

Indirect Effects of Moose on the Birds and the Bees

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Abstract

Large herbivores are important drivers of ecosystem processes, affecting plant species richness and composition, primary productivity, habitat structure as well as nutrient cycling. Large herbivore activities may therefore have important indirect effects on other plants and animals in the same ecosystem. The effect of herbivore activity on ecosystem processes varies with habitat productivity, herbivore selectivity, herbivore density and may be modified by different wildlife management practices. Therefore indirect effects of herbivores may also vary with these factors. In this thesis, I focus on indirect effects of moose (*Alces alces*) on plants and animals in the boreal forest and how these effects are modified by moose density, habitat productivity and supplementary winter feeding of moose. I studied effects of moose density and habitat productivity on species composition, growth and reproduction in the field layer vegetation and on abundance and family richness of flower-visiting insects. I also studied effects of a gradient in moose density around supplementary winter feeding stations for moose on bird species richness, abundance and reproduction. Selective moose browsing on preferred species affected species composition in the field layer vegetation, increasing abundance and reproduction in unbrowsed plant species, and decreasing abundance and reproduction in browsed species. Moose browsing in the tree canopy increased light availability and flowering in the field layer as well as family richness of Hymenoptera at sites with high productivity. Moose winter browsing around supplementary feeding stations led to reduced species richness and abundance of insectivorous birds and birds nesting at browsing height. Furthermore, high moose densities led to lower reproduction and food availability for great tits (*Parus major*), and higher reproduction and food availability for pied flycatchers (*Ficedula hypoleuca*). Supplementary feeding stations for moose brought nutrients into the system and had a positive effect on species richness and abundance of insectivorous birds, and the size of insect prey. These results show that moose activity can have indirect effects on plants and animals through changed resource availability and habitat structure, and that these effects are modified by habitat productivity and supplementary feeding of moose.

Keywords: *Alces alces*, boreal forest, browsing, cascading effects, field-layer vegetation, flower-visiting insects, habitat productivity, insectivorous birds

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Dedication

To Mum & Dad

*Let me tell you 'bout the birds and the bees
And the flowers and the trees and the moon up above
And a thing called love ...*

(Barry Stuart)

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List of Publications

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

- I *Mathisen, K. M. , F. Buhtz, K. Danell, R. Bergström, C. Skarpe, O. Suominen, I. L. Persson. 2010. Moose density and habitat productivity affects reproduction, growth and species composition in field-layer vegetation. *Journal of Vegetation Science*. 21 (4). 705-716. DOI: [10.1111/j.1654-1103.2010.01180.x](https://doi.org/10.1111/j.1654-1103.2010.01180.x)
- II Effects of browsing disturbance on abundance and species richness of flower visiting insects – The role of light availability and flower density. Authors: Widenfalk, O., Mathisen, K. M., Danell, K., Skarpe, C., Bergström, R. and Persson I.-L. (Submitted to *Oikos*)
- III *Mathisen, K. M and Skarpe, C. Cascading effects of moose (*Alces alces*) management on passerine birds. (Accepted by *Ecological research*) DOI: 10.1007/s11284-011-0815-6.
- IV Contrasting responses of two passerine bird species to high moose densities. Authors: Mathisen, K. M., Pedersen, S., Nilsen, E.B. and Skarpe, C. (Submitted to *European Journal of Wildlife Research*)

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1 Introduction

1.1 Indirect effects of large herbivores in ecological communities

Ecologists have traditionally focused on studying direct interactions between trophic levels, but indirect effects may be even more important than direct ones in determining ecosystem patterns and processes (Hobbs, 1996). Large herbivores can cause indirect effects through food webs or habitat modification, but how important these indirect effects are in structuring ecological communities is not known (Rooney & Waller, 2003). For example, interactions between large herbivores and soil nutrients may affect the plant community, while feedbacks between herbivores and decomposers may determine community structure (Hobbs, 1996; Pastor & Naiman, 1992). An indirect effect is defined as how one species alters the effect that a second species (or more) has on a third (Wootton, 1994; Strauss, 1991). Interactions mediated through a non-living resource, such as soil nutrient content, may also be considered as indirect effects (Strauss, 1991). Exploitative competition, where two species affect each other through the use of a common resource, is probably the indirect effect that is most studied, however, it is not always considered as an indirect effect (Wootton, 1994; Strauss, 1991). Other examples include trophic cascades, where changes at one level in the food web, affect other levels in the food web than the level directly below or above (Polis *et al.*, 2000). Little is known about the strength of indirect versus direct effects, mainly because indirect effects are complex to study and analyze (Wootton, 1994; Strauss, 1991).

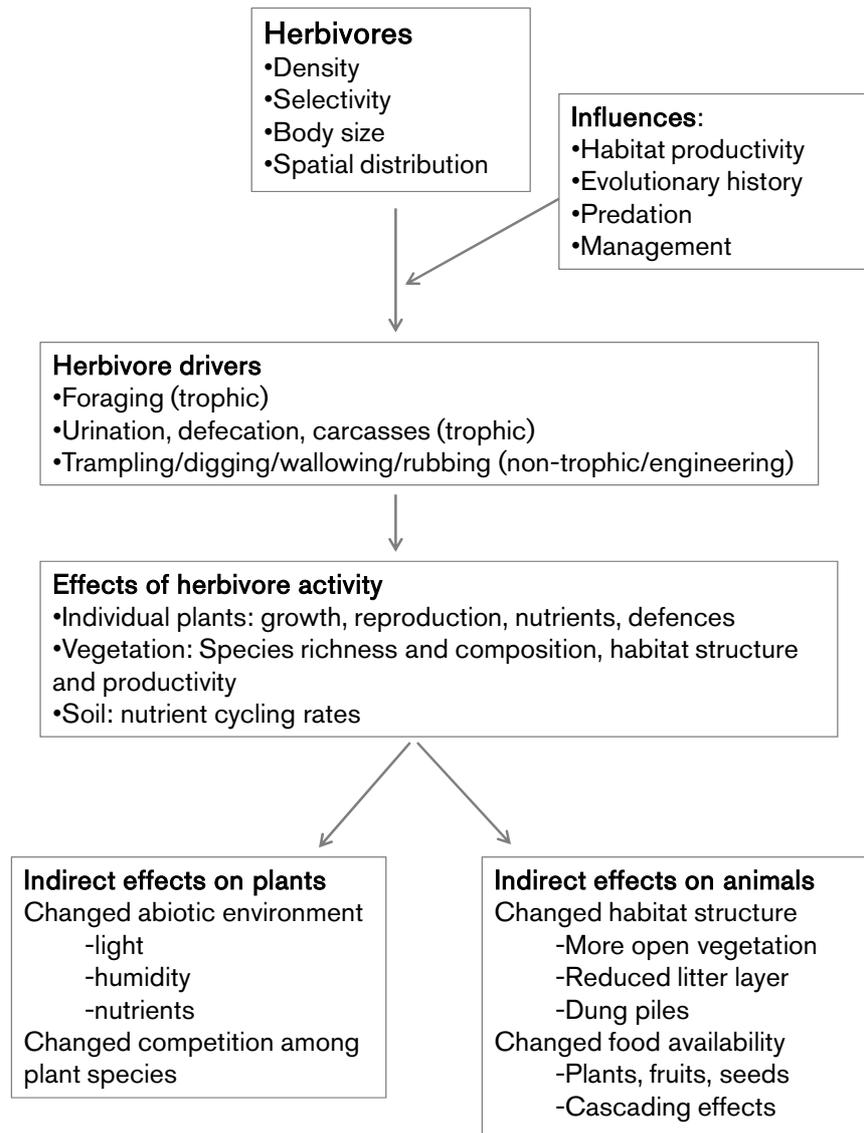


Figure 1. Herbivores may have indirect effects on plant and animals through changed environment and resource availability, and these effects depend on herbivore traits, density, predation, management and environmental variables.

Large herbivores may affect the dynamics of communities and ecosystems by acting as sources of disturbance, and by modifying the environment by foraging and non-foraging activities in a heterogeneous manner in time and

space (Hobbs, 1996; Huntly, 1991). Their large size, often high densities and wide spatial distributions make them important factors in structuring ecological communities (Hobbs, 1996). They play an important part in the food web, as a food resource for carnivores, as a predator on plants, and affecting decomposers indirectly through effects on the plant community. The role of herbivores in the ecosystem is mediated by their interactions with plants (Augustine & McNaughton, 1998), predators (Schmitz *et al.*, 2000; McLaren & Peterson, 1994) and decomposers (Pastor *et al.*, 2006). Their ecosystem effects are also influenced by environmental variables, evolutionary history and productivity (Proulx & Mazumder, 1998; Milchunas *et al.*, 1988) as well as by habitat and wildlife management (Garrott *et al.*, 1993). Herbivores may through their foraging, deposition of dung and urine and trampling therefore affect many other species of plants and animals through indirect effects (Figure 1), although these indirect effects are often given little attention (Suominen & Danell, 2006; Rooney & Waller, 2003). The density of herbivores is important in modifying the indirect effects of herbivores, since effects of herbivores on plant species richness and nutrient cycling may vary strongly with density, and follow non-linear response curves (Pastor *et al.*, 2006; Suominen & Danell, 2006; Milchunas *et al.*, 1988). The sum of the various direct and indirect effects will be what drives community dynamics, but to predict the direction of change, we should know more about the mechanisms that control them (Huntly, 1991).

1.1.1 Mechanisms behind indirect effects of large herbivores

The most important indirect effects of large herbivores on other fauna occur through changing of the habitat, or changed availability of food resources (Suominen & Danell, 2006) (Figure 1). Indirect effects can be both trophic and non-trophic, or a mix of both (Strauss, 1991). Trophic effects include effects through foraging, such as competition with other herbivores. For example, red deer (*Cervus elaphus*) grazing in Scotland reduced the height of bilberry (*Vaccinium myrtillus*) and the abundance of geometrid moth larvae foraging on the same resource (Baines *et al.*, 1994), while reindeer browsing on willow (*Salix lanata*) in northern Finland reduced densities of the most common insect herbivores (Den Herder *et al.*, 2004). Also large herbivores may eat other herbivores while foraging, i.e. domestic sheep and Spanish ibex in Sierra Nevada in Spain affected weevils negatively both by exploitative competition and by incidental predation (Gomez & Gonzalez-Megias, 2002). Large herbivore foraging may also change the chemical composition of plants, making them more or less susceptible to herbivory by

arthropod herbivores (Olofsson & Strengbom, 2000; Danell & Huss-Danell, 1985). Herbivores may also have indirect effects on plants by affecting competition between plant species for light, water and nutrients as well as by affecting nutrient cycling and habitat structure (Rooney & Waller, 2003; Augustine & McNaughton, 1998; Pastor & Naiman, 1992). By foraging on one species, herbivores may affect another competing plant species indirectly, through apparent mutualism (Wootton, 1994). Herbivores may also have indirect effects on the decomposer community, as herbivore foraging may change the input of plant litter, deposition of faeces and urine, affect nutrient cycling rates and soil microclimate (Suominen *et al.*, 2008; Stewart, 2001; Stark *et al.*, 2000; Pastor *et al.*, 1988). Large herbivore foraging may also have cascading effects on other trophic levels. Herbivore exclusion in an African savanna led to increased vegetation cover and tree density, increased number of beetles and their predator lizard (Pringle *et al.*, 2007), while deer grazing in a temperate forest in England led to reduced abundances of small mammal prey species, affecting diet, density and reproduction in their predators owls and kestrels (Van Wieren, 1998).

Large herbivores may also act as “environmental engineers” (Jones *et al.*, 1994), modifying the environment for other species through non-trophic effects. Non-trophic effects include activities such as trampling, wallowing, rubbing against trees, urinating, defecating and digging which may provide sites for new colonists (Hobbs, 1996). Bare soil patches created by soil or canopy disturbance can serve as regeneration sites for plant species, and increased light availability can enhance germination rates and seedling survival (Bakker & Olf, 2003; Bakker & Devries, 1992). Also herbivore foraging can modify the environment for other species by affecting vegetation structure and productivity and therefore indirectly affecting habitat structure, microclimate, nutrient dynamics and soil structure (Larson & Paine, 2007; Pedersen *et al.*, 2007; Vazquez & Simberloff, 2004; Hartley *et al.*, 2003; Jones *et al.*, 1994). For example, changed vegetation structure due to deer browsing in Japan led to reduced abundance of web-building spiders due to a shortage of web-sites (Miyashita *et al.*, 2004). Herbivory may open up the vegetation, increasing insolation and decreasing moisture levels, with negative effects on arthropod species that depend on shady, moist habitats (Suominen, 1999; Gardner *et al.*, 1997). Effects of herbivory on vegetation structure tends to have negative impact on small mammals and birds, probably through increased predation risk in more open vegetation (Suominen & Danell, 2006).

