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Interactions between ungulates and forest insects

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Cover: Sawfly larvae feeding on a browsed pine branch
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Abstract

In forest ecosystems ungulates and insect herbivores often co-occur and utilise the same host trees. Herbivores that share a host plant can indirectly affect each other through plant induced responses. Such changes may affect plant growth, interactions with other species, and population dynamics. Studies investigating indirect interactions between taxonomically distant herbivores are lacking. Ungulates, as well as many herbivorous insect species, are considered pests and cause substantial damage to trees. Thus, interactions between these species may alter the level of damage and affect tree growth. In this thesis I investigate indirect interactions between ungulates and insects in forest ecosystems, with Scots pine (*Pinus sylvestris*) as the focal tree species, and the European pine sawfly (*Neodiprion sertifer*) as the focal insect. By combining controlled field experiments, observational studies, and modelling, I explore how ungulate browsing and grazing affect insect performance, abundance and population dynamics, and study the consequences for pine growth. I found that *(i)* sawfly fecundity was increased but larval survival decreased on browsed pines; *(ii)* browsing influenced the arthropod predator community on pines, *(iii)* browsing potentially could mitigate sawfly outbreaks, and that *(iv)* sawfly defoliation combined with ungulate browsing can, depending on the sequence and frequency, cause non-additive growth responses in pine. Lastly, I show that abundance, and diversity of and predation pressure on herbivorous insects can be influenced by habitat characteristics, which are commonly affected by ungulate grazing. I conclude that ungulates can have profound effects on forest insects and that indirect effects should not be neglected in ecological research and may have implications for e.g. forestry.

Keywords: indirect interactions, trait-mediated effects, plant-herbivore interactions, mammal-insect interactions, ungulate browsing, *Pinus sylvestris*, *Neodiprion sertifer*, tree growth, exclosures

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Interaktioner mellan klövvilt och insekter

Sammanfattning

Både klövvilt och växtätande insekter är vanligt förekommande i skogsekosystem, och har dessutom ofta samma värdträd. Växtätare som utnyttjar samma växt kan indirekt påverka varandra genom växtens inducerade responser, vilket i sin tur kan påverka växtätarnas interaktioner med arter och deras populationsdynamik men också växtens tillväxt. Detta ämnesområde är särskilt outforskat när det kommer till interaktioner mellan taxonomiskt skilda arter, så som klövvilt och insekter. Både klövvilt och flertalet växtätande skoginsekter räknas som skadegörare och interaktioner dem emellan kan således förändra skadenivåerna och därmed trädens tillväxt. I den här avhandlingen undersöker jag indirekta interaktioner mellan klövvilt och insekter i skogsekosystem med huvudfokus på tall (*Pinus sylvestris*) och röd tallstekel (*Neodiprion sertifer*). Genom att utföra kontrollerade fältexperiment, observationer och populationsmodellering studerade jag hur klövviltsbete påverkar insekters förekomst, överlevnad, reproduktion och populationstillväxt samt vilka konsekvenser det kan få för tallens tillväxt. Jag fann minskad överlevnad men ökad reproduktiv kapacitet hos tallsteklar som ätit på klövviltsbetade träd. Jag fann också att dessa förändringar eventuellt kan hindra tallstekelutbrott under vissa förutsättningar. Däröver fann jag att bete från klövvilt och tallsteklar, beroende på hur det är kombinerat i tid (sekvens och frekvens), kan orsaka icke-additiva effekter på tallars tillväxt. Till sist visar jag att abundans och diversitet av växtätande insekter samt predationstryck påverkas av habitatstrukturen, vilken ofta påverkas av klövvilt. Sammantaget visar denna avhandling att bete från klövvilt kan ha stora effekter på insekter och att denna typ av interaktioner inte kan försummas i ekologisk forskning, samt att de kan ha konsekvenser som kan vara viktiga att ha hänsyn till inom skogsbruket.

