in Ritchie & Johnson 2009). In Australia, the absence of the dingo (*Canis dingo*) has resulted in a mesopredator release of foxes and cats, which in turn has caused devastating cascading effects on the marsupial fauna (Johnson, Isaac & Fisher 2007). In North America, wolves (*Canis lupus*) exert control on coyotes (*Canis latrans*) both via direct predation and indirectly through intimidation and food competition (Berger & Gese 2007; Miller *et al.* 2012), which also cascades further on to red foxes that benefit from reduced coyote numbers (Newsome & Ripple 2015). When top predators are reintroduced to their former ecosystems, they may regain control over mesopredator populations. In Germany, a recolonizing avian superpredator, the eagle owl (*Bubo bubo*), suppresses the numbers of two mesopredators, the goshawk (*Accipiter gentilis*) and the common buzzard (*Buteo buteo*) (Chakarov & Krüger 2010).

Studies on terrestrial vertebrate IGP have largely focused on within-class guilds, i.e. interactions between mammals or birds alone (**mammals**: Palomares *et al.* 1995; Courchamp, Langlais & Sugihara 1999; Henke & Bryant 1999; Helldin, Liberg & Glöersen 2006; Elmhagen *et al.* 2010; Letnic *et al.* 2011; **birds**: Hakkarainen and Korpimäki 1996; Fielding *et al.* 2003, Sergio and Hiraldo 2008; Lourenço *et al.* 2011). Nonetheless, diet

studies of large raptors show that mammalian mesopredators succumb to predation by birds, too (Korpimäki & Norrdahl 1989; Sulkava, Tornberg & Koivusaari 1997; Sulkava, Lokki & Koivu 2008; Watson 2010). This brings forth the question of whether large birds of prey can influence the abundance and behaviour of mammalian mesopredators.

Avian predators can provide protection to smaller birds breeding in the vicinity of their nests (Quinn & Ueta 2008), as in the case of forest grouse that seem to optimize the trade-off between predation and protection from nest predators by breeding at intermediate distances from goshawk nests (Mönkkönen *et al.* 2007; Tornberg *et al.* 2015). However, these type of IGP studies rarely gather data on the numerical response of nest predators, and accordingly there are only a few studies conducted to investigate how avian top predators reduce the numbers of mammalian mesopredators (Korpimäki & Norrdahl 1989; Roemer, Donlan & Courchamp 2002; Moehrensclager, List & Macdonald 2007) and alter their behaviour (Salo *et al.* 2008). Therefore, more extensive knowledge from various systems would be important in order to properly assess the role of avian top predators in the ecosystems and also to make more informed conservation decisions.

## 1.5 Aims of the thesis

In the boreal forest ecosystems, the earlier decline and current recovery of several top predators (Linnell *et al.* 2005; Chapron *et al.* 2014; Ripple *et al.* 2014) may have brought about notable, cascading changes. In this thesis, I tested the strength of these terrestrial trophic cascades and the relative importance of individual trophic levels in order to assess the effects the predators can have. My aim was to provide new insight on the functioning of boreal ecosystems. The experimental study designs used in the first two chapters allowed a feasible way to manipulate herbivore browsing on tree seedlings. The two nationwide, observational data sets utilized in the latter two chapters provide unique long-term abundance information of several bird and mammal species, gathered with vast efforts from volunteers.

In chapters I–II, I used two large-scale field experiments (2008–2011) to compare the browsing effect of varying combinations of herbivores (voles, hares and cervids) on tree seedlings common in the boreal region of Eurasia, i.e. silver birch (*Betula pendula*), Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). Effects of different herbivore groups on seedlings of these economically important trees have been examined in many studies. Yet, the joined effects of all these herbivores together have not been tested, although such information would be useful in determining how abundance changes of the said herbivores, and also their predators, may affect structure of forest stands. It could further be used to assess the need for protection measures on seedlings.

Hypothesising that the effects of herbivores are at least partially additive, I predicted that [1] the pooled effects of all the herbivores cause more damage to seedlings than that of any individual herbivore group. I also wanted to find out [2] whether the browsing effects of large-sized cervids are more detrimental than those of smaller herbivores. Further, I asked [3] whether the threat of a predator affects the foraging of voles and cascades onto seedlings, and [4] whether the browsing effect of an enclosed, predation-free vole population differs from that of a natural vole and hare population. These questions were examined separately on each tree species used in the studies.

Assemblages of herbivores were spatially manipulated using exclosures (I), which enabled to compare the relative importance of the three herbivore groups studied. Additionally, the exclusion of cervids was considered to simulate the presence of large carnivores. In chapter II, the browsing effect of an enclosed, predation-free vole population was compared with that of a natural herbivore community consisting of voles and hares, taking into account also the varying density of the vole populations. Furthermore, the enclosed vole population was subjected to a playback experiment (II) to test whether a simulated intimidation by avian predators, namely hooting owls, causes cascading effects on tree seedlings. The impacts of the herbivore browsing were studied by measuring the growth, damage and survival of the planted seedlings.

In the latter two chapters, I examined the intraguild interactions between an avian top predator and its mesopredator prey (III), and also the possible cascading effects on their shared herbivore prey (IV), using country-wide observational data from 1989–2011. The golden eagle (*Aquila chrysaetos*) preys relatively often on mesopredators, such as the red fox and the pine marten (*Martes martes*) (Sulkava *et al.* 1999; Valkama *et al.* 2005; Watson 2010; Lourenço *et al.* 2011). Based on this information, I hypothesized in chapter III that [5] eagles can reduce the abundances of these mesopredators by direct predation and/or indirectly through perceived predation risk. In chapter IV, I studied [6] whether this could benefit the shared herbivore prey, forest grouse.

The study system included the black grouse (*Tetrao tetrix*), the hazel grouse (*Tetrastes bonasia*), the red fox and the pine marten, whose abundances were acquired from a national wildlife census scheme. In addition, I used the nesting data of the golden eagle to calculate proxies of its predation risk. In the IGP chapter (III), the effect of predation risk by golden eagle on the winter abundances of red fox and pine marten was examined. In the mesopredator suppression chapter (IV), the joint impact of the eagle and mesopredators on the summer abundance and reproductive success of black and hazel grouse were examined, with the supposition that the IGP risk imposed by eagle on mesopredators could reduce the overall predation pressure on grouse.