In summary, of the three major categories of herbivore drivers discussed (Figure 1), foraging is often assumed to be the most important driver of ecosystem dynamics (Hobbs, 2006) and indirect effects on other species (Suominen & Danell, 2006). However, it is also important to understand how herbivores may affect the ecosystem through non-foraging activities, which so far rarely have been quantified. As plants influence many features of the environment, such as light penetration, temperature, wind, humidity, soil moisture, nutrient cycling and hydrology (Jones *et al.*, 1994), the effects of herbivores on plants indirectly affect the physical properties of habitats. To understand the effect of herbivores on communities and ecosystems, it is thus important to understand how herbivores affect the vegetation through different activities, and how these effects differ with environmental variables and herbivore density (Figure 1).

1.1.2 Effects of herbivores on plants and plant species richness

Herbivores may, through foraging and non-foraging activities, affect growth and reproduction in plants and hence plant species richness, plant species composition and primary production (Hester *et al.*, 2006; Hobbs, 2006). Selective foraging is probably one of the most important drivers of ecosystem dynamics, as it creates differential pressure on plant populations and may drive changes in species composition and succession rates (Augustine & McNaughton, 1998; Pastor & Naiman, 1992). Herbivore selectivity depends on different plant traits that may affect accessibility and palatability to herbivores, such as the presence of physical defence structures or the production of secondary compounds (e.g. phenolics, resins, tannins and alkaloids) (Skarpe & Hester, 2008; Bryant *et al.*, 1991). Selectivity also depends on herbivore body size, as large-bodied herbivores can tolerate lower food quality and feed less selectively than small herbivores (Davidson, 1993; Bryant *et al.*, 1991; Demment & Van Soest, 1985). Therefore effects on plant diversity may differ with the community composition of herbivores as large generalist herbivores may impact dominant plant species and increase plant diversity (Milchunas & Lauenroth, 1993), whilst small selectively feeding herbivores may decrease diversity by selectively feeding on nutritious plant species (Bakker *et al.*, 2006; Olofsson *et al.*, 2004).

“The intermediate disturbance hypothesis” (Connell, 1978) is often used to explain the effects of herbivore foraging on plant species richness. If disturbance is defined as any relatively discrete event in time that removes organisms or parts of organisms (Begon *et al.*, 1996), large herbivore foraging and non-foraging activities can be considered as disturbance factors in

ecosystems (Hobbs, 1996). Disturbance may open up space or release resources that can be taken over by new individuals. Therefore disturbance may affect competition between species, relative abundance of species and community structure. Herbivore activity may affect species diversity by increasing spatial heterogeneity and affecting patch-scale dynamics of colonization and extinction (Olf & Ritchie, 1998). At high disturbance intensity or frequency, extinction rates will increase, only disturbance-tolerant species will survive, and plant species richness will decrease. At low disturbance frequency or intensity, competitive exclusion by dominant species may reduce species diversity. Therefore species richness is commonly considered to have bell-shaped response to disturbance intensity or frequency, with the highest species richness at intermediate disturbance levels (Connell, 1978).

Some authors have suggested that an intermediate grazing intensity may also maximize animal species richness (Van Wieren, 1998), as diversity of insect communities is closely related to plant diversity (Haddad *et al.*, 2001). However, although some animal groups (beetles (Suominen *et al.*, 2003b), lagomorphs and macro-arthropods (Milchunas *et al.*, 1998)) show a unimodal response to grazing intensity, others (mammals, birds, web spiders and terrestrial gastropods) show a monotonic decline in diversity with grazing intensity (Suominen & Danell, 2006). Animal and vegetation diversity may also show contrasting responses to grazing intensity (Kruess & Tschamtker, 2002). The effect of disturbance on plant and animal species richness may be modified by resource availability and evolutionary history (Kondoh, 2001; Milchunas *et al.*, 1988) so the unimodal response curve may only be observed under certain conditions. This may partly explain why both positive, negative and unimodal responses of species richness to disturbance have been documented (Mackey & Currie, 2001). Herbivore disturbance due to foraging and non-foraging activities may occur on different scales in space and time, from small scale disturbances such as plant module death to long-term changes in structure of the vegetation. Large scale effects depend on herbivore population densities and distribution in space and time, as herbivores often migrate over large distances, and may have large fluctuations in population size (Illius, 2006; Senft *et al.*, 1987).

1.1.3 Effects of herbivores on plant species composition

Plants have evolved various strategies to minimise the negative effects of herbivory on plant fitness, such as avoidance strategies (including escape strategies or physical and chemical defences) and tolerance strategies (i.e.

rapid compensatory growth) (Rosenthal & Kotanen, 1994). Herbivory may change plant community composition through favouring plants with certain strategies. The direction of change depends on several factors, such as nutrient availability, herbivore density, herbivore selectivity, plant community composition and recovery time between herbivory events (Augustine & McNaughton, 1998). When herbivory is relatively non-selective, or the herbivore community together affects most species in a plant community, plant species with high growth rates and the ability to recover quickly after herbivory (tolerance) may increase in dominance with increasing levels of herbivory. For example, reindeer grazing on tundra can replace mosses, lichens and dwarf shrubs with grazing-tolerant graminoids at high levels of summer grazing (Olofsson *et al.*, 2001), browsing by white-tailed deer in temperate forest can convert the forest from conifer to deciduous dominated species due to the inability of slow-growing conifers to tolerate tissue loss (Augustine & McNaughton, 1998), and increasing wildebeest populations in Serengeti lead to increased abundance of a fast-growing palatable sedge (*Kyllinga nervosa*) and no change in unpalatable species (Sinclair, 1995).

When herbivory on the other hand is highly selective, and affects plant species unequally, unpalatable species (avoidance) may increase in dominance relative to palatable species that are more heavily affected by herbivory. For example, browsing by moose in boreal forest may give spruce (*Picea* spp.) which is practically not browsed due to chemical defences an advantage over more heavily browsed species such as balsam fir (*Abies balsamea*) or deciduous species (Pastor & Cohen, 1997; McInnes *et al.*, 1992). Also selective grazing by white-tailed deer in oak savannas can reduce the abundance of palatable legumes compared to unpalatable grasses (Ritchie *et al.*, 1998). Similarly, impala and kudu in nutrient poor savanna show highly selective foraging and may maintain dominance of slow-growing chemically defended woody species (Scholes & Walker, 1993; Owen-Smith & Cooper, 1987).

Herbivores may also affect succession rates (Kielland & Bryant, 1998; Ritchie *et al.*, 1998; Kielland *et al.*, 1997; Davidson, 1993). Palatable fast-growing plant species are often more common early in succession and slow-growing unpalatable plant species are more common late in succession (Grime *et al.*, 1997). As growth rates and palatability to herbivores are positively correlated, herbivores may graze selectively on the more palatable fast-growing species, and hasten their replacement by slow growing

defended species (Augustine & McNaughton, 1998; Grime *et al.*, 1997; Pastor & Naiman, 1992), thus hastening succession rates. However, if the more palatable species occur late in succession, herbivores may retard succession (Ritchie *et al.*, 1998; Pastor & Naiman, 1992). If herbivores accelerate or decelerate succession may also depend on the successional stage that the herbivore forages in. Herbivore feeding on fast growing plants at intermediate stages of succession may retard early succession and hasten late succession (Davidson, 1993).

1.2 Influence of habitat productivity on effects of herbivory

Herbivore disturbance may also interact with habitat productivity, as plant responses to herbivory are related to resource availability (Hawkes & Sullivan, 2001), and nutrient availability is one of the major drivers of plant specialisation (Grime *et al.*, 1997). Environments with low resource availability favour plants with low growth rates and high levels of anti-herbivore defences, while plants with faster growth rates and lower defence levels are favoured under conditions of high resource availability (Grime *et al.*, 1997; Coley *et al.*, 1985). Therefore herbivory may increase the abundance of herbivore-tolerant plants in an environment with high resource availability, and herbivore-defended plants in an environment with low resource availability (Augustine & McNaughton, 1998). Since high palatability and high growth rates are correlated (Grime *et al.*, 1997), herbivores tend to prefer the dominant plant species and, at moderate densities, may reduce competition by limiting growth of fast growing dominant species, and increase species richness according to the intermediate disturbance hypothesis (Connell, 1978). As species with high growth rates may tolerate higher levels of disturbance, the intermediate disturbance level that is assumed to maximise species richness, may increase with habitat productivity (Kondoh, 2001; Huston, 1979). In contrast, in environments where herbivory does not lead to reduced competition with the most dominant species, either because growth rates are limited by resource availability rather than competition, or because the dominant plant species has evolved adaptations to herbivory, herbivory may not have the unimodal effect on plant species richness predicted by the intermediate disturbance hypothesis, but rather a negative effect (Milchunas *et al.*, 1988). The “grazer reversal hypothesis” states that grazing reduces plant species richness in nutrient-poor environments, but increases plant species richness in nutrient rich environments because of higher resource availability and higher capacity

for compensatory growth after disturbance in nutrient rich environments (Bakker *et al.*, 2006; Proulx & Mazumder, 1998).

1.2.1 Effects of herbivores on the soil community

Changes in the plant community may affect the soil biota through changed litter quality and quantity and changed allocation to plant roots, affecting soil respiration, mycorrhiza and N-fixation (Persson *et al.*, 2009; Bardgett & Wardle, 2003; Rossow *et al.*, 1997). Herbivore selectivity and decomposition of plant litter are linked through chemical plant defences, as the same compounds that reduce palatability to herbivores also reduce litter decomposability (Harrison & Bardgett, 2008; Pastor *et al.*, 2006; Wardle *et al.*, 2002; Augustine & McNaughton, 1998; Bryant *et al.*, 1991). Therefore herbivores may affect decomposers through exploitative competition for the most palatable plant parts. Changed decomposition rates may again affect nutrient availability for plants, and affect plant species composition and productivity, leading to feedbacks between herbivores, plant populations and soil communities. Large mammalian herbivores can have stronger effects on rates of nutrient cycling than what is expected from their direct influence by foraging, suggesting magnified effects by positive and negative feedbacks with other trophic levels (Pastor *et al.*, 2006; Bryant *et al.*, 1991). Deposition of dung, urine and carcasses may also affect nutrient cycling rates, usually increasing nutrient availability (Melis *et al.*, 2007a; Pastor *et al.*, 2006; van der Wal *et al.*, 2004; Danell *et al.*, 2002; Stark *et al.*, 2000; Towne, 2000), but very nutrient poor dung may decrease nutrient cycling rates (Pastor *et al.*, 2006). Herbivores may convert plant material to more easily decomposable components in dung and urine thus increasing mineralisation rates, but if the plant material has low nutrient content, most of the nutrients are extracted by the digestive system, and only slowly decomposable components are excreted in dung (Pastor *et al.*, 2006). I.e. moose winter dung may have lower mineralisation rates than the soil in boreal forest, and may slow down mineralisation rates (Pastor *et al.*, 1993).

1.2.2 Herbivores may affect nutrient cycling and habitat productivity

Due to the changes in litter composition and nutrient availability, and feedbacks with decomposers described above, herbivores may change habitat productivity by affecting nutrient cycling (Bardgett & Wardle, 2003; Pastor & Cohen, 1997; Hobbs, 1996). Hence herbivory may affect plants both through top down and bottom up processes (Martin *et al.*, 2010). Nutrient limitation of the plant community may control whether herbivores increase or decrease nutrient cycling rates. Herbivores tend to increase nutrient

cycling rates if plant nitrogen content is high, such as in the Serengeti grasslands, or decrease nutrient cycling rates if plant nitrogen content is low, as in a boreal forest (Pastor *et al.*, 2006; Ritchie *et al.*, 1998). If plant nitrogen content is high, nitrogen concentrations excreted in dung is also high, and herbivores may accelerate nutrient cycling rates. If plant nitrogen is low, most of the nitrogen is assimilated in the animals digestive system, and the nitrogen contents excreted in dung is low, and herbivores may decelerate nutrient cycling rates (Pastor *et al.*, 2006). Also if plant nitrogen content is high, herbivores are less selective, and may increase abundance of fast growing herbivore-tolerant species with fast-decomposing litter (Augustine & McNaughton, 1998). But if plant nitrogen content is low, herbivores are more selective, and may shift plant species composition towards more slowly growing species with slowly decomposing plant litter (Pastor & Naiman, 1992). Hence herbivores may affect nutrient cycling both through changing litter composition and through nutrients excreted through dung and urine.