Keywords: Klövviltsbete, tall, indirekta interaktioner, växt-växtätarinteraktioner, tillväxt, röd tallstekel, hägn, skadegörare, inducerade responser

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Contents

List of publications

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

I. Nordkvist M*, Klapwijk MJ, Edenius L, Gershenzon J, Schmidt A, Björkman C (2019). Trait-mediated indirect interactions: Moose browsing increases sawfly fecundity through plant-induced responses. Ecology and Evolution, 9 (18), 10615-10629.

II. Nordkvist M*, Björkman C, Klapwijk MJ (2020). Plant mediated interactions; how moose changes pine traits to reduce sawfly survival. (Submitted manuscript)

III. Nordkvist M*, Björkman C, Klapwijk MJ (2020). The effect of ungulate browsing on forest insect populations (Manuscript)

IV. Nordkvist M*, Klapwijk MJ, Edenius L, Björkman C (2020). Interacting effects of insect and ungulate herbivory on Scots pine growth. (Re-submitted manuscript)

V. Nordkvist M, Klapwijk MJ*, Barets S, Björkman C (2020). The relationship between moose browsing, habitat structure and predation pressure on insect herbivores. (Re-submitted manuscript)

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The contribution of Michelle Nordkvist to the papers included in this thesis was as follows:

I. Developed research question and experimental design with CB, LE and MJK. Performed data collection and statistical analyses. Led the writing of the paper with contributions from co-authors. JG and AS performed the chemical analysis. First author of the paper.

II. Developed research question and experimental design with CB and MJK. Performed data collection and statistical analyses. Led the writing of the paper with contributions from co-authors. First author of the paper.

III. Developed research question with CB and MJK. Developed model with assistance from PC and MPH. Led the writing of the paper with contributions from co-authors. First author of the paper.

IV. Developed research question and experimental design with CB, LE and MJK. Performed data collection and statistical analyses. Led the writing of the paper with contributions from co-authors. First author of the paper

V. Contributed with input to the research questions and experimental design, which was developed by MJK, CB and SB. Collected the data together with SB. MJK performed the statistical analyses. Wrote the paper together with MJK, with contributions from co-authors. First author of the paper

Abbreviations

C:N ratio	Carbon:Nitrogen ratio
DC	Direct consumption
DMII	Density-mediated indirect interaction
TMII	Trait-mediated indirect interaction

1. Introduction

Where there are plants, there are herbivores. Almost all plants are associated with a suite of herbivores (Fig. 1), some more ravaging than others. However, plants are not powerless. They respond in various ways to counteract the negative effects of herbivore damage. Interactions between plants and herbivores have fascinated scientists for decades and while it has been studied intensively we still do not fully understand the underlying mechanisms and ecological consequences.

1.1 Indirect interactions

Herbivory can have far reaching effects beyond plant damage. Through plant induced responses and altered plant communities, herbivory can affect other organisms. When one herbivores affects a second herbivore, through such changes, it is known as an indirect interaction (Abrams 1995). Indirect interactions are of great importance for ecological communities as they can alter community composition and strengthen or weaken trophic interactions (van Zandt & Agrawal 2004, Gómez & González-Megías 2007a, Ali & Agrawal 2014), thereby potentially affecting population dynamics. This may consequently alter damage levels (Muiruri *et al.* 2015), and by extension plant growth (Strauss 1991). Herbivory can have various consequences for plant growth, resulting both in reduced, unchanged and increased growth (Belsky 1986). When multiple herbivores feed on the same plant, due to indirect interactions and due to multiple plant responses, the outcome may be non-additive (Strauss 1991, Stephens *et al.* 2013, Gagic *et al.* 2016). The effect of multiple herbivory can accordingly be larger or smaller than expected from the individual effects, i.e. synergistic or antagonistic.