## 2 METHODS

### 2.1 Study species

#### 2.1.1 Seedlings and their herbivores

Scots pine, Norway spruce and silver birch are the three most common tree species in Finnish forests. They are both ecologically and economically very important, as they form 85 % of the wood volume in Finnish forests (Peltola 2014). Therefore, it is noteworthy that in the early stages of their growth these species suffer from browsing by various herbivore species (Huitu *et al.* 2009). Many herbivores damage the bark of the seedlings, which lowers the viability of the seedlings and may also expose them to pathogens (Roll-Hansen & Roll-Hansen 1980; Uotila & Kankaanhuhta 2003). In addition, browsing on the tops of young seedlings can significantly lower the value of the full-grown stands as timber.

The group of wood-browsing mammalian herbivores in Finland entails both small and large species. The largest herbivore in the Finnish forest stands is the moose (*Alces alces*), and this common herbivore typically browses on young pines and deciduous trees, sometimes breaking the stem to access the main shoots (Jalkanen 2001; Poteri 2008). The Finnish population of moose is regulated by high annual hunting quotas (Luoma, Ranta & Kaitala 2001), while smaller cervids, the roe deer (*Capreolus capreolus*) and the introduced white-tailed deer (*Odocoileus virginianus*), are only moderately culled despite their growth in numbers (Nylander 2012). Roe deer and white-tailed deer damage young trees with preference to pines and spruce, but they may also damage birches (Gill 1992a; Heikkilä & Härkönen 1996; Bergman, Iason & Hester 2005; Poteri 2008), mainly in Southern and Central Finland where their populations are most numerous (Poteri 2008; Bjärvall & Ullström 2011). Cervid-induced damage on conifers occurs mostly during autumn and winter whereas deciduous seedlings are typically browsed upon in summer as well (Gill 1992a; Uotila & Kankaanhuhta 2003; Poteri 2008).

There are two hare species of the genus *Lepus* in Finland, the mountain hare and the European hare (*L. europaeus*). Mountain hare is a forest species found in the whole country, while European hare is encountered only in southern and central parts of Finland (Bjärvall & Ullström 2011). Both of these species typically feed on the bark and branches of pine and deciduous seedlings, occasionally also cutting the main stem (Gill 1992b; Hjältén, Danell & Ericson 2004; Poteri 2008). In particular they cause damage in cultivated birch stands, typically from early spring to summer (Poteri 2008). The

population of the European hare has been increasing in Finland, while the numbers of mountain hares have decreased, likely due to environmental changes and competition with European hares (Kauhala & Helle 2007; Wikman 2010; Nylander 2012) and possibly also by a spreading viral disease (Syrjälä, Nylund & Heinikainen 2005).

Voles are periodically the most severe pest to young forest stands (Huitu *et al.* 2009). Two species in particular, the field vole (*Microtus agrestis*) and the bank vole (*Myodes glareolus*) are very harmful. Field voles can damage both coniferous and deciduous stands in winter by girdling seedlings under the snow cover, and also damage birch seedlings in summer (Gill 1992b; Uotila & Kankaanhuhta 2003; Poteri 2008). In comparison, bank voles typically feed on the buds of coniferous seedlings or the bark of pine and birch, which results in patchy defects in timber quality (Gill 1992b; Uotila & Kankaanhuhta 2003). In Finland, vole populations exhibit 3-year cyclic fluctuations in abundance, which are synchronous in wide regions (Hanski *et al.* 2001; Korpimäki *et al.* 2005). Voles cause damage to tree seedlings mainly during winters following the increase phase of the vole cycle, when their numbers are high and food availability is low (Norrdahl *et al.* 2002; Huitu *et al.* 2009).

### **2.1.2 Forest grouse and their predators**

Two of the most common forest grouse species in Finland are the black grouse and the hazel grouse, which occur in the whole country excluding the most northern parts beyond the spruce tree line (Valkama, Vepsäläinen & Lehtikoinen 2011). Although their distribution has remained largely unchanged, the population densities of black and hazel grouse, as well as capercaillie (*Tetrao urogallus*) and willow grouse (*Lagopus lagopus*) have declined since 1960's (Valkama, Vepsäläinen & Lehtikoinen 2011). Regarding their habitat use, black grouse is a species of young-to-mid aged forests and open areas such as peatland bogs, which are utilized in particular during lekking (Swenson & Angelstam 1993; Jansson *et al.* 2004). Hazel grouse prefer good coverage of tree tops, thus residing most often in thickets of young deciduous trees and in old-growth spruce forests (Åberg, Swenson & Angelstam 2003).

Forest grouse face a multitude of predators, some of which prey only on nests and fledged juveniles while others are able to capture also adults. Two relatively common mammalian predators of forest grouse are red fox and pine marten. The latter occur mainly in old forests, whereas the former use a wider selection of different habitats, such as fragmented landscapes of young forests and farmlands (Kurki *et al.* 1998; Brainerd & Rolstad 2002; Pereboom *et al.* 2008; Holmala & Kauhala 2009). Both species are found in the whole country, excluding the treeless tundra where marten is absent and fox found only occasionally (Bjärvall & Ullström 2011).

Red foxes weigh typically 5–10 kg, and their main prey are small rodents and hares, especially *Microtus* voles, but they also prey on ground nesting birds, their eggs and chicks, and will utilize carrions if they come across any (Kauhala, Laukkanen & von Rége 1998; Dell'Arte *et al.* 2007). Although the number of foxes in Finland increased during the 20<sup>th</sup> century, from 1990 onwards (study period in chapters III–IV), there has been some decrease in the population.

During the same time period, the abundance of pine martens in Finland has stayed quite stable. The diet of the pine marten consists of rodents, hares and squirrels, and is complemented by birds (e.g. grouse), but there seems to be strong variation within and between years due to the availability of prey (Storch, Lindström & de Jounge 1990; Pulliainen & Ollinmäki 1996). Like foxes, also martens are able to forage on carrions of e.g. moose and reindeer. Pine martens weigh 0.5–1.9 kg, which is considerably less than red foxes and thus renders them susceptible to intraguild predation by foxes (Lindström *et al.* 1995) and may also force them to reduce foraging at the cost of increased vigilance (Wikenros, Ståhlberg & Sand 2014).