Species richness also shows a unimodal response to increasing primary productivity with the highest diversity at intermediate productivity (Rosenzweig & Abramsky, 1993; Grime, 1973), similar to the intermediate disturbance hypothesis (Connell, 1978). How herbivore disturbance changes productivity along the unimodal species-productivity curve, may therefore be used to predict how herbivores affects species richness in different habitats (Wright & Jones, 2004). A herbivore that reduces productivity would have a positive effect on richness in highly productive habitats, and a negative effect in low productivity habitats, whilst a herbivore that increases productivity would have the opposite effect (Wright & Jones, 2004). This is consistent with the “grazer reversal hypothesis” of Proulx & Mazumder (1998) and Milchunas (1988). Indirect effects of herbivores may therefore also vary with productivity. Trophic cascades may vary with productivity as the level of primary productivity may determine whether top-down or bottom-up control is predominant (Chase, 2003). Compensatory growth after herbivory is faster in high-productivity sites, which may dampen the effect of trophic cascades in high-productivity habitats (Pringle *et al.*, 2007).

1.3 Study system: moose in boreal forests

The role of large herbivores as agents of change in ecosystems is an important issue for management and conservation (Garrott *et al.*, 1993), and grazing by large herbivores is often used as a management tool for

conservation in some habitats (Van Wieren, 1998). The recent increase in many cervid species due to land-use changes in Europe, North-America and Japan raises concern over the effects they may have on their respective ecosystems and biodiversity (Côte *et al.*, 2004; Fuller & Gill, 2001; McShea *et al.*, 1997; Hobbs, 1996). The moose (*Alces alces*) in the boreal forests of Fennoscandia is an example of a cervid species that has experienced a dramatic population increase during recent decades, and now occurs at quite stable high densities (in Norway on average 0,9–1.0 moose km⁻² but densities at county level vary between 0.2–1.5 (Solberg *et al.*, 2003)). The most important causes of this increase have been an increase in food availability associated with modern forestry clear-cutting practices, selective hunting of moose to increase the harvest yield, low numbers of predators such as wolf and bear, and possibly lower competition with domestic herbivores (Austrheim *et al.*, 2008; Cederlund & Bergström, 1996).

The moose is a large herbivore (300–370 kg for cows, 390–470 kg for bulls in Sweden (Sand *et al.*, 1995)) with a strong potential to affect ecosystem processes and biodiversity in the boreal forest ecosystem (Persson *et al.*, 2000). Consequently it may have indirect effects on other flora and fauna. The moose is a selective browser that prefers early successional tree species that are palatable and have high growth rates, such as rowan (*Sorbus acauparia*), aspen (*Populus tremula*) and willow (*Salix* spp.). In Fennoscandia, birch (*Betula* spp.) and pine (*Pinus sylvestris*) are of medium preference, but spruce (*Picea abies*) is almost never eaten (Månsson *et al.*, 2007; Shipley *et al.*, 1998; Pastor & Naiman, 1992; Bergström & Hjeljord, 1987). Moose browsing therefore has the potential to increase successional rates, by giving non-browsed unpalatable species such as spruce a competitive advantage (Pastor & Naiman, 1992). Habitat productivity in boreal forest is rather low and often nutrient limited (Bonan & Shugart, 1989). Moose browsing may reduce habitat productivity and decrease nutrient cycling rates by reducing the quality and quantity of litter in the short term (Persson *et al.*, 2005b) and in the long-term by changing species composition towards unpalatable species with low litter quality (Pastor & Cohen, 1997). Moose would therefore be predicted to reduce plant species diversity in a low productivity environment, but increase plant species diversity in a high productivity environment (Wright & Jones, 2004). It is therefore important to take habitat productivity into account, when evaluating ecosystem effects of moose and other large herbivores.

Supplementary winter feeding of cervids is a widespread management practice across Northern-Europe and North-America for reasons such as maintaining high densities of cervids for hunting, or avoiding damage to vegetation of commercial or conservation value (Putman & Staines, 2004; Smith, 2001). Supplementary feeding of moose with baled silage is popular in Norway and increasing also in Sweden, to sustain high moose populations, reduce browsing damage to forestry and to divert moose away from main roads and railway lines (Sahlsten *et al.*, 2010; van Beest *et al.*, 2010a; van Beest *et al.*, 2010b; Gundersen *et al.*, 2004). This management practice brings biomass, nutrients and seeds into the boreal forest system. This affects moose population density and distribution, but also local nutrient cycling and availability, and possibly modifying the effects of moose on nutrient cycling. How this type of management interacts with the effects of moose on the ecosystem is not known.

Changed vegetation structure and species composition due to moose browsing, as well as changes in soil properties and nutrient cycling may potentially affect many other species living in the boreal forest. Moose activities may potentially have indirect effects on plants through changing light competition, nutrient availability and microclimate (Persson *et al.*, 2009; Persson *et al.*, 2005b; Pastor & Cohen, 1997). Moose browsing may affect animals through changed habitat or resource availability. For example, moose browsing has been found to have negative effects on spider richness and abundance as well as gastropod abundance, probably through reduced litter fall and changed microclimate (Suominen *et al.*, 2008; Suominen, 1999). However, moderate moose browsing can have positive effects on abundance of leaf eating insects and ground-living invertebrates (Melis *et al.*, 2007b; Danell & Huss-Danell, 1985). Effects of browsing on flower densities and microclimate may in turn affect flower-visiting insects, and important ecosystem processes such as pollination. Moose browsing may change the structure of the canopy affecting the abundance of birds dependent on vegetation layers at browsing height for nesting or foraging (Berger *et al.*, 2001; Fuller, 2001). Browsing may also affect arthropod abundance and have cascading effects on bird food availability (Suominen *et al.*, 2008; Pedersen *et al.*, 2007). An overview of the role of moose in the ecosystem is given in Figure 2.

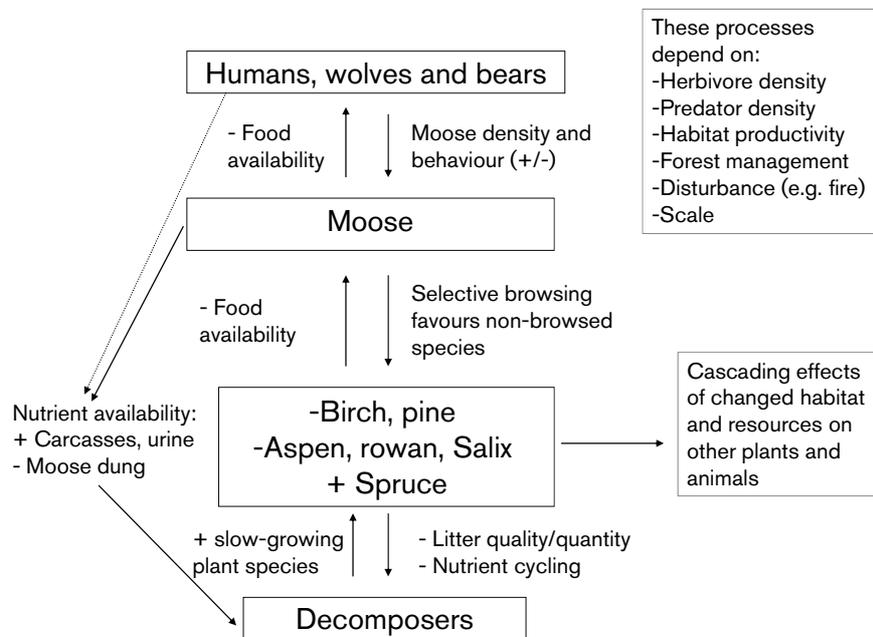


Figure 2. A simplified illustration of the role of moose in the food web in boreal forest, and some of the most important mechanisms.

Traditionally, studies of moose browsing have focused on direct effects on plants. However, also indirect effects on non-browsed species may be important for the role of moose in the ecosystem (Pastor & Cohen, 1997; Pastor & Naiman, 1992). This thesis focuses on indirect effects of different moose densities on plants and animals, specifically on the field layer vegetation and flower-visiting insects, and on bird species composition and reproduction. It also investigates how moose browsing interacts with habitat productivity and management actions, such as supplementary feeding, that bring nutrients into the ecosystem. Identifying guilds or functional groups that respond similarly to modifications of the environment may increase our ability to anticipate the response of unstudied organisms to changes in ungulate densities (Rooney & Waller, 2003). I have therefore investigated how different moose densities affect different functional groups of these three different trophic levels. I have focused mostly on the mechanisms of how moose activities affect birds, insects and field-layer vegetation, and asked the following questions:

1.4 Questions addressed

1. How do moose density and habitat productivity affect species composition, growth and reproduction in field-layer vegetation?
2. How do moose density and habitat productivity affect richness and abundance of flower-visiting insects?
3. How do moose browsing and nutrient input affect species richness and abundance of functional groups of birds?
4. How do moose browsing and nutrient input affect reproduction in insectivorous bird species?

2 Study sites

This study was performed in two study areas, one around Umeå (63°50'N, 20°18'E) in northern Sweden and one in Stor-Elvdal (~61°N, 11°E) municipality in south-eastern Norway (Figure 3). In Umeå I investigated effects of moose density and habitat productivity on field layer vegetation and flower-visiting insects and in Stor-Elvdal the effects of a gradient in moose density around moose winter supplementary feeding stations on bird species composition and reproduction. Both study areas are situated in the boreal forest zone, with similar vegetation and with forests managed for timber production of mainly Scots pine (*Pinus sylvestris*) and Norway spruce. The forest in these areas consists of pure or mixed stands of pine, spruce, downy birch (*Betula pubescens*) and silver birch (*B. pendula*) interspersed with species such as grey alder (*Alnus incana*), rowan, aspen and willows. The field layer vegetation is generally dominated by dwarf shrubs such as cowberry (*Vaccinium vitis-idaea*) and bilberry (*V. myrtillus*), heather (*Calluna vulgaris*) and wavy hair grass (*Avenella flexuosa*).

2.1 Umeå, northern Sweden

In northern Sweden I worked in an existing experimental setting on a small spatial scale to study the effects of moose and habitat productivity on species composition, growth and flowering of the field layer vegetation and abundance and diversity of flower-visiting insects. The effects of different moose densities and habitat productivity were studied in an experiment with simulated moose densities which has been described in many previous studies (Persson *et al.*, 2009; Suominen *et al.*, 2008; Persson *et al.*, 2007; Persson *et al.*, 2005a; Persson *et al.*, 2005b). The experiment was designed as a randomized block experiment with eight study sites and four treatment plots (i.e. moose density plots) within each site.



Figure 3. Study areas; Stor Elvdal municipality in Hedmark, south-eastern Norway, and the area outside Umeå in Västerbotten, northern Sweden.

Each treatment plot was 25 x 25 m, and the four plots were separated by a buffer zone of 5 m between plots and a fence of 5m height that surrounded the site (Figure 4). The experimental treatment included simulation of browsing, defecation and urination corresponding to four levels of moose population density on a landscape scale, from 0 moose per km² (control), through 1, 3 and 5 moose per km², the last corresponding to the highest density experienced locally in Sweden (Figure 4). The eight study sites were selected to cover the entire productivity gradient in the middle boreal zone (Ahti, 1968). An index of site productivity was developed by ranking the study sites from the poorest to the most productive according to productivity of *P. sylvestris*, litter production, *Betula* spp. browse production and field-layer vegetation composition and using the mean of these four

ranks as a productivity index. The index has proven to be a good estimate of habitat productivity and was tested in Persson *et al.* (2009; 2007) and Suominen *et al.* (2008).

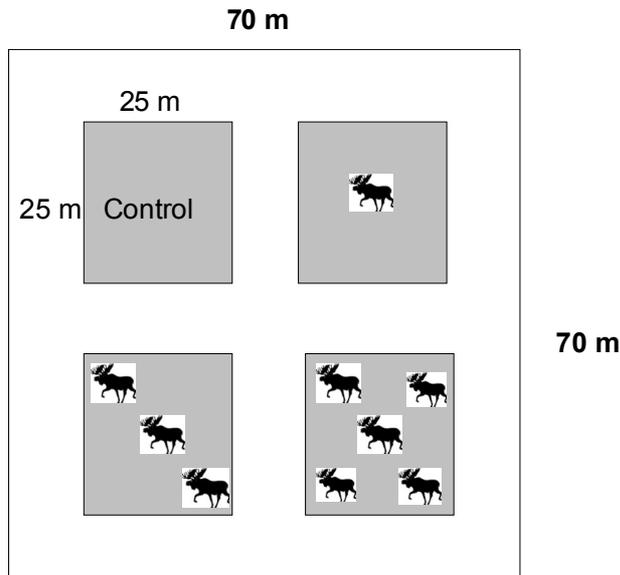


Figure 4. Experimental setup showing one enclosure with 4 treatment plots corresponding to simulation of 0, 1, 3, and 5 moose per km².