Interactions between taxonomically distant herbivores, such as mammals and insects are less well studied than interactions between taxonomically close species (Ohgushi 2005). Large mammalian herbivores, such as ungulates or large grazers, can have profound effects on plants and habitats (McInnes *et al.* 1992, Suominen *et al.* 2008, Wallgren *et al.* 2014) and are common in many types of ecosystems, thus mammal-insect indirect interactions should be a common phenomenon. Moreover, interactions between large mammals and small insects are often asymmetrical and has a much larger effect on the insect than on the mammal (Gómez & González-Megías 2002), and mammals can even directly affect insects numbers through accidental predation while ingesting plant material (Gish *et al.* 2017) (from here on referred to as direct consumption). Mammal-insect interactions can be divided into four distinct categories of two types (Abrams et al 1996, Gómez & González-Megías 2007b); density- and trait mediated indirect interactions (TMII and DMII) and density- and trait mediated direct interactions (TMI and DMI) (Table 1). These different interaction types are governed by different mechanisms and occur at different spatial scales (Table 1). DMIIs have been studied to a larger extent than TMIIs despite the fact that TMIIs can be as strong as or even stronger than DMIIs (Werner & Peacor 2003).

Table 1. Types of interactions between mammals and insects. Column one: type of interaction, column two: which mechanisms govern the interaction, column three: the spatial scale in which this interaction occur.

Type of interaction	**Mechanism**	**Spatial scale**
Indirect		
Density-mediated (DMII)	Decrease in shared resource(s)	Habitat level
Trait-mediated (TMII)	Modification of plant phenotype(s)	Plant level
Direct		
Density-mediated (DMI)	Direct consumption (accidental predation of insects during ingestion of plant material)	Plant level
Trait-mediated (TMI)	Change(s) in insect behaviour in presence of mammal	Plant level

1.2 Interactions between ungulates and insects

In forest ecosystems ungulates and insect herbivores co-occur and often utilise the same host trees (Fig. 1). Ungulates can alter growth (Edenius *et al.* 1995, Hódar *et al.* 2008, Wallgren *et al.* 2014), morphology (Edenius *et al.* 1993, Danell *et al.* 1994), nutritional quality and production of defences (Nykänen & Koricheva 2004) in trees. They are also ecosystem engineers and can fundamentally modify habitats through several processes (Hobbs 1996, McInnes *et al.* 1992, Martin *et al.* 2010), such has selectivity. Through all these effects, ungulate browsing and grazing create a large potential for indirect interactions with other organisms, such as insects (both DMIIs and TMIIs) (Suominen *et al.* 2008, Tabuchi *et al.* 2010). Studies have demonstrated both negative (den Herder *et al.* 2004), neutral (den Herder *et al.* 2009) and positive (den Herder *et al.* 2009, Danell & Huss-Danell 1985) effects of ungulate herbivory on insects. Ungulates can impact both performance (Tabuchi *et al.* 2010), numerical responses (such as abundance) (Danell & Huss-Danell 1985, Bailey & Whitham 2003, den Herder et al 2004) and damage levels (Schwenk & Strong 2011, Muiruri *et al.* 2015) of herbivorous insects. In terms of TMIIs the effect of ungulate browsing on damage and abundance (and other numerical responses) of insect herbivores has been studied to a larger extent than the effects on insect performance. Browsing can also affect predatory insects and other arthropods, both at the tree (Danell & Huss-Danell 1985) and habitat (Suominen *et al.* 2008, Lilleeng *et al.* 2018) level, which could have consequences for herbivorous insects, through altered predation rates. Ungulates can also directly influence insect herbivores through direct consumption (DMIs) (Gish *et al.* 2017) but in which systems this occur and to what extent is largely un-explored. Overall, these direct and indirect effects of ungulates on insects can potentially scale up and influence insect population dynamics, as well as cause non-additive effects on growth of the shared host tree (Strauss 1991).