In addition to mammalian predators, grouse are also preyed upon by avian predators, such as the goshawk (Tornberg 2001). Another important avian predator of grouse is the golden eagle, which is the second largest avian predator in Finland after the white-tailed sea eagle (*Haliaeetus albicilla*). The golden eagle can prey on a wide range of species from small birds and rodents even to ungulates as large as deer. The main prey of this top predator in Fennoscandia include hares (Leporidae), grouse (Tetraonidae and Phasianidae) and squirrels (Sciuridae) (Watson 2010). In contrast to many other raptors, golden eagles have a relatively high percentage (2–20 %) of mammalian predators in their diet (Valkama *et al.* 2005; Watson 2010; Lourenço *et al.* 2011). Consequently, the absence of the golden eagle may have contributed to the increase of mesopredators in many ecosystems during the past decades (Korpimäki & Nordström 2004).

Most of the golden eagle territories are concentrated in northern Finland (regions of Lapland and North Ostrobothnia, see Fig. 3), but there are some breeding pairs also in the more southern regions. Golden eagles were heavily persecuted in Finland from the late 19<sup>th</sup> century to mid-20<sup>th</sup> century, and declined both in numbers and range (Ollila & Koskimies 2006), and a concurrent trend for the same reasons was seen in many other countries too (Whitfield *et al.* 2004; Watson 2010). Since the species was protected by Finnish legislation in 1962 (Ollila & Ilmonen 2009), the number of breeding golden eagles has slowly increased towards the levels preceding active decimation and bounties. In 2015, there were 355 inhabited golden eagle territories in Finland, 182 of them with a breeding pair (Ollila 2015). Yet, the species is still categorised as endangered, and its historical nesting regions in the southern parts of Finland are mostly lacking breeding residents.

## 2.2 Seedling experiments

The seedling experiments (chapters I and II) were conducted with two different experimental set ups during 2008–2011. Chapter I aimed to compare the relative importance of individual herbivore groups, and for this purpose varying combinations of voles, hares and cervids were excluded from accessing and browsing on seedlings of silver birch, Scots pine and Norway spruce. The experiment was conducted in Kauhava, western Finland (63°08'N, 23°03'E), using two sites. The Kauhava airport site has a high fence that prevents cervids from entering the area, whereas the adjacent field site is open to all herbivores. To further manipulate the assemblage of herbivores accessing the seedlings, three types of treatment plots (10×10 metres) were established at both sites. In the airport, these treatments included the following (abbreviations of allowed species group in parenthesis): voles and hares allowed (VH), voles only allowed (V), and no herbivores allowed (N); four replicate plots in each. In the open field site, the treatments were: all herbivores allowed (VHC), hares and cervids allowed (HC), and cervids only allowed (C); five replicate plots in each. This resulted in 27 study plots with five different treatments and a control (VHC), in which the access of herbivores was not manipulated. Any treatment plots, where undesired species had browsed on seedlings, were discarded as unsuccessful, resulting in exclusion of treatment C (see Fig. 1).

The study design allowed to compare the effect of varying herbivore assemblages on the growth and survival of tree seedlings. In summer 2008, seedlings of silver birch, Scots pine and Norway spruce were planted in the study plots (nine per species in each) and were then measured three times per year (May, July, September–October) from autumn 2008 until spring 2011. Measures of height, diameter and number of tops were taken from each live seedling, and additionally dead seedlings were recorded. Some of the seedlings died due to drought and were replaced in autumn 2008 and summer 2009 to maintain the original seedling density. The replanting batch of 2008 was discarded from the analyses to avoid planting season from affecting the results.

My prediction was that the pooled effects of all the three herbivore groups would cause clearly more severe damage to tree seedlings than that of any individual group. I also wanted to find out whether the effects of large-sized cervids, usually considered the most detrimental herbivore group, would be more damaging than the browsing effects caused by the temporally peaking vole populations.

The goal of experiment in chapter II was to examine whether the threat of avian predators, owls, affects the browsing behaviour of voles and cascades further on to tree seedling growth and survival. Additionally, I wanted to compare the browsing effects of a predation free vole population with that of voles and hares under natural predation



and varying vole abundances. For these purposes, the study system in Lapua, western Finland (63°01'N, 22°57'E), consisted of 1 ha enclosures and adjacent 1 ha open fields at three different sites: NE, NW and SW. The enclosures contained introduced field voles and sibling voles (*Microtus levis*), but no other mammalian herbivores or any predators were able to enter. Fields were open to all herbivores, which mainly comprised voles and hares, and to all predators.

A playback experiment with four trials was conducted during 2009–2010 within the enclosures to examine potential cascading effects of a simulated threat by owls. As a predator treatment, vocalisation of Tengmalm's owl (*Aegolius funereus*), short-eared owl (*Asio flammeus*) and long-eared owl (*Asio otus*) was played at night in one site for three weeks. The playback was a 4-hour recording containing 1 h of vocalisation of each species, with two 30-minute pauses in between. These avian predators are common in the study area, and a large portion of their diet consists of voles (Korpimäki & Norrdahl 1991; Korpimäki & Hakkarainen 2012). As a control treatment, vocalisation of sedge warbler (*Acrocephalus schoenobaenus*), thrush nightingale (*Luscinia luscinia*) and corn crake (*Crex crex*) was played at another site, using intervals identical to the owl treatment. These birds are typical to the study region and exhibit a loud nocturnal vocalisation but pose no threat to voles.