The simulation of different moose densities was based on an extensive literature review (Persson *et al.*, 2000). The removal of biomass was based on an estimated daily food intake of moose of 5 kg dry mass in winter and 10 kg in summer (Persson *et al.*, 2000), and the year was divided into winter and summer seasons (180 days each). The species composition of food plants removed was based on studies of the diet composition and browsing patterns of moose (Shipley *et al.*, 1998; Bergström & Hjeljord, 1987; Cederlund *et al.*, 1980). During winter, live shoots of *P. sylvestris*, *Betula* spp., *S. aucuparia*, *P. tremula* and *Salix* spp. were clipped from 50 cm above ground (normal snow depth) and up to 3 m height. The diameter and number of shoots clipped per tree for *P. sylvestris* and deciduous trees were based on field studies of natural moose browsing in the area (Persson *et al.*, 2007; 2005a). *P. sylvestris* was clipped at around 4 mm in diameter, *Betula* spp. at 2.5 mm and the highly preferred species *S. aucuparia*, *P. tremula* and *Salix* spp., were

clipped hard at 4mm diameter whenever encountered. In summer deciduous trees and raspberry (*Rubus idaeus* L.) were leaf-stripped. The trees that were clipped or leaf-stripped were chosen at random within each treatment plot. In the field layer, *V. myrtillus* and *C. vulgaris* were clipped by taking one handful at a time of leaves and current shoots also based on studies of natural moose (K. Danell and R. Bergström, pers. obs.). *E. angustifolium* was clipped at a height where 70 % of the stem was removed (R. Bergström, pers. obs.).

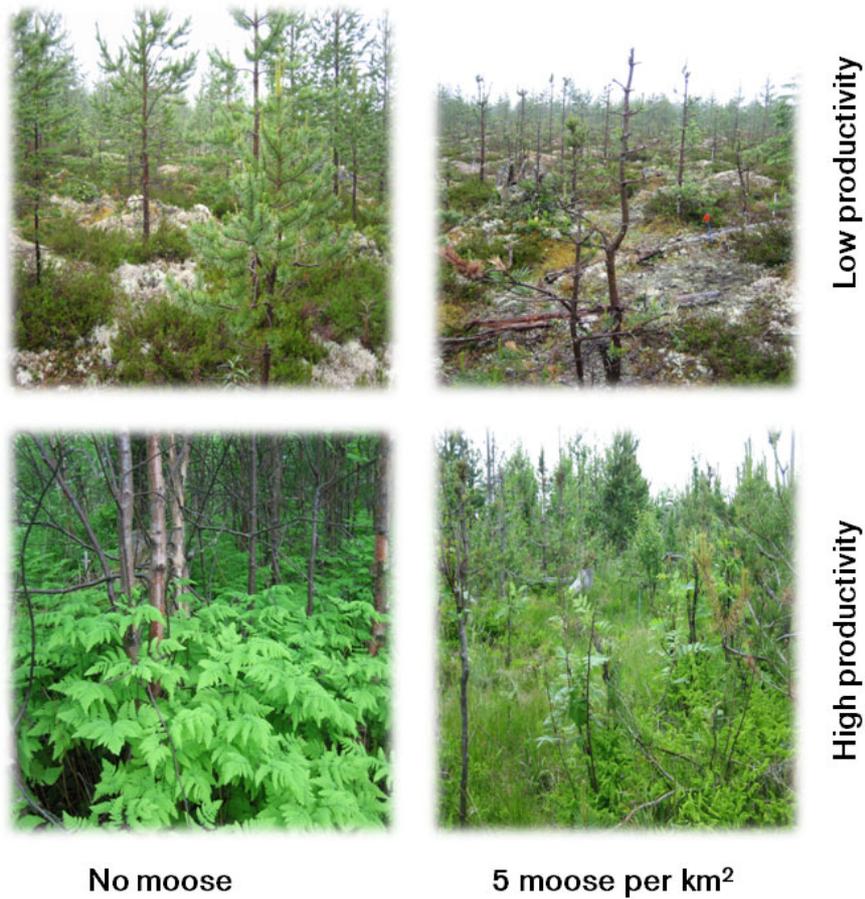


Figure 5. Simulated moose browsing in the experiment in Umeå. The pictures compare the control plot (left) with the high moose density plot (right) at low (above) and high productivity sites (below) after 7 years of simulated browsing. Photos: Inga-Lill Persson.

A random spot within each treatment plot was chosen for clipping of the field layer vegetation each time. Thus, a temporally and spatially variable clipping pattern was applied. During the growing season the clipping and

leaf stripping were done once a month. For winter, when plants are dormant, the clipping for the whole winter was done in April before the growing season started. Natural moose dung was added from a farm nearby where moose were fed a natural diet (Nyberg & Persson, 2002), and artificial urine (urea dissolved in water) was added in proportion to the clipping intensity (Suominen *et al.*, 2008; 2007; Persson *et al.*, 2005a; 2005b). Simulation of defecation and urination was also random within the treatment plot, and was carried out twice a year at the end of the summer and winter season. The effects of the simulation experiment were very similar to natural moose browsing, and are illustrated in Figure 5. Simulated moose density and browsing in this experiment will for practicality be called “moose density” or “moose browsing” hereafter.

2.2 Stor-Elvdal, south-eastern Norway

To study bird species composition and reproduction, a larger scale was required. I used a gradient in moose winter density around moose supplementary feeding stations in Stor-Elvdal to study effects of moose density and how nutrient input through supplementary food modified the impact of moose density on bird species composition and reproduction. This can be considered a “quasi-experimental” design (Shadish *et al.*, 2002) where moose density in the area is manipulated by the presence of feeding stations. The moose population in the area is mainly migratory, spending the summer at higher altitudes and migrating down to the valley bottom where the snow depth is lower in winter. Since 1990 local landowners have carried out organised supplementary winter feeding of moose with grass silage (Gundersen *et al.*, 2004), to attract moose away from the main road and railway line, reduce traffic accidents and browsing damage to young pine stands. The amount of food supplied has more than doubled during the study period, from 800 tonnes during the winter season 2003/2004 to 1700 tonnes in 2007/2008 (Stor-Elvdal landowner association, unpubl.). The overall moose density in the municipality varies between 1.1–3.4 moose per km² (Storaas *et al.*, 2005; Gundersen *et al.*, 2004), but in winter the effective moose density may be many times higher in the vicinity of feeding stations. In 2007, moose density at 1 km distance from feeding stations was 3.6 ± 1 moose per km² (estimated from pellet counts (this study, see methods Paper III) assuming 14 pellet groups per moose per day in winter (Persson *et al.*, 2000) and a winter period of 180 days). At a local scale of 25–50 m radius around feeding stations, pellet group density corresponded to a moose

density of 130 ± 20 moose per km^2 . However, this reflects intensive use of feeding stations by moose, rather than population density in the area.

Feeding stations for moose represent points of high moose density in the landscape with high browsing pressure and nutrient input (though silage, dung and urine) and both effects decrease with distance to feeding stations (van Beest *et al.*, 2010a; Gundersen *et al.*, 2004). Nutrient input and browsing intensity at feeding stations operate on different scales. Nutrient input through dung and urine is intense at a local scale (up to 50 m from feeding station) and then decreases rapidly, caused by high processing of supplementary food at feeding stations. Browsing pressure on birch is intense up to 500 m and decreases gradually with distance from feeding station but at a larger scale than dung density. Pine browsing pressure is high up to 1 km from feeding stations, whilst spruce browsing occurs almost only up to ~50 m from feeding stations (van Beest *et al.*, 2010a; Pedersen *et al.*, 2007; Gundersen *et al.*, 2004). Dung, silage remains and browsing at feeding stations are illustrated in Figure 6.



Figure 6. Top: Supplementary feeding station for moose in winter. Middle: Paths of moose dung and browsed birches at a feeding station. Bottom: Silage remains in front and heavily browsed spruce and birch at a feeding station.

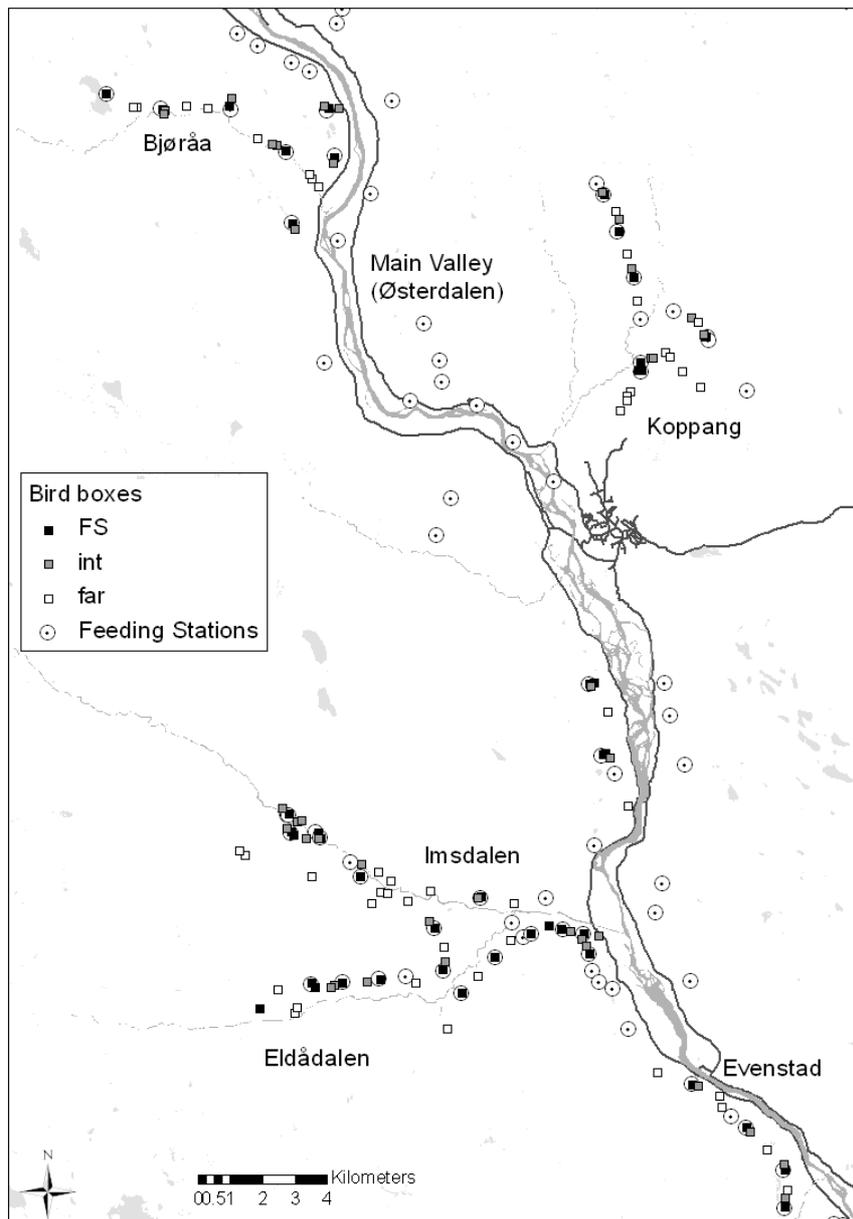


Figure 7. Map of supplementary feeding stations for moose and bird boxes used in Paper III and IV in Stor-Elvdal municipality, Hedmark County, Norway. Bird boxes were grouped into 3 categories in Paper IV: FS: Bird box at a feeding stations (overlapping feeding station points), int: boxes 50-499 meters from feeding stations, far: bird boxes 500m-1800 m from feeding stations. The main roads and rivers are also displayed.

3 Field methods:

3.1 Field layer vegetation and flower-visiting insects (Paper I and II)

The field layer vegetation was surveyed in the simulated browsing experimental area in 2006 and 2007, and pollinators were surveyed in 2007. The most extensive field layer vegetation survey was carried out in 2006 with repeated surveys in the months June, July and August, where we measured vegetation cover and height, and counted buds and flowers of all plant species in the field layer to investigate reproduction and growth. This survey was carried out in 16 plots of 1 m² systematically distributed in each moose density plot in all eight sites, but avoiding edge zones. Light availability was also measured in 2006, to investigate how moose browsing changed light availability under the tree canopy. Photosynthetic active radiation (PAR) was measured at 1.5 m height with a light meter (see Paper I for details).

In 2007 we followed up with a survey of flower-visiting insects during July, where we trapped insects using yellow pan traps filled with water, glycol as a preservative and detergent to reduce surface tension. One trap was placed in the middle of each treatment plot. The traps were emptied every four days for a period of 20 days, and all insects were later identified to family level. We counted flowers in the field layer vegetation in the same period, to relate insect data to flower abundance. Flower density was counted in ten 2.25 m² plots in each treatment in all sites (see Paper II for details). For the analysis, we used the flower density of *Vaccinium vitis-idaea* and *Melampyrum pratense*, as these were the main flowering plant species during July. These plant species are also important nectar resources for pollinators (Nielsen,

2007), and showed indirect positive effects of increasing moose density on flower density the previous year (Paper I).