1.2.1 Ungulate induced responses

Plant induced responses (i.e. changes in plant traits) are the basis of TMIIs. Ungulates can alter both chemical and morphological traits of trees. The effect of ungulates on chemical traits depend on the timing of browsing (winter vs. summer) and on the tree species (Nykänen & Koricheva 2004, den Herder *et al.* 2009). Winter browsing on conifers can be expected to increase nutritional quality (Danell *et al.* 1994, Nykänen & Koricheva 2004). The reduction in photosynthetic capacity on browsed trees, could lower the production of carbon based defences such as terpenes (Bryant *et al.* 1983, duToit *et al.* 1990). Browsing has also been shown to affect level of phenolics in woody plants (Stolter 2008), which is an important group of defence compounds. Ungulate browsing also alters tree morphology/architecture (Danell *et al.* 1994), by for example altering re-growth patterns, decreasing biomass, and altering the number of shoots and the branching pattern. The intensity of browsing is an important factor influencing induced responses, as demonstrated in birch (*Betula* sp.) (Danell & Huss-Danell 1985).

1.2.2 Insect responses to altered plant quality and architecture

Plant quality is of importance to insect herbivores, and can affect both their abundance, diversity (Forkner & Hunter 2000, van Zandt & Agrawal 2004) and performance (Mattson 1980, Björkman *et al.* 1991, Awmack & Leather 2002). One of the most important, and most studied, plant quality traits is nitrogen, which frequently affects the performance abundance of herbivorous insects (Mattson 1980). Increased nitrogen or decreased C:N ratio commonly increases the performance of herbivorous insects (Joern & Behmer 1997, Awmack & Leather 2002). Defensive compounds are also of great importance for insect performance (Björkman *et al.* 1997, Awmack & Leather 2002) and abundance (Poelman *et al.* 2009). Increased levels of defensive compounds usually decreases insect performance, but this is dependent on the specificity of the defence, i.e. some defence compounds only affect certain herbivores (Agrawal 2000). Plant architecture can shape arthropod communities in several ways: structurally complex plants tend to harbour a greater diversity and abundance of both herbivorous (Lawton

1983) and predatory arthropods (Langellotto & Denno 2004), and plant architecture can influence predator consumption rate and behaviour (Reynolds & Cuddington 2012a, Reynolds & Cuddington 2012b).

1.2.3 Ungulate habitat alteration

Habitat modification by ungulates can cause both DMIIs and TMIIs. Ungulates modify habitats through a variety of processes such as selectivity, trampling, induced responses and much more (Hobbs 1996). Ungulate selectively decreases the abundance certain plant species, and favours others, altering plant community composition (Kolstad *et al.* 2018a, Kolstad *et al.* 2018b). Several studies have reported richer herb layers in grazed/browsed areas (Faison *et al.* 2016a, Boulanger *et al.* 2018) dominated by herbs that are adapted to open habitats (Faison et al 2016a, Boulanger et al 2018). Studies have also reported a decrease in biomass of herbs (Kolstad et al 2018b) and richness of shrubs (Boulanger *et al.* 2018) in areas grazed by ungulates. In boreal forests, ungulates commonly decrease the density of deciduous trees (Faison *et al.* 2016b, Kolstad *et al.* 2018b).

1.2.4 Insect responses to altered habitat structure

Arthropod communities respond to altered habitat structure in various ways. Insect herbivores are highly affected by increases or reductions in their host plant(s) and by plant species composition (Jactel & Brockerhoff 2007) Arthropod predators respond to habitat alterations in various ways. Overall, arthropod predator abundance is higher in more structurally complex habitat and lower in structurally simple ones (Langelotto & Denno 2004) but the response depend on how the habitat is altered, on the type of ecosystem (Suominen & Danell 2006) and on the specific predator group (Landsman & Bowman 2017, Lilleeng *et al.* 2018). For example, sparse vegetation tend to favour mobile predators at ground level, whereas denser vegetation favours ants and web-hunting spiders (Suominen & Danell 2006). In boreal forests, ungulate grazing has been shown to reduce richness of arthropod predators (