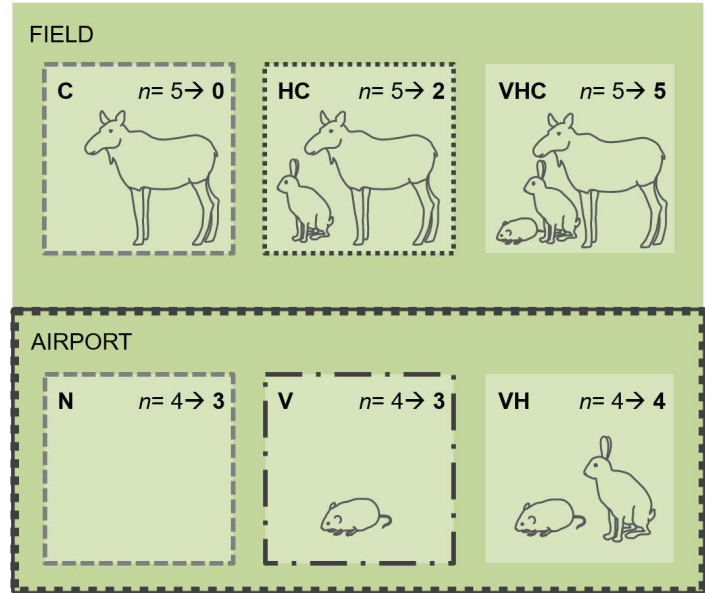
The playback experiment was carried out in the enclosures of sites NE and SW, and repeated twice both in 2009 (August and September) and in 2010 (June–July and July–August). The first trial played the owl treatment in site NE (control in SW) and the second in SW (control in NE); in 2010 the order was reversed (3rd owl in SW, control in NE; 4th owl in NE, control in SW). Height of the seedlings was measured before and after each trial to find out whether the playback had an effect on seedling growth rate. In both years the measurements taken between the two trials were used as the following measurement of the first and preceding measurements of the second trial.

Seedlings of birch, pine and spruce were planted in June 2008 in the enclosures and open fields to compare the effects of different herbivore communities, and to examine the effects of the playback experiment on vole browsing (see Fig. 2). Seedlings were set in an even pattern at a density of approximately 40 seedlings per species per ha (total of 741). Supplementary planting (239 seedlings) was done in July 2009 due to high winter mortality. Seedling growth rate (change in height), damage (observed or not) and survival were measured every spring, summer and autumn. Additionally, measuring was done before and after each playback trial.

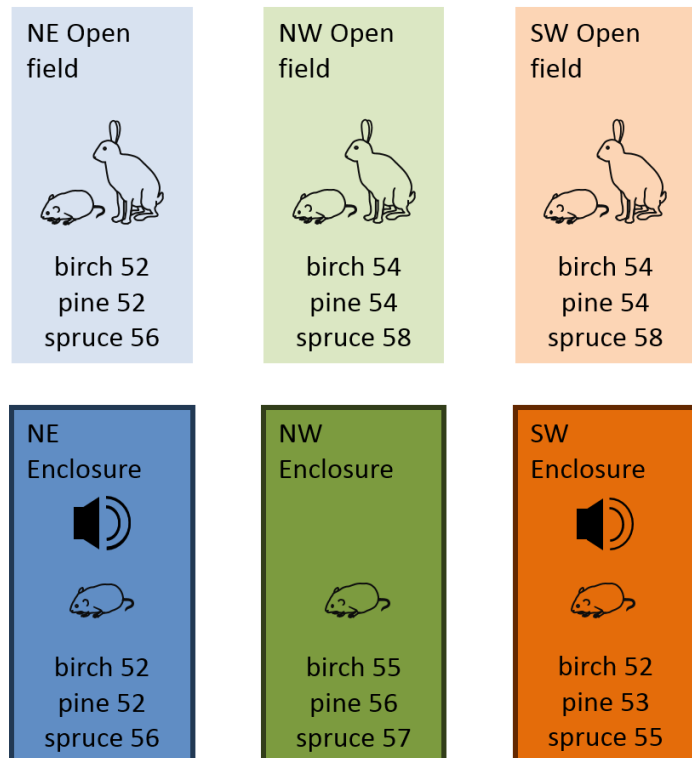
To monitor vole densities, live trappings using standard capture-mark-recapture techniques were carried out in the enclosures and open fields three times per year (spring, summer, autumn), and before and after each playback trial. The *Microtus*

capture-recapture data was transformed to a jackknife density estimate using program CAPTURE (Otis et al. 1978), and then complemented with the number of bank voles captured (which were not marked and thus it was not possible to identify the individuals and reconstruct trapping histories).

**Figure 1.** The study system in chapter I, representing the six different treatments. Letters refer to herbivore groups allowed inside the plot (C=cervid, H=hare, V=vole). Number of plots per treatment ( $n$ ) is given, and the final number after removal of unsuccessful treatments is in bold (note that treatment C was discarded).



**Figure 2.** The study system in chapter II, showing enclosures and open fields at sites NE, NW and SW. Herbivores allowed within the areas are shown with figures, notably open fields were also accessible to any predators. The total number of seedlings planted is given per species. Speaker motif shows enclosures included in the playback experiment in 2009–2010.



## 2.3 Studies on eagle-game interactions

### 2.3.1 Game abundance estimates

The Finnish wildlife triangle scheme is a permanent census system for game species initiated in 1988 (Lindén *et al.* 1996; Pellikka, Rita & Lindén 2005) and coordinated by the Natural Resources Institute Finland. It consists of fixed triangular transect lines (3 × 4 km), established in forested areas and monitored biannually by volunteering hunters. The objective of the census is to monitor as many triangles as possible each winter (typically February) and summer (August). In winter, snow tracks of mammalian species are counted on the transect lines, and additionally sightings of forest grouse species are noted. The length of the snow track accumulation period varies upon conditions, and is therefore also recorded. In summer, the number of visually observed forest grouse is counted from the same transect lines, with distinction between adult and juvenile individuals.

In chapter III, the winter snow track counts of two mesopredator species, red fox and pine marten, from 1989–2011 were used as response variables (17 808 observations). In addition, sightings of capercaillie, black grouse, hazel grouse, and willow grouse were summed together and used as an explanatory prey covariate. Similarly, the track count of mountain hare, corrected by accumulation days, was used as a prey covariate. For pine marten, the abundance of red fox was included as a predator covariate.

In chapter IV, data from both winter and summer censuses from 1989–2011 were used. In a given year, only the triangles that had been observed twice were included in the data (14 774 observations, Fig. 3). The summer abundances (no. of all individuals observed) and reproductive success (no. of juveniles out of all observed) from black and hazel grouse were used as response variables. The snow track indices of fox and marten were set as explanatory mesopredator variables, corrected with the track accumulation time.