3.2 Bird diversity and reproduction (Paper III and IV)

Bird diversity and reproduction was investigated along a gradient of moose winter density around supplementary feeding stations for moose. Bird diversity was investigated using point counts, where singing males were registered at feeding stations and points 1 km from feeding stations in 2007. Songbird vocalisations were surveyed early in the morning, for ten minutes at each station, during April - June, once a week, for five weeks. Observers were rotated systematically among sites and time of day, to avoid bias due to observer differences. Birds were grouped in functional groups according to diet and nesting height, to investigate if certain groups responded differently to moose density than others (see Paper III for details). Bird reproduction was studied in nest-boxes placed along the same gradient but at a finer scale, including boxes at feeding stations, at intermediate distances (50-499 m from feeding stations) and far from feeding stations (500-1800 m) over five years, 2004-08, (Figure 7 and Paper IV, study design). Number of bird boxes varied with year, from 38 boxes in 2004 to 145 boxes in 2007. The number of eggs, fledglings and the mass of fledglings were recorded for the two most common species, the pied flycatcher (*Ficedula hypoleuca*) and the great tit (*Parus major*). Frequency of parents bringing food to nestlings was surveyed in 2007 by using nest-box activity loggers. Diet composition in great tits was also surveyed in 2007 by video filming of prey brought to nest boxes by the parents. The food items were identified to group (Lepidoptera, Hymenoptera, Coleoptera, Aranea, and Diptera) and to life stage (larvae, pupae, and imago). Prey length and width was measured relative to beak size, and a volume index was calculated for each prey item, assuming a cylindrical form. Habitat and moose variables were recorded at all bird boxes and point count stations in 2007. Vegetation cover (%) of trees and field layer vegetation was recorded in a plot of 10m radius around each nest box. Moose browsing pressure (% shoots browsed/shoots available) and moose pellet density were counted in 5 circular plots of 50 m², one under the box, and one in each cardinal direction (see Paper IV for details).

4 Results and discussion

4.1 Moose density, productivity and field-layer vegetation (Paper I)

We have shown that simulated moose browsing led to a change in the field layer community from a vegetation type dominated by a browsed dwarf-shrub (*V. myrtillus*) to a community dominated by an unbrowsed graminoid (*A. flexuosa*) (Paper I, Fig 1b & 2a). Browsed species (*V. myrtillus*, *C. vulgaris*, *E. angustifolium*, *R. ideaus*) showed negative effects of increasing moose density on growth and flowering, whilst the opposite was the case for non-browsed species, confirming our predictions. The most important indirect effect of moose browsing was a change in light availability (Figure 8), which resulted in an increase in cover of species adapted to an open habitat (Paper I, Fig 1a), a decrease in height in most species (Paper I, Fig 2b) and an increase in total reproductive effort with increasing moose density (Paper I, Fig 1 c-f). This result resembles one from a study of natural moose browsing in central Sweden by Suominen et al. (1999) that suggested that in the ground layer of a pine forest moose browsing led to increased cover of light demanding lichens at the expense of shade tolerant mosses.

A. flexuosa most likely increased in cover and reproductive effort (Paper I, Fig 2a,c) because of increased light availability and/or because of decreased competition with *V. myrtillus* with increasing moose browsing. However we cannot disentangle these two simultaneous effects. Similar effects of herbivory, plant competition and light availability have been shown in studies of cyclic succession where defoliation of *C. vulgaris* led to increased light availability and increased cover of *A. flexuosa* (Bokdam, 2001). Also *V. vitis-idaea* increased in reproductive effort with increasing

moose density, but not in cover (Paper I, Fig 2a, c). This may be explained by reduced competition with *V. myrtillus*, as removal of *V. myrtillus* has been shown to increase berry production in *V. vitis-idaea* (Shevtsova *et al.*, 1995). Increased flower density of *V. vitis-idaea* could potentially increase food abundance for flower-visiting insects, which was investigated in Paper II.

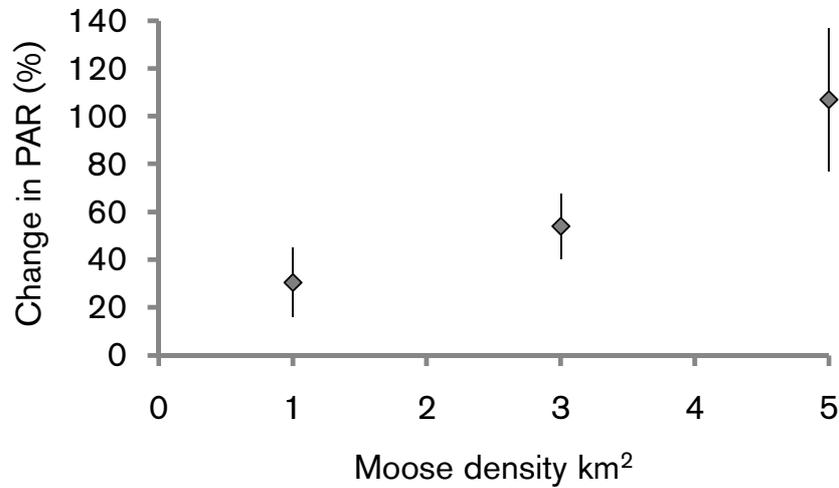


Figure 8. Relative increase (%) in light availability (PAR measured at 1,5 m) in moose treatment plots compared to the control plot for 3 simulated moose densities (mean and SE of 8 sites).

Total reproductive effort increased with increased light availability (Paper I, Fig 1h). This may indicate that reproduction in the field-layer vegetation is light-limited at low moose densities and that when moose browsing opens up the canopy, increased light availability leads to increased reproductive effort. This is also supported by the relatively higher increase in total reproductive effort in the productive areas where light was a more limiting factor (Figure 5). Only plant groups adapted to nutrient poor and dry habitats increased their reproductive effort with increased light availability, indicating that nutrients and moisture may be limiting reproduction at high moose densities. Increased moose density has had documented negative effects on litter quantity, N-return to soil and soil respiration, but weak effects on soil moisture (Persson *et al.*, 2009; Persson *et al.*, 2005b; Pastor & Naiman, 1992). The observed positive effects of moose density on reproductive effort in the field layer in this study, indicates that positive effects of moose browsing on increased light availability and reduced

competition with bilberry on the field layer vegetation were stronger than negative effects of reduced nutrient availability.

The effects of moose density were modified over the gradient of habitat productivity. The trend was the same for all species (*A. flexuosa*, *V. myrtillus*, and *T. europaea*), total reproductive effort (Paper I, Fig 1g and 3a-c) and light availability, with positive effects of moose density increasing with increasing productivity, and negative effects decreasing with increasing productivity. These results are similar to other studies from the same experiment (Suominen *et al.*, 2008; Persson *et al.*, 2007), indicating that generally the relative effect of moose browsing is negative in poor environments, whilst in more productive environments the relative effect of moose browsing may be positive. This interaction may be caused by two mechanisms: 1) More productive areas tend to have taller and denser vegetation and are more affected by light competition than less productive areas, therefore the opening up of the canopy creates a greater relative increase in light availability in a productive habitat, 2) In a more productive environment plants have more nutrients available, and are able to compensate for browsing by growth, hence negative effects of browsing on growth and reproduction may be stronger in a resource poor environment, where compensatory growth is limited by nutrients (Proulx & Mazumder, 1998; Coley *et al.*, 1985).

4.2 Moose density, productivity and flower-visiting insects (Paper II)

The insects caught in the traps were mainly dominated by Hymenoptera and Diptera, and reflected common groups of flower-visiting insects in the boreal forest (Nielsen, 2007). In general, Hymenoptera showed stronger responses to changed moose density than Diptera. Moose density had a significant positive effect on Hymenoptera family richness, but only in high productivity sites (Paper II, Table 2, Fig. 2). In contrast, moose density showed a marginally significant positive effect on Diptera family richness, but only in low productivity sites (Paper II, Table 2). Other studies of effects of herbivores on arthropod richness have also shown that responses to herbivore density differ strongly between arthropod groups (Suominen *et al.*, 2008). We found no significant effects of moose density on abundance of flower-visiting insects (Paper II, Table 2).

The weak positive effect on Diptera richness in low productive sites, but not in high productive sites, may be due to different initial species composition in low and high productivity sites. A path analysis of effects of moose density through light availability and flower density (Figure 9) showed that increasing moose density had a positive effect on Hymenoptera family richness through increased light availability in high productive sites, and not through effecting flower density.

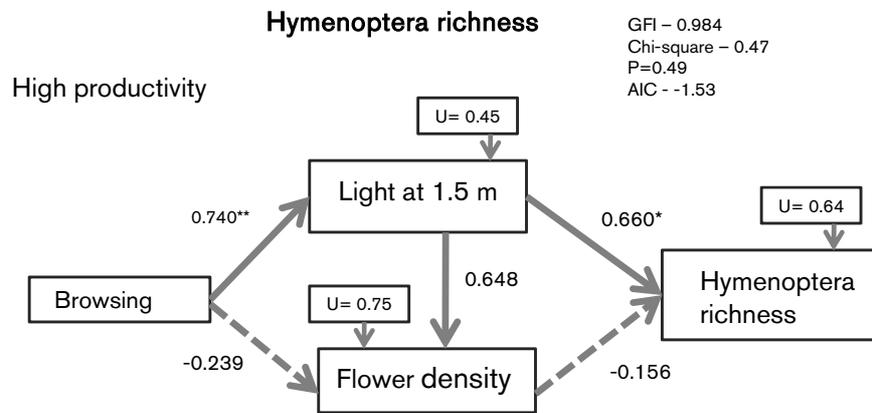


Figure 9. Illustration of the path analysis of the indirect effect of moose browsing through light availability and flower density on Hymenoptera richness at high-productivity sites. (Fig. 4a, Paper II). Solid lines indicate significant or marginally significant relationships ($p < 0.10$), dotted lines indicate non-significant relationships. Line numbers are path (standardized regression) coefficients. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$. U - unexplained variance, $1-R^2$

This may explain why the increase in Hymenoptera family richness occurred only in high productive sites, as the relative increase in light availability was higher in highly productive, shady sites, as shown in Paper I. It also indicated that the effects of moose density on flower density found in Paper I, had little effects on flower-visiting insects. However, this study was restricted to July, and effects of flower density in June or August may also be important for the community of flower-visiting insects. Moose browsing opens up the canopy, increasing light availability (Figure 7) and temperature, and this may favour activity and habitat suitability for many species of Hymenoptera (Campbell *et al.*, 2007; Cartar, 2005; Moretti *et al.*, 2004). Also reduced field layer vegetation height (Paper I) and a more open canopy may contribute to increased mobility and activity of flower-visiting insects (Sjodin *et al.*, 2008; Sjodin, 2007). Hence moose browsing may affect arthropod richness by changing the abiotic environment. The mechanism

revealed in this study is similar to effects of moose browsing on abundance of gastropods, where browsing opens up the environment, reducing humidity and habitat suitability (Suominen, 1999).

4.3 Moose browsing, nutrient input and the bird community (Paper III)

Abundance and species richness of insectivorous birds and birds nesting at browsing height were negatively related to moose browsing pressure on birch (Figure 10 & Paper III, Fig. 3b). This indicates that moose browsing reduced food availability or habitat cues for insectivores (Pedersen *et al.*, 2007), and also changed the structure of the habitat leading to fewer nesting places or increased predation risk (Fuller, 2001). Maybe the most interesting result in this study was a positive effect of feeding stations on species richness and abundance in general (Paper III, Fig. 1bc), and of insectivorous birds in particular (Figure 10). This indicates a positive bottom-up effect of increased nutrient input at feeding stations, but the mechanisms behind this increase are not clear. Granivorous birds showed a positive relationship with birch browsing, and a negative relationship with feeding stations (Figure 10).

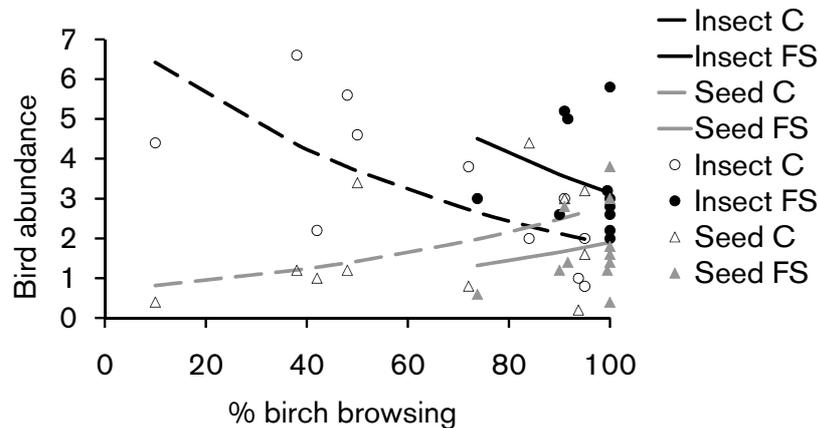


Figure 10. Abundance of seed- and insect-eating birds with increasing birch browsing pressure (% shoots browsed of shoots available) at supplementary feeding stations for moose (FS) and control sites 1 km from feeding stations (C.) (Fig. 3a, Paper III).