### 2.3.2 Golden eagle predation effect

To analyse the impact of golden eagles on the game species in chapters III and IV, locations of all active eagle nests in Finland during 1989–2011 were used (6 569 records from 477 territories and 1 137 individual nests, see Fig. 3). Kernel smoothers (Diggle 1985) were applied on the nest locations to estimate annual territory and fledgling densities in the extent of the whole country. All active territories were used for territory density (TD) maps, while only the successful nests (fledged offspring) were used for fledgling density (FD) maps, weighed by the number of chicks fledged. The maps were

computed at five different radii (smoothing kernel SD 1–5 km) to detect the spatial extent within which the eagle predation might have the strongest effect. In addition, a linear variable of distance to nearest active eagle nest (DNN) from the centres of wildlife triangles (i.e. the observation points for game abundances) was used as an explanatory variable. The value of DNN for each triangle varied annually based on the location of the active territory closest to a given triangle.

The eagle densities were linked with the game abundances of the same year based on the location of wildlife triangles. This way, the TD values reflect the abundance of eagle pairs settled on their territories already during winter (McGrady *et al.* 2002; Watson 2010) while FD values were a proxy of nesting eagle pairs that hunt also for the juveniles. However, in chapter III the response variables of mesopredator abundance were from winter and therefore were connected with FD values from the previous year, as the hunting pressure posed by eagles in late summer and autumn was thought to reflect on the mesopredator abundance the following winter.

### **2.3.3 Habitat data**

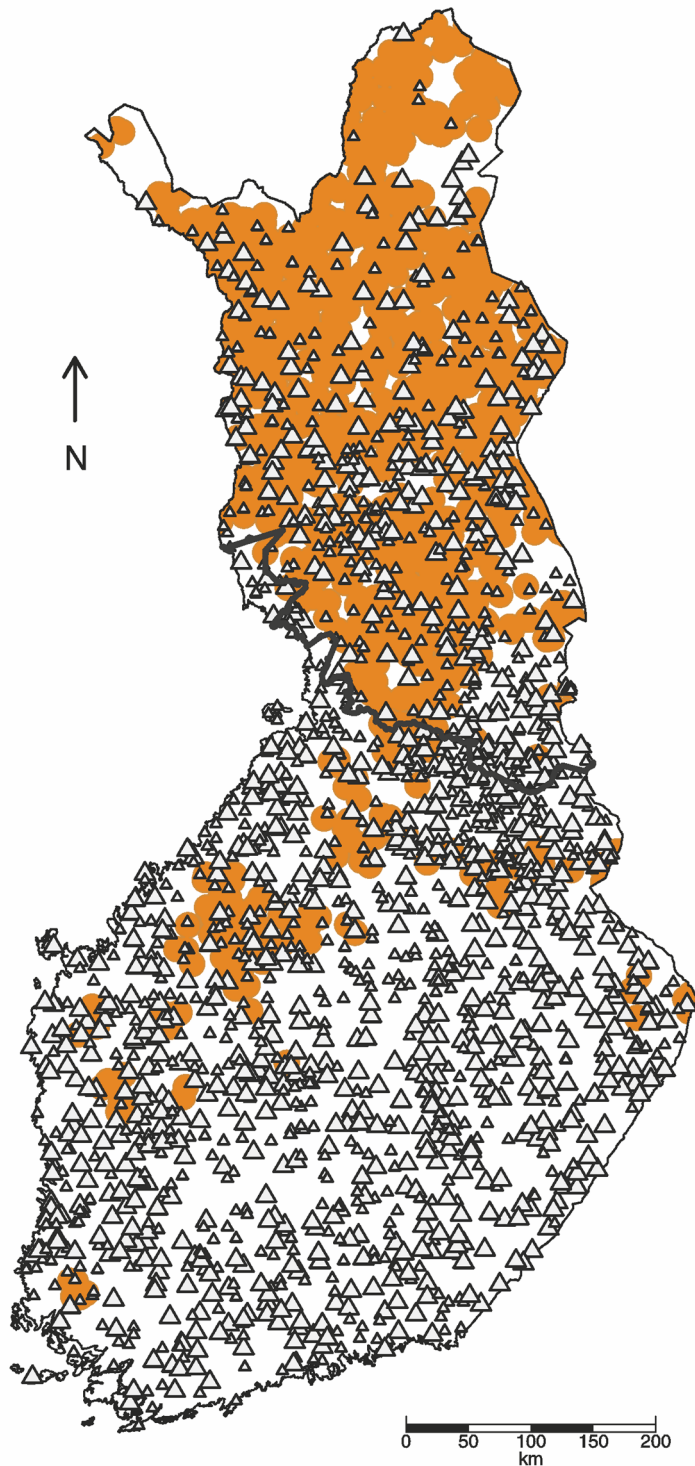
Several habitat variables were included in the analyses of chapters III and IV to account for any large-scale environmental effects on the abundance of mesopredators and grouse, and also the reproductive success of the latter. For this, CORILIS data (based on Landsat imagery 2000, European Environment Agency 2009) was used, giving coverage percentages of habitat classes within a 5 km radius on a 1 km grid. In chapter III, the coverage of farmland and forest, thought relevant for the mesopredators (Kurki *et al.* 1998), were calculated. The general forest habitat group used in chapter III was divided to forests and open areas in chapter IV according to the different habitat preferences of black and hazel grouse. Additionally, classes of farmlands and peatland bogs were used in chapter IV. For each triangle, the percentages of habitat types were extracted based on triangle centre point location.

### **2.3.4 Weather data**

The breeding success and consequently the abundance of grouse populations is affected by weather during spring and early summer, when cold and rainy conditions can notably increase mortality in the juveniles (Ludwig *et al.* 2006). In winter, a sufficient snow cover enables grouse to roost in snow and save energy (Marjakangas, Rintamäki & Hissa 1984). Therefore, weather variables describing spring and winter conditions were accounted for regarding grouse abundance and the proportion of juveniles (IV). Data was provided by the Finnish Meteorological Institute (2014), and variables used were the mean snow cover, mean winter temperature, mean spring temperature and spring

rainfall sum (winter: November–April, spring: May–June). All observations were retrieved for individual triangles from the closest location on the 10×10 km weather data grid.

**Figure 3.** Map of Finland showing the locations of wildlife triangles used in chapter IV (triangle symbol; larger size refers to more observations within the study period 1989–2011). Orange colour depicts golden eagle nesting area, and is presented by plotting active nest sites with a 10 km buffer and a  $\leq 10$  km random offset per coordinate to protect the exact locations of eagle nests. The dark grey line represents the southern border of reindeer husbandry area.



## 3 RESULTS AND DISCUSSION

### 3.1 Effects of herbivores on seedling growth and condition

The herbivore exclusion experiment (I) showed that pooled hare and cervid browsing had harmful effects on the height growth of silver birch seedlings, but there were no obvious growth limitations found in Scots pine and Norway spruce in any of the treatments. As the main group of herbivores causing growth limitations in the study seemed to be cervids, it is possible that this pattern accrued during winters when the smaller coniferous seedlings remained better protected by snow cover than the faster-growing birches.

In the herbivore composition study, damage on pine and spruce was more probable in the presence of both hares and voles (open fields) than in the vole enclosures, almost throughout the three-year study (II). However, possibly due to the overall low probability of damage occurrences, there were no differences in seedling survival rates between herbivore composition treatments (II). Indeed, the overall survival of conifers was high in both seedling studies (I, II), in particular for spruce. This may have resulted from the abundance of more highly preferred food for herbivores, namely grassy herbs and second growth shrubs. The results support earlier studies from other areas showing low palatability of spruce to mammalian herbivores when other food is available (Hjältén, Danell & Ericson 2004), but do not clarify why there are high amounts of damage in spruce-dominated forest stands during vole peaks (Huitu *et al.* 2009). The availability of more preferred herbaceous forage could also explain why I found spruces to survive best at the highest vole densities (II), as there is usually more preferred grass and forb forage available in the increase phase of vole cycle whereas in the decrease phase voles have to resort to woody plants more often (Norrdahl *et al.* 2002; Vehviläinen & Koricheva 2006). Survival of Scots pines (I, II) suggested a minor-to-intermediate susceptibility to browsing by voles and hares. In earlier studies, the palatability of pine has varied greatly, likely depending on the herbivore species studied (Heikkilä & Härkönen 1996; Rao *et al.* 2003; Hjältén, Danell & Ericson 2004).

In contrast to conifers, birch seedling mortality was dramatically higher in the presences of voles and hares (open fields) than within the vole enclosures (II), which stresses the importance of hares as herbivores of deciduous trees. In the exclusion study (I), treatments with small herbivores only (voles, voles+hares) showed highest mortality compared to any other treatment, which would suggest that voles are more harmful to birch seedling survival than cervids. Voles and hares do have a higher tendency to cause lethal damage by girdling and cutting the seedling from stem (Gill 1992b; Baxter &

Hansson 2001). Nonetheless, there may have also been variance in herbivore abundances between the fenced airport and open field site (I) that could explain the high survival when all herbivores were allowed to browse on the seedlings.

### 3.2 Cascading effects of predators on seedlings

Birch seedlings under simulated owl risk showed increased growth rate but only in late summer, while for pine and spruce there was no obvious effect. The nutritional “midsummer crisis” has been documented in field voles when the quality and quantity of their preferred food is decreased after midsummer (Myllymäki 1977). The main food of field voles within study area are grasses (e.g. timothy *Phleum pratense*, Norrdahl *et al.* 2002), and it is possible that voles preferred new grass over birch seedlings in early summer but used birch seedling as alternative food when grass was less palatable. Thus a probable explanation for the results is that simulated owl predation risk prevented voles from actively searching for their optimal forage, grasses, resulting in unchanged, low browsing level on birch seedlings at all times in the owl playback. In contrast, in the control treatment voles were free to use their preferred food, which in early summer was new grasses, while in late summer voles switched to birch seedling as alternative food.

Owl vocalisations can impact the behaviour of passerine birds, e.g. by reducing their dusk chorus activity (Schmidt & Belinsky 2013), but the results of chapter II indirectly suggest that this would be the case also for voles. The importance of predator auditory cues for voles (Eilam *et al.* 1999; Pusenius & Ostfeld 2000) and rodents in general (Schmidt 2006) has been demonstrated previously, but to the best of my knowledge this is the first experimental test of their cascading effects on the growth of rodent food plants. How exactly the behaviour of voles is modified still requires further studies. The results of chapter II suggest that voles are prevented from selecting their preferred forage when under owl threat, and thus reduced mobility (Korpimäki, Koivunen & Hakkarainen 1996; Banks, Norrdahl & Korpimäki 2000) seems a likely explanation, as well as reduction in the overall time that voles spend foraging.

The results of manipulated herbivore assemblages (I) highlighted cervids as the most harmful group for birch growth, although they seem not to be killing the plants but rather browsing on the tops. Yet, such foraging may cause growth defects (Gill 1992a; Heikkilä & Löyttyniemi 1992), which can be costly in forest management due to the reduced value of timber and increased need for replanting. Top predators in many ecosystems have been shown to limit cervid populations (McLaren & Peterson 1994; Boutin 2005; Ripple & Beschta 2012b) and further, cervids have been shown to have extensive browsing effect on seedlings in predator-free areas (Côté *et al.* 2004;

Tremblay *et al.* 2005; Beschta & Ripple 2009). When reintroduced or recovered, these top predators have reinstated limitation on herbivore numbers and thus reduced the browsing pressure (Wolff & van Horn 2003; Dussault *et al.* 2005; Ripple & Beschta 2012a). The results of chapter I indirectly suggest, that similar beneficial effects of top predator presence could be expected in Finnish forests, too, regarding silver birch and perhaps other deciduous trees.

Obviously an increase in top predator numbers can also suppress the numbers of mesopredators, which may then benefit smaller herbivores – even those that are a shared prey for both the top predator and the mesopredator, as in the case of lynx, red fox and mountain hare (Elmhagen *et al.* 2010). Therefore, from the perspective of trees, more top predators does not explicitly mean that the overall browsing pressure is reduced but instead, the relative importance of different herbivore groups may change.

### **3.3 Predation impact of eagle on mesopredators and cascading effects on grouse**

The results of chapter III show, contrary to the initial hypothesis, that the abundance of pine marten and red fox to increase when moving to areas of high eagle territory density and areas close to active eagle nests. This could result from both the avian top predator and the mammalian mesopredators benefitting from the availability of shared prey, which would be expected especially for foxes (Kauhala, Laukkanen & von Rége 1998; Sulkava *et al.* 1999; Dell'Arte *et al.* 2007). The availability of hare and grouse was accounted for in the analyses, but there are other shared prey, like rodents, and availability of carrions that could enable the two species to thrive within same areas.