A possible explanation for this pattern may be that granivores benefit from increased seed size in birch with increasing moose browsing on birch (Bergström & Danell, 1987), but suffer from reduced seed availability in

spruce because of spruce browsing at feeding stations. Although different functional groups showed contrasting responses, total bird diversity and abundance showed the same pattern as that of insectivores, as they were the dominant group in the species assemblage (Paper III, Fig. 1b, c). This study shows that changed habitat structure due to browsing is important for bird species dependent on vegetation at browsing height, in accordance with several other studies (Berger *et al.*, 2001; Fuller, 2001). This study is the first to show evidence of possible cascading effects of browsing on bird food availability and effects of nutrient input at supplementary feeding stations.

4.4 Moose browsing, nutrient input and bird reproduction (Paper IV)

Reproduction, habitat selection and feeding activity showed opposite responses to a gradient in moose density in the two study species, great tits and pied flycatchers (Paper IV, Figs. 1, 2 and 4). Great tits showed a negative relationship with moose density while pied flycatchers showed a positive relationship, for all three variables. Also mass of flycatcher fledgings was highest at high moose densities (Paper IV, Fig. 3). The different responses of the two bird species studied may be explained by their foraging behaviour and habitat preferences. Great tits are leaf-gleaners and may suffer from reduced birch biomass at high moose density (Naef-Daenzer *et al.*, 2000; Slagsvold, 1975). Flycatchers may catch insects in the air, prefer a more open habitat and may profit from moose browsing (Sanz, 1998; Slagsvold, 1975).

Habitat selection changed over time, as great tits were more common at feeding stations in 2004–2005, but in 2007–2008 they preferred to nest far from feeding stations (Paper IV, Fig. 1). During the same time period, activity of moose around feeding stations had increased, and the change in nest box selection might be due to accumulated browsing effects on the vegetation at feeding stations (van Beest *et al.*, 2010a). Bird feeding frequency showed the same response to moose density as reproduction, and we saw no differences in diet composition in great tits (Paper IV, Appendix 3). We therefore assume that food availability (quantity) is the mechanism behind changed reproduction with increased moose density. This study therefore supports the theory that herbivory may have cascading effects on bird reproduction through affecting food availability (Pedersen *et al.*, 2007; Evans *et al.*, 2006; Baines, 1996).

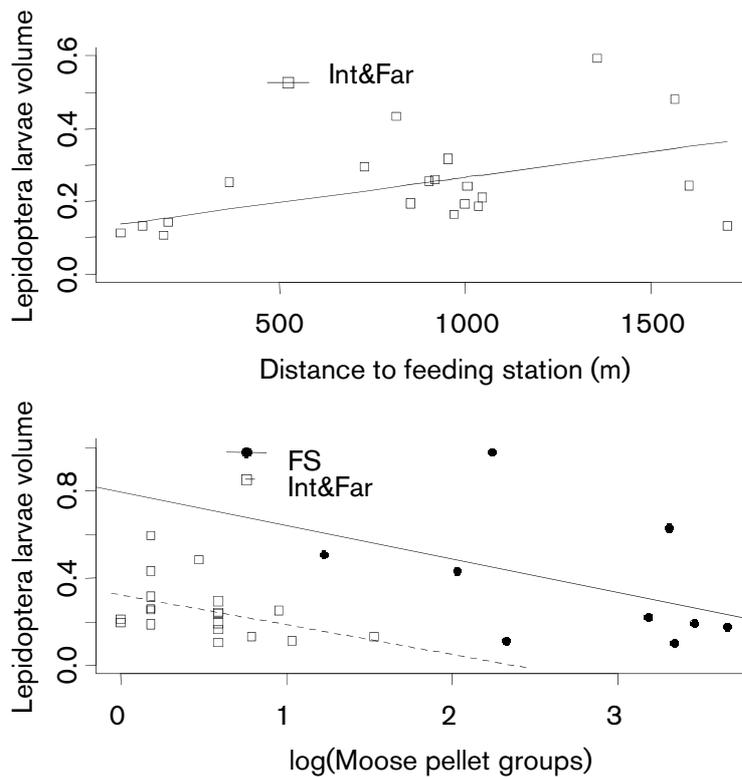


Figure 11. Caterpillar volume index of items brought to great tit nest boxes increased with distance to supplementary feeding stations (FS) for moose (upper) but decreased with increasing moose pellet density, and was larger at feeding stations compared to sites at 50–1700 m from feeding stations (Int & Far) with similar moose density (lower).

Filming of great tit nest boxes showed a negative relationship between the size of caterpillars and moose density, and a positive effect of feeding stations (Figure 11). This indicates that nutrient input at supplementary feeding stations may have a positive effect on the size of insectivorous prey. This result also shows the same trend as the effects of feeding stations and birch browsing found on diversity and abundance of insectivorous birds (Paper III). The reproduction responses of the two bird species appear to be related to the gradient in browsing intensity, and show few effects of nutrient input at feeding stations, as observed in the bird diversity study. As great tits showed a lower reproduction at feeding stations than far from feeding stations, and a reduced feeding frequency, the increase in larvae size at feeding stations (Figure 11) may not compensate for a general decrease in food quantity at feeding stations for the great tits.

4.5 Potential biases and limitations

Although the experimental simulation of moose density was as realistic as possible, experiments always have some limitations or “experimental artefacts”. One thing that was not simulated that potentially may be very important for the field layer vegetation (Paper I) was trampling. To simulate trampling in a scientific manner was not possible as field workers had to walk around in the different treatment plots. However, as human activity during clipping was higher in the high moose density plots, human trampling was also correlated to moose density. During fieldwork other than clipping, trampling was avoided as much as possible by walking in the buffer zones.

In the field layer vegetation, only plant species that were common in the moose diet such as *V. myrtillus*, *R. ideaus*, *C. vulgaris* and *E. angustifolium* were clipped in the experiment whilst species that are rare in the diet such as *Melampyrum pratense* were not clipped (Bergström & Hjeljord, 1987; Cederlund *et al.*, 1980). However, although some species in the field layer may not be very significant in the moose diet, moose browsing may have a significant impact on growth and reproduction in these species, as many of these species are of small stature and moose may well remove the whole aboveground part of the plant. Another advantage or disadvantage of the enclosure is that other large herbivores, such as roe-deer, reindeer and red deer were excluded. However, this may be a realistic scenario, as in many areas in the boreal forest in Scandinavia, moose is the dominant herbivore. Smaller herbivores, such as hares and rodents had access to the enclosures, and were sometimes observed foraging on the field layer vegetation, so our results on effects of moose browsing on growth and flowering in the field layer could potentially include also indirect effects via small herbivores. These limitations of the experiment mean that what I have studied is the indirect effect of moose browsing, urination and defecation on the field layer vegetation, not including trampling and other large herbivores. This may also be an advantage when investigating the strength of relative effects.

We used yellow pan traps to attract flower-visiting insects (Paper II), simulating the color of yellow flowers. Such traps may catch a selection of insect species that do not visit flowers, but fall into the trap by accident, or exclude flower-visiting insects that search for other specific cues than yellow. However, the main flowering plant at this period was *Melampyrum pratense*, which has yellow-white flowers, and the trap material contained many known flower-visiting groups, suggesting that the trap material was

representative. The observed changes in species richness and abundance of Hymenoptera with different moose treatments could also potentially be a result of different trapability in the different treatments. However, as insects had to actively seek the trap to get trapped, we assume that the trap material reflects insect activity, and not different trapability.

A similar issue of detectability might affect the bird observations in point counts (Paper III). It is commonly assumed that bird song is more easily detected in a more open environment (Bibby *et al.*, 2000; Bibby & Buckland, 1987). As species richness and abundance increased with increasing moose browsing, and moose browsing opens up the canopy, such a bias would only mean that the effect of moose browsing is even more negative than we found. For Paper IV, we could not avoid the fact that there was a dependency in nest box choice between the two bird species since the great tit usually arrives first, and the flycatcher could only choose from the boxes that were left after the great tits had nested. However, every year there were empty boxes after the flycatcher had made its choice, indicating that the choice of boxes near feeding stations for moose was an active one.

In paper III and IV, feeding stations was used as a way to manipulate moose density, and study effects of moose density on bird diversity and reproduction. Moose browsing at feeding stations may be comparable to natural browsing pressure in areas with high moose density. However supplementary feeding over a long time period may convert moose into central-place foragers, and lead to accumulating affects of high browsing on the vegetation close to feeding stations (van Beest *et al.*, 2010a; van Beest *et al.*, 2010b). Feeding stations also lead to increased browsing on spruce, which is normally a non-preferred species, so this is probably an artefact of the supplementary feeding (van Beest *et al.*, 2010a). Also input of dung and urine is higher than at corresponding natural high browsing pressures, because of the processing of supplemental forage. However, by comparing areas with high browsing pressure with feeding stations, we could to some degree separate the effects of nutrient input and browsing.

5 General discussion

5.1 Trophic and non-trophic mechanisms behind effects of herbivores

The mechanisms linking effects of herbivores on vegetation species richness and composition, and cascading effects on animals, are complex. Indirect effects are often suggested to be weaker than direct effects (Hebblewhite *et al.*, 2005; Wootton, 1994; Strauss, 1991). Hence animal responses may be similar to vegetation responses to herbivory, but with lower amplitudes. The mechanisms here still need further investigation, but our results point to some important pathways (Figure 12). Moose activity had two main indirect effects; changing habitat structure and changing resource availability. Browsing in this study had indirect effects on other fauna through changed vegetation structure and changed abiotic factors, such as increased light availability. This is a mix of trophic and non-trophic effects, as herbivore foraging on plants is a top-down trophic controller that changes physical properties of the environment for other species, affecting birds, flower-visiting insects and non-browsed plants in the field-layer vegetation. This mechanisms can therefore not be described as that of an ecosystem engineer as they include trophic effects (Jones *et al.*, 1994). They may better be described as indirect effects through modification of the environment (Strauss, 1991). The trophic mechanisms described include the cascading effect through moose browsing on vegetation structure and abundance of seeds and insectivorous prey for passerine birds. This is similar to the observed mechanisms behind indirect effects of other herbivores (Suominen & Danell, 2006; Rooney & Waller, 2003).

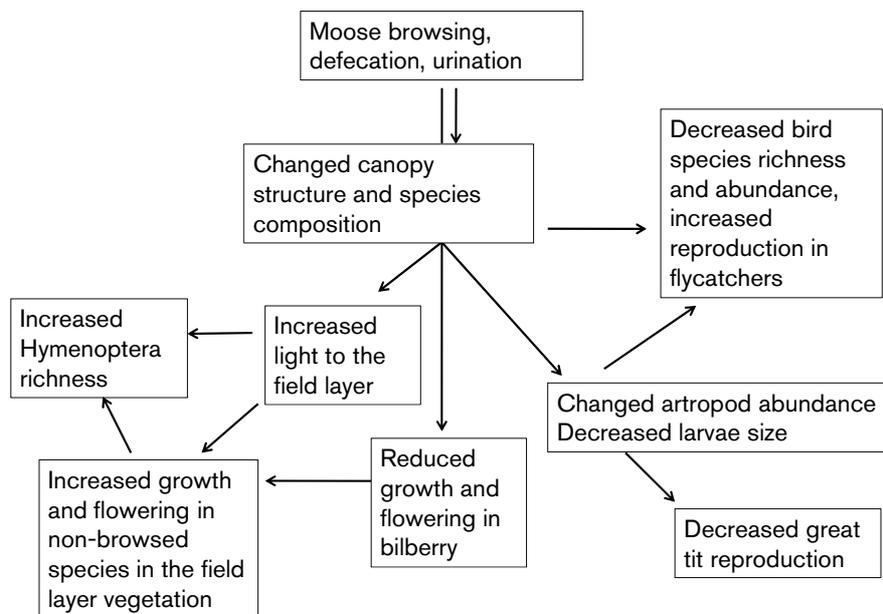


Figure 12. The mechanisms behind moose-driven indirect effects on the birds, field-layer vegetation and hymenopterans in this thesis

5.1.1 Indirect effects on plants

As described above, herbivory may change the competition between plant species, affecting resource competition for light, water and nutrients and possibly also interference competition. Moose browsing in the tree canopy may affect the field layer vegetation indirectly, as increased light availability lead to an increase in total reproductive effort and changed species composition (Paper I). Also browsing on bilberry may have had an indirect positive effect on neighbouring plant species (Paper I), which may be described as an indirect mutualism (Wootton, 1994) between moose and non-browsed species. So the changes in the field layer may be caused by competition both within the field-layer, and between the field layer and the tree canopy (Paper I). In deciduous forest understories, graminoids and ferns benefit from heavy browsing pressure from cervids, as graminoids are tolerant to herbivory, whilst ferns generally avoid herbivory (Rooney & Waller, 2003; Gill, 1992). However, the mechanisms may differ; deer browsing may increase the abundance of grazing-tolerant graminoids (Rooney, 2009), whilst in Paper I, the increase in graminoids was caused by the indirect effects of browsing on other species.