Also overlapping habitat preferences of martens and eagles may explain the results opposing my initial prediction. Pine martens reside in old, coniferous forests (Brainerd & Rolstad 2002), which overlap with the nesting habitats of golden eagles. Nevertheless, preferences in habitat use can be quite detailed and consequently, they were perhaps not optimally detected from the robust habitat variables (1 km raster size; temporally restricted to one year only). Furthermore, there is partial separation in the habitat use too, as martens actively avoid open areas (Brainerd & Rolstad 2002; Pereboom *et al.* 2008) while large, long-winged eagles mainly use these habitats for hunting (Watson 2010). Actually, this could even be a causal connection if martens actively avoid open areas in fear of the eagle (Korpimäki & Nordström 2004). Interestingly though, the results gave some indication that eagles could be harmful for pine martens at very high territory densities. Due to the low number of triangles located at very high eagle territory density, this cannot be stated for certain without further research.

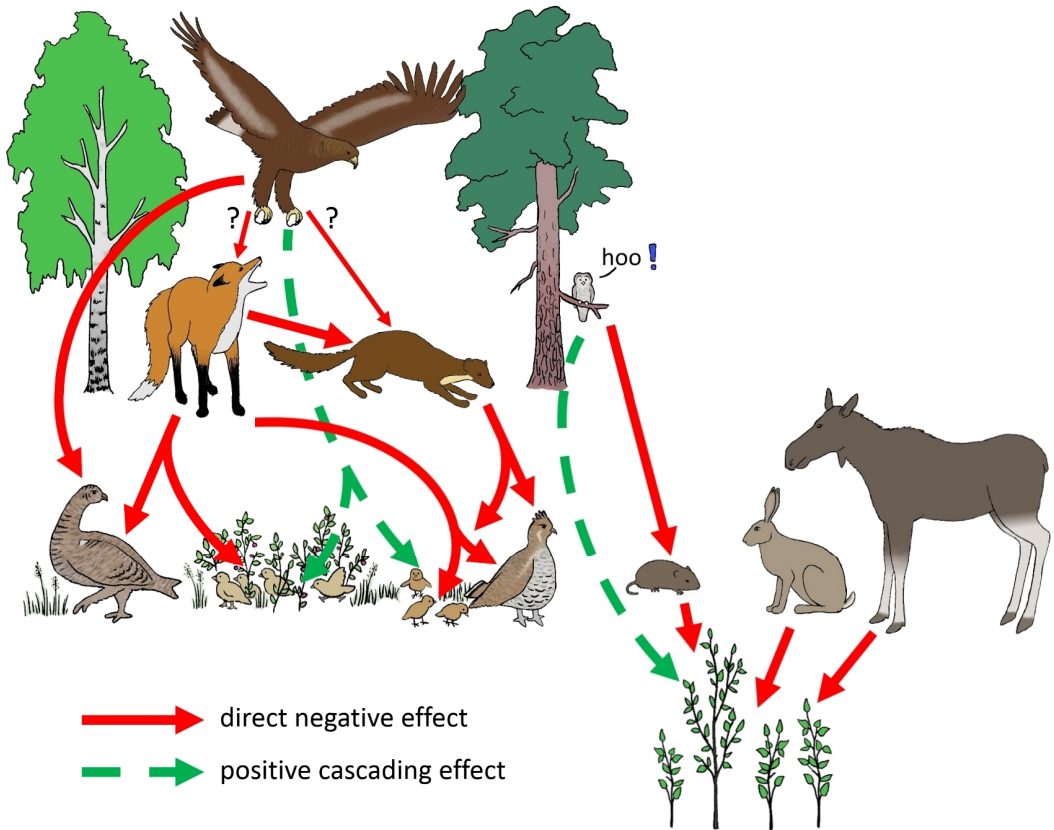


In chapter III, I also examined the interaction between foxes and martens, and found that at high abundance of foxes the abundance of martens was decreased. This can be interpreted to further support the idea of IGP (Lindström *et al.* 1995) and food competition between the larger fox and the smaller marten, although earlier studies from Finland have found no clear negative effect from foxes on martens (Kurki *et al.* 1998). In addition, this result too may have been influenced by habitat preferences. Foxes use more varied types of habitats, in particular the fragmented, human-influenced landscapes (Kurki *et al.* 1998; Brainerd & Rolstad 2002; Pereboom *et al.* 2008; Holmala & Kauhala 2009) whereas martens are typically found in more forested areas (Storch, Lindström & de Jonge 1990; Brainerd & Rolstad 2002).

Although I did not find any strong influence of golden eagle on the abundance of mesopredators, high territory density of eagles was associated with higher proportions of juveniles in black and hazel grouse populations (IV). These results could mean that eagles provide protection for the grouse by reducing nest and chick predation from mesopredators. However, the protection effect of eagle was not dependent on the abundances of the mesopredators (no significant eagle-mesopredator interactions), even though fox was negatively associated with both grouse species and marten with hazel grouse. One explanation could be that eagle intimidation is very effective, preventing mesopredators occurring at any densities from hunting, and therefore this effect is not dependent on the abundance of the studied mesopredators. Alternatively, the protection effect may be mediated by other mammalian nest predators not accounted for here, such as the invasive raccoon dog (*Nyctereutes procyonoides*) (Pekkola *et al.* 2014). Interestingly, similar protection effect on juvenile grouse has recently been found also with another avian predator that relies heavily on forest grouse, namely the goshawk (Tornberg *et al.* 2015).

Increased eagle territory and fledgling density were associated with a low overall abundance of black grouse but not with the abundance of hazel grouse (IV). Apparently, eagles reduce the abundance of an important prey species, the black grouse, but kill smaller hazel grouse less frequently (Sulkava *et al.* 1999). This is supported also by habitat use of the grouse species: black grouse prefer open habitats (Swenson & Angelstam 1993; Angelstam 2004) where they consequently are more prone to be caught by eagles, while hazel grouse are more protected by the dense forest habitats they prefer (Åberg, Swenson & Angelstam 2003).

In summary, eagles seem to protect juvenile grouse while being a threat to the adult individuals. I propose that the protection effect of eagles may be mediated by changing the behaviour and microhabitat use of several mammalian mesopredators, in addition to fox and marten included in the study.