Changed competition between plant species in the canopy may change the rate of succession in boreal forests (Pastor & Naiman, 1992). Changed succession rate may also occur in the field-layer as deer browsing may retard succession in forest field-layers (Rooney, 2009). In our case, succession was also retarded, as bilberry – a more shade tolerant late-successional species was replaced by a more light-demanding early successional grass (Paper I). In the canopy, moose browsing in boreal forests may cause spruce to increase in dominance compared to preferred species (Pastor & Cohen, 1997; McInnes *et al.*, 1992). Indirect effects of moose on non-browsed plants may be more common in boreal forest than in other systems as some plant species such as spruce are practically not eaten (Augustine & McNaughton, 1998). Moose, as browsers, also eat fewer species in the field layer than mixed feeding or grazing species of deer. In other systems with higher productivity where most of the plant species are eaten (or trampled), direct effects of herbivores on plants play a larger role (Pastor *et al.*, 2006; Augustine & McNaughton, 1998). But in systems with low productivity, selective herbivores and a high abundance of unpalatable species (Augustine & McNaughton, 1998; Ritchie *et al.*, 1998; Owen-Smith & Cooper, 1987), indirect effects on plants may be expected to play a larger role.

5.1.2 Indirect effects on animals

According to Paper III and IV, moose browsing may affect the bird community both through indirect effects on habitat structure and on food availability. Previous studies have suggested that changed structure of the browsed vegetation is the main driver behind indirect effects of browsing cervids on birds (Berger *et al.*, 2001; Fuller, 2001; McShea *et al.*, 1997), but other studies have suggested that effects of herbivory on invertebrate prey may also be important (Dennis *et al.*, 2008; Pedersen *et al.*, 2007; Evans *et al.*, 2005; Bailey & Whitham, 2003). Our results support both these hypotheses and show that large herbivores may have cascading indirect effect on other levels of the food web through their foraging (Larson & Paine, 2007). Exclusion of megaherbivores in an African savanna showed that herbivores affected bird diversity and abundance both through changing vegetation structure and changed arthropod food availability (Ogada *et al.*, 2008; Cumming *et al.*, 1997), suggesting that the mechanisms may be similar across ecosystems. Few studies have investigated the actual mechanism linking herbivory and bird diversity and abundance, mainly because of the difficulties with carrying out experimental studies at a larger scale. The few studies that link herbivory and bird food availability, have a more

experimental approach, but at a smaller scale (Dennis *et al.*, 2008; Pedersen *et al.*, 2007; Evans *et al.*, 2005; Bailey & Whitham, 2003). Overall, herbivory seems to have a negative effect on bird diversity and abundance, but a positive effect on certain species that are adapted to open grassland or forest patches (Evans *et al.*, 2006; Suominen & Danell, 2006; Evans *et al.*, 2005; Fuller, 2001) (Paper IV) . One reason that studies of herbivory register negative effects on birds and mammals may be that such studies are often performed in areas of extremely high herbivore density, and do not include low herbivore densities (Suominen & Danell, 2006). The study presented in Paper III was also carried out in an area of high moose density, with high moose density even far from feeding stations. In contrast, some studies have shown that moderate grazing pressure by sheep in alpine pastures may have none or positive effects on bird diversity (Loe *et al.*, 2007). However, grasslands and forest may not be directly comparable when considering birds, because of the more complex vertical structure of forests.

Several studies show that herbivores affect pollination through direct foraging effects on plants (Vazquez & Simberloff, 2004; Juenger & Bergelson, 2000; Allison, 1990), but to my knowledge Paper II is the first study of indirect effects of large herbivores on environmental variables and flower-visiting insects. Although invertebrate responses to large herbivore activity are very diverse, there is a general tendency that invertebrate herbivores feeding on the same plant as vertebrate herbivores decrease in abundance with increasing vertebrate herbivore abundance (Suominen & Danell, 2006). This can have several explanations. First, herbivores can affect plant attractiveness for pollinators through reducing flower density or plant height (Juenger *et al.*, 2005; Vazquez & Simberloff, 2004). Second, flower-visiting insects may compete with ungulate herbivores for the same plants, and reduced flower density and flower diversity by grazing may reduce abundance and diversity of flower-visiting insects (Sjodin *et al.*, 2008; Sjodin, 2007). We found that a third mechanism can explain the patterns observed, as my results indicate, light-availability was the main mechanism linking moose density to Hymenoptera family richness (Paper II). Invertebrates are sensitive to small changes in microclimate, such as temperature and humidity, and are thus often indirectly affected through physical habitat modification by large herbivores (Stewart, 2001; Wardle *et al.*, 2001; Suominen *et al.*, 1999). It has been shown that forest logging leads to an increase in bumble bees (*Bombus* spp.), through an opening up of the environment (Nielsen, 2007; Cartar, 2005), and it has been suggested that lower vegetation height may increase the mobility of flower-visiting insects

(Sjodin, 2007). Our study shows that effects of moose density on flower density might also be a potential mechanism affecting flower-visiting insects. However, in the case of Paper II, the main flowering plants at the time were not browsed. As browsing herbivores in forests eat only some of the plants available compared to more nutrient rich ecosystems where herbivores eat many of the plant species available (Augustine & McNaughton, 1998), responses to herbivores may be more difficult to predict in a boreal forest because herbivorous invertebrates respond to both browsed and non-browsed species.

This study illustrates the complexity of indirect effects of large herbivores, with the possibility of several effects operating simultaneously and obscuring each other if they act in opposite directions (Rooney & Waller, 2003; Strauss, 1991). In the field layer vegetation, positive effects on reproduction and growth in non-browsed species were probably caused both by the effects of reduced competition from bilberry and effects caused by increased light availability (Paper I). Positive effects of moose density on light availability and negative effects on flower density affected Hymenoptera richness simultaneously, although path analysis identified light availability as the strongest driver (Paper II). In the case of bird diversity at supplementary feeding stations for moose, the negative effects of browsing and the positive effects of nutrient input on bird diversity and abundance at feeding stations lead to a net zero effect of supplementary feeding stations on bird species richness (Paper III). In addition, there may be other pathways that we have overlooked.

5.2 How does moose density affect biodiversity?

In this study I have looked at how moose affects species richness at a small to medium scale, in both time and space. I have found mainly negative effects of moose browsing on species richness in low productivity habitats, and positive effects in high productivity habitats. Therefore, an important finding of this study is that productivity should be included when discussing effects of moose and other larger herbivores on biodiversity. Furthermore, I found that responses to moose density differ with trophic level, as vegetation and insects showed both positive and negative responses, but bird diversity showed only negative responses, consistent with other studies (Suominen & Danell, 2006). A small scale is often necessary in ecology to establish experiments and investigate mechanisms. To evaluate effects of moose on the ecosystem and to discuss management implications, a larger scale

perspective than in this study is needed. On a larger scale in space, ecosystem effects of moose browsing will depend on moose spatial behaviour and heterogeneous use of habitats. As moose may prefer to forage more heavily in some patches than in others, or moose avoid some habitats because of the presence of humans or predators, patch selectivity by moose may create heterogeneity in the habitat, and have a positive effect on diversity (Edenius *et al.*, 2002a). However, this also depends on population density, as a low-moderate population density tends to increase diversity due to effects on habitat heterogeneity, while a high population density might decrease diversity due to a homogenization of the environment (Olf & Ritchie, 1998).

On a longer time scale, the effects of moose on forest succession will be important for the ecosystem. Moose may retard succession by reducing growth in birch and pine in low productivity sites (Persson *et al.*, 2007; Persson *et al.*, 2005a), where spruce cannot colonize, and by opening up the canopy, increasing light availability to the field layer, and increasing dominance of early successional shade-intolerant species (Paper I). Moose may also retard succession in the canopy if moose browsing increases productivity in early successional species such as birch or aspen, but this is only likely in high productivity habitats with moderate browsing pressure (Persson *et al.*, 2007; Pastor & Naiman, 1992). In the enclosure experiment, high moose density (5 moose per km²) retarded succession in most sites, by reducing canopy growth. But in one site, with a relatively high productivity and where a spruce seed source was present in the vicinity, spruce colonized in the browsed plots. This supports the theory that moose may hasten succession by giving late successional species such as spruce a competitive advantage (Pastor & Naiman, 1992), but only under certain conditions.

5.3 Interaction between herbivory and productivity

The community studies of field layer vegetation, flower visiting insects and birds gave little support for the intermediate disturbance hypothesis (Connell, 1978) alone. I found that species richness in both field layer vegetation and birds decreased with increasing browsing pressure, and that Hymenoptera family richness increased, but only at high productivity sites. Several results from the experiment with simulated moose browsing over a productivity gradient thus show that there is an important interaction between habitat productivity and moose density, as both positive and negative responses (relative to the control site) were positively correlated

with habitat productivity (Figure 13). My results concur with the general hypothesis of Larson and Paine (2007) that low productive areas are more susceptible to herbivory than high productive areas. The interaction between effects of productivity and effects of herbivory may explain why studies of herbivory in different habitats give contrasting results.

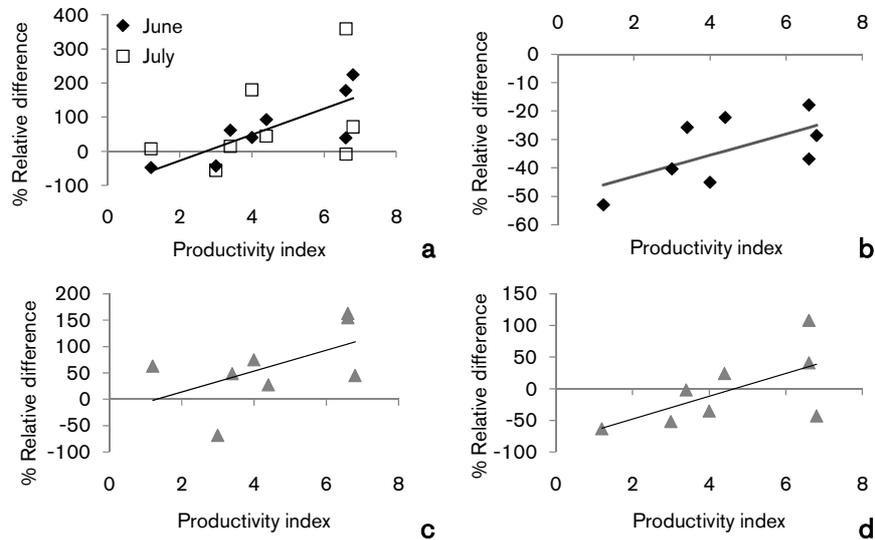


Figure 13. Relative difference of high moose density treatment ((response at 5 moose per km² – control)*100/control) for total reproductive effort in field layer vegetation (a), height in bilberry (b), Hymenoptera abundance (c) and Hymenoptera richness (d).

The consequence of this interaction is that an effect of herbivore density may switch from negative to positive with increasing productivity (i.e. Figure 13 d), which is consistent with both the grazer reversal hypothesis (Bakker *et al.*, 2006; Proulx & Mazumder, 1998) and the model of grazing in grasslands with varying resource availability (Milchunas *et al.*, 1988). Furthermore, it is consistent with the hypothesis that an ecosystem engineer that reduces productivity has a positive effect on species richness in high productivity habitats, and negative effects on species richness in low productivity habitats (Wright & Jones, 2004). These related hypotheses could therefore be unified in a more general theory concerning the interaction between habitat productivity and disturbance. Since both productivity and disturbance are assumed to maximize species richness at intermediate levels, there is a balance between productivity and disturbance that maximizes species richness (Kondoh, 2001). At low levels of

productivity, disturbance will have a negative effect on richness by increasing extinction rates, at intermediate levels of productivity disturbance will have a unimodal effect on richness by preventing competitive exclusion and at high levels of productivity, disturbance will have an increasingly positive effect on richness, because plant growth and competitive exclusion is high (Kondoh, 2001; Milchunas *et al.*, 1988). According to my results, the pattern of plant species richness in the field layer (Paper I) conforms to this pattern (Figure 14).

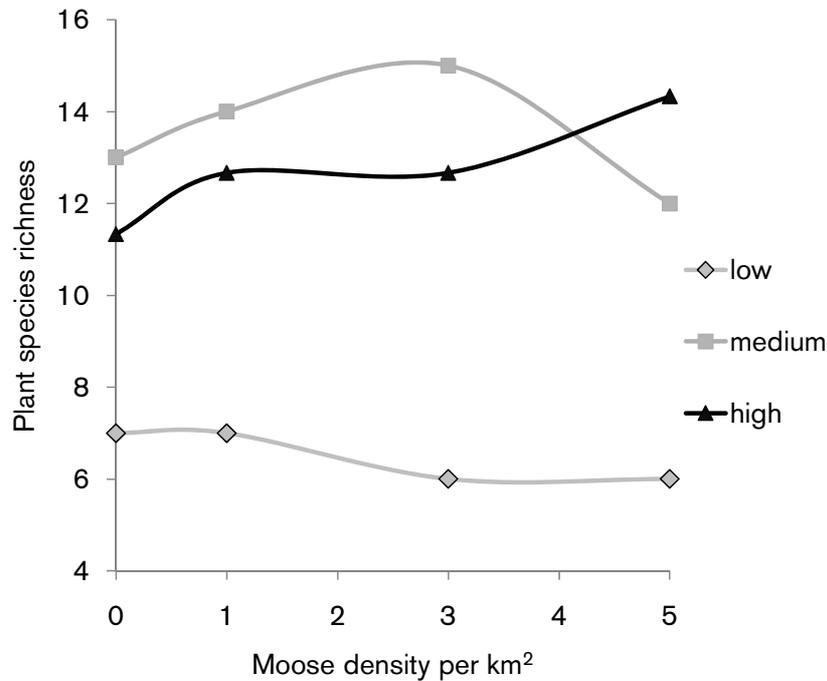


Figure 14. Species richness (mean) of field layer vegetation in relation to simulated moose density at low productivity sites (n= 3), medium productivity sites (n=2) and high productivity sites (n=3).

The input of nutrients at supplementary feeding stations for moose can be seen in a similar context (Paper III and IV, Figure 10, 11). Here productivity was increased, as nutrients were added, which modified the effect of moose density through bottom-up control. This led to an increase in species richness and abundance of birds, and increase in cover of herbs and grasses in the field layer vegetation (Paper IV) (Torgersen, 2008), and an increase in volume of caterpillars, compared to areas with similar browsing pressure but no nutrient input.

5.4 Management implications

My study of the effects of moose on the birds and the bees investigated in this thesis, has shown that moose can change species composition, species richness and reproductive output of birds and flowers. The direction of these documented changes supports the idea that increasing numbers of ungulates in many areas can have adverse effects on biodiversity and ecosystem processes (Garrott *et al.*, 1993), depending on site productivity. None of the bird species observed in this study are listed as threatened species to date in Norway (Kålås *et al.*, 2010), but birds may serve as useful indicators of ecosystem change. To determine whether high ungulate densities are a conservation issue needs to be evaluated on a larger scale. Bilberry can be regarded as a keystone species in boreal forest, and was observed to decline in abundance even at low moose densities in this study. Effects of moose on bilberry may have cascading effect on a wide range of other species (Baines *et al.*, 1994), and this may be a topic for further research. Habitat productivity has been a very important factor modifying species responses to moose browsing in this thesis, indicating that management goals for herbivore densities should consider that habitats vary greatly in their ability to sustain dense populations. However, the tipping point (Figure 10) from negative to positive effects of moose density relative to the control plot differs among responses, which makes it difficult to indicate any optimal moose density recommendations for management purposes. This highlights the importance of clear management priorities.

From a biodiversity conservation perspective, the effects of moose on the preferred tree species, rowan, aspen and *Salix* spp. (Edenius *et al.*, 2002a), which are important for the conservation of biodiversity of fungi, arthropods and birds (Griffis-Kyle & Beier, 2003; Suominen *et al.*, 2003a; Siitonen & Martikainen, 1994), may be more important than the effects of browsing on birch and pine that were dominant in this study. Even low moose densities today may prevent the growth of saplings of highly preferred species into trees, as these species are browsed hard whenever encountered (Edenius *et al.*, 2002b; Ericsson *et al.*, 2001). In addition, increasing commercial damage by moose browsing on pine has led to increased planting of spruce by forest owners in Scandinavia. This is carried out even in low productive areas that are more suitable for pine production, leading to spruce-dominated forests and lower biodiversity. This may have long-lasting ecosystem effects.

My results show that supplementary feeding stations for moose have a strong local effect on the vegetation, with cascading effects on birds. On a

larger scale, supplementary feeding stations may create a more heterogeneous forest, and therefore increase biodiversity. In certain areas, this management tool has become increasingly popular (Putman & Staines, 2004), i.e. more than 100 feeding stations in Stor-Elvdal municipality alone. Supplementary feeding of moose as a management tool has been shown to reduce moose-vehicle collisions (Andreassen *et al.*, 2005), but to increase long term browsing damage on pine (van Beest *et al.*, 2010a), and to be inefficient in diverting moose from young pine forest (van Beest *et al.*, 2010b). Furthermore they might also contribute to a higher population density than the natural browse production can sustain (Putman & Staines, 2004; Smith, 2001), with correspondingly high browsing pressures over a large spatial scale. Therefore I would recommend trying to adjust moose populations in relation to the quantity of natural forage produced through forestry management, rather than continuing to establish supplementary feeding stations with silage bales to solve management problems associated with high moose densities.

5.5 Future perspectives

There is a need for more research on the mechanisms behind indirect effects of herbivore activities, responses of animals and plants, and the relative strengths of direct and indirect interactions. This area has received little attention with few studies explicitly studying the mechanisms involved (Suominen & Danell, 2006; Rooney & Waller, 2003). There is also a general lack of studies at larger spatial and temporal scales, which would be important for understanding the mechanisms and implications of indirect effects by large herbivores. As wild cervid populations have increased in many areas, there is a need for more research on the effect this may have on ecosystem processes and possible conservation issues (Côte *et al.*, 2004; McShea *et al.*, 1997; Garrott *et al.*, 1993). Herbivore selectivity is a key to understanding ecosystem effects of herbivores, which is linked to how herbivores affect plant species distribution and productivity (Augustine & McNaughton, 1998; Pastor & Cohen, 1997). Therefore comparing systems with different herbivore populations and factors that modify their selectivity and the indirect effects of their activities (such as browsing/grazing, herbivore density, body size, and nutrient availability) may be useful to uncover general patterns. One approach may be to investigate how changes in the plant community are linked with changes in the animal community, and if animal responses can be predicted from plant community responses that are already modelled (Olf & Ritchie, 1998; Van Wieren, 1998;

Milchunas & Lauenroth, 1993; Milchunas *et al.*, 1988). Non-foraging activities, such as trampling, digging, rubbing, wallowing, fraying etc. have also not been well investigated, and deserve more attention. In addition, the importance of dung fertilization and urine on nutrient cycling, and how this affects nutrient cycling and feedbacks within the soil community, is important for understanding ecosystem effects of large herbivores (Pastor *et al.*, 2006). To develop management goals for large herbivore populations that are in accordance with ecosystem functioning and biodiversity conservation, the indirect effects of moose and other herbivores need to be evaluated at scales in space and time that are relevant for management, i.e. scaled up from mechanisms to ecosystem effects. A possible way to do this is to build ecosystem models that include large herbivore space use at a landscape scale. It is also important to include how global warming and changed atmospheric composition, in addition to management of herbivores, their food resources and predators (hunting, supplementary feeding, habitat management, forestry and agriculture), will modify effects of large herbivores and ecosystem dynamics in future scenarios. To investigate what the mechanisms are, and how they are modified by other factors, is best done in an experimental approach.

In the case of moose in boreal forests, some issues might be worth investigating closer. This study showed that moose browsing may have a negative impact on bilberry growth and reproduction, even at low moose densities (Paper I). As bilberry is a keystone species in boreal forest, and may affect other animals using the same resource such as arthropods, rodents, forest grouse and brown bears, cascading effects on these species should be investigated. Moose is also a potential competitor of pollinators for species such as bilberry, fireweed, raspberry and *Salix* spp., and may affect pollinator populations with cascading effects on plant reproduction. The boreal forest with low nutrient availability and strong selective foraging by moose is a unique system (Pastor *et al.*, 2006; Augustine & McNaughton, 1998; Pastor *et al.*, 1988) and the effects of moose on nutrient cycling through foraging, deposition of dung and urine, and how this affects plant and arthropod responses to browsing should be investigated further. These processes may also be modified by climate change, atmospheric composition, deposition of nitrogen from the atmosphere and from forest fertilizers and supplementary feeding. Large carnivores such as wolves and bears are recolonizing Scandinavia, which may have cascading effects on ecosystem effects of moose (Kauffman *et al.*, 2010; Hebblewhite *et al.*, 2005). How this changes moose behaviour and density, and potentially indirect effects of moose on

plants and animals may also be important for ecosystem restoration. On a larger scale, it would be interesting to combine recent knowledge of the spatial distribution of moose from GPS-collared animals (van Beest *et al.*, 2010c) with the ecosystem effects of moose, and to model this on a landscape scale, and test predictions. From a management perspective, it would be useful to know more about how effects of moose interact with forestry management, and how long-term supplementary feeding of moose affects moose density and ecosystem effects at a landscape scale. Such an understanding could be used to develop better moose management models including ecosystem management.

6 Summary and conclusions

My research had shown that moose browsing can have effects on vegetation structure, richness and composition that drive changes in the bird and pollinator communities, at a small-to medium scale. The effects of moose browsing are strongly dependent on habitat productivity, and tend to be negative in poor habitats, and positive in rich habitats. The interaction with habitat productivity corresponds to several hypotheses that state that herbivores may have negative effects on species richness in low productivity habitats, but positive effects in high productivity habitats (Wright & Jones, 2004; Kondoh, 2001; Proulx & Mazumder, 1998; Milchunas & Lauenroth, 1993). Supplementary feeding stations counteract the effects of moose browsing at a small scale by adding nutrients to the system, increasing productivity and modifying the effects of moose. However at a larger scale, they may sustain a high moose population with correspondingly high browsing pressure. The results in this thesis suggest that moose is potentially a strong driver of ecosystem processes and has indirect effects on other flora and fauna leading to changes in community composition. The effects on a larger scale, and how the mechanisms link moose activity to other parts of the ecosystem, have to be investigated in further studies.

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7 Sammendrag

Indirekte effekter av elg på blomstene og biene

Store herbivorer kan bidra til både stabilitet og endring av økosystemer. Gjennom beiting, urinering, møkk og tramping kan store planteetere påvirke plantediversitet, vegetasjonssammensetning, primærproduksjon, habitatstruktur og sirkulasjon av næringsstoffer. Dette kan igjen ha mange indirekte effekter på andre planter og dyr i samme økosystem. Effekten av store herbivorer varierer med habitatets primærproduksjon, tettheten av herbivorer, herbivorenes selektivitet og hvordan herbivorer og habitatet deres blir forvaltet. Elg i boreal skog er en stor selektiv herbivor som har hatt en høy tetthet i Skandinavia de siste 30–40 årene, og har et høyt potensial til å påvirke økosystemet. I denne doktorgradsavhandlingen har jeg undersøkt hvordan ulike tettheter av elg kan påvirke andre dyr og planter gjennom indirekte effekter, og hvordan effektene varierer med elgtetthet, habitatproduktivitet og vinterfôring av elg. Jeg har undersøkt hvordan elgtetthet og habitatproduktivitet påvirker diversitet, vekst og reproduksjon i feltvegetasjonen og diversitet og abundans av blomsterbesøkende insekter. Disse studiene ble utført i et eksperiment med simulert elgtetthet over en gradient i habitatproduktivitet utenfor Umeå i Västerbotten, Sverige. Jeg har også undersøkt hvordan elgtetthet og vinterfôring av elg påvirker diversitet, abundans og reproduksjon hos fugl i Stor-Elvdal i Hedmark, Norge. Elgbeiting i feltvegetasjonen førte til redusert vekst og reproduksjon hos de artene som ble beita på, og økt vekst og reproduksjon hos ubeita arter. Elgbeiting i trevegetasjonen førte til økt lystilgang og økt blomstring i feltvegetasjonen. Dette førte igjen til økt diversitet av blomsterbesøkende insekter i ordenen Hymenoptera, spesielt i høyproduktive habitat. Hardt beitepress på bjørk rundt fôringsstasjoner for elg førte til redusert diversitet av fugl, spesielt fugl som hekker i beitehøyde og insektspisende fuglearter.

Høy elgtetthet rundt fôringsstasjoner førte til lavere reproduksjon og mattilgang for kjøttmeis, men høyere reproduksjon og mattilgang for fluesnapper. Fôringsstasjoner brakte næringsstoffer inn i økosystemet via silo, møkk og urin, og hadde en positiv effekt på diversitet og forekomst av insektetende fugler, og størrelsen på insektbytte. Disse resultatene viser at elgen kan påvirke andre arter og biologisk mangfold i boreal skog via endret ressurstilgang og habitatstruktur, og at effektene påvirkes av habitatets produktivitet. I tillegg kan fôringsstasjoner for elg påvirke elgtetthet og bringe næringsstoffer inn i systemet som endrer effekten av elg.