**Figure 4.** Trophic interactions and cascades examined in the thesis. Bold lines refer to observed interactions, thin lines to supposed ones. The direct negative predation or herbivory effects are presented with solid red lines, the indirect cascading effects of predators with dashed green lines.

## 4 CONCLUSIONS

The landscape-level seedling experiments (I, II) provided new insight on the food webs of boreal forests. Information about the interactive roles of herbivores in the boreal food webs is important ecologically, as the trees they browse on form an essential and influential part of the forest flora. In addition, there is also vast monetary value in the forests and their successful regeneration. Results of this thesis suggest no synergistic effects of herbivores, i.e. they do not seem to facilitate the browsing effects of one another. Overall, the impact of mammalian herbivores on spruce seedlings was found to be relatively small, at least in mixed forest stands where more preferred food is available. In contrast, the condition and survival of pines was negatively affected by voles and hares, and very high vole abundances were associated with more damaged pine seedlings. Pine and spruce are the two most abundant species in Finnish forests, and damage on young stands caused by cervids and voles is a major concern in forestry (Huitu *et al.* 2009; Huitu, Rousi & Henttonen 2013; Peltola 2014). Although studies from other areas have shown mountain hares not to be a very prominent browser of pines (Rao *et al.* 2003), the results of this thesis highlight hares as relevant pest of pine stands, too.

From the tree species studied in this thesis, silver birch appears to be the most palatable for the mammalian herbivores, which is supported also by earlier studies (Gill 1992a; Baxter & Hansson 2001; Hjältén, Danell & Ericson 2004). All in all, it seems probable that the high mortality and the growth limitations observed from cervids, hares and voles weaken the regeneration in birch stands. Consequently, lowered cervid abundances could improve birch regeneration and decrease the need for damage control and prevention (I). Therefore, the results in this thesis give indirect support to the idea that increase in the abundance of key predators of cervids, such as wolves, bears (*Ursus arctos*) and lynxes, could cause cascading effects also in the boreal forests of the Fennoscandia. As mammalian top predators are currently recovering and increasing in numbers across the boreal ecosystems (Chapron *et al.* 2014), we could anticipate cascading effects on deciduous trees, notably on birch seedlings. The results of this thesis showed little effect from cervids on coniferous seedlings, but it is still plausible that also pine and spruce could benefit from increased predation on cervids. After all, for example winter browsing by roe deer is known to cause growth reduction and stem deformations on spruce (Bergquist, Bergström & Zakharenka 2003), while moose are known to be a severe pest for young pine seedlings (Heikkilä & Härkönen 1996).

Another three-level cascade was examined in the playback experiment (II), where I found that the foraging effect of voles on birches was reduced under simulated owl

predation risk in late summer, when voles would normally turn to browse more on seedlings instead of the less palatable old grass. This is novel information about the cascading effects triggered by auditory cues from avian predators and mediated by voles, and it can even have applications in the protection of birch seedlings against vole browsing during late summer, autumn and winter, when voles induce the majority of damages to seedlings. The presence of an owl may, in addition to direct consumption effect, indirectly benefit birch seedlings. Furthermore, a playback of small owls could possibly be used to protect birch seedlings against vole browsing in new planting areas, which often are on abandoned agricultural fields or grassy clear-cut areas, the preferred habitat of field voles.

The third cascade examined in this thesis is the eagle–mesopredator–grouse system (III–IV). Golden eagles, red foxes and pine martens seem often to be numerous within the same areas, so eagles do not effectively decrease the abundance of these mesopredators, although there was some indication that when very abundant, the eagles could reduce numbers of the smaller pine marten (III). These results, based on combining two long-term national data sets, are novel as studies on the population effects of avian top predators on mammalian mesopredator have been lacking previously. Furthermore, there are several other mesopredator species in the boreal ecosystems, which may be preyed upon by the golden eagle. More insight on how different mesopredators respond to the threat of the golden eagle, or other large avian predators like the eagle owl, could be gathered by tracking the mesopredators in the presence and absence of large avian predators.

When forest grouse species were included in the study design, I observed that eagles had a negative effect on adult black grouse but a positive, protective effect on the juveniles of both black grouse and hazel grouse (IV). As could be anticipated by the results of chapter III, the positive effect of eagle was not dependent on the abundance of fox and marten. Instead, the results indicate that eagles have a non-lethal intimidation effect on the mesopredators. In addition to – or instead of – red fox and pine marten, this group of grouse-preying mesopredators probably includes other species too, such as the alien American mink (*Neovison vison*) and raccoon dog, and the native stoat (*Mustela erminea*) (Kurki et al. 1997; Saniga 2002). In the case of the mink, it has already been shown that their movement activity can be decreased in the presence of an avian top predator, the white-tailed eagle (Salo et al. 2008). Large avian predators can also deter avian nest predators, such as corvids, from breeding grouse (Tornberg *et al.* 2015). An interesting question remains whether eagles could expel smaller raptors that prey on both the young and the adult grouse (Tornberg 2001).

In conclusion, in this thesis I have provided novel information about the species interactions on several trophic levels of the boreal food webs. Already earlier the effects

of mammalian herbivores on tree seedlings have been very evident, but this thesis highlighted how different herbivore groups vary in their effects on the growth and condition of seedlings, depending on the tree species. Furthermore, I examined the possible cascades in the boreal forests. Browsing on birches seems to be reduced by the non-lethal intimidation effect of owls, and the recovery of large carnivores may also have a similar effect through lowered cervid abundance and reduced foraging. Also the golden eagle was found to have a protective effect, not on the plants but on herbivorous grouse. The results of this thesis provide further support on the idea that there are indeed cascading effects rippling through the boreal food webs, in addition to those already shown in previous studies conducted in the northern continents. In the systems examined in this thesis, there seems to be both direct and non-lethal effects of predators that trigger these trophic cascades. Top predators may even be considered to benefit humans by providing ecosystem services with their predation effects, cascading on to young tree stands or valued herbivorous game, such as grouse. Also smaller predators, e.g. owls, are important as they may provide protection on seedlings by reducing the browsing behaviour of voles.



*An overview of the study area in the Alajoki region, Lapua.*

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*Mari Lyly*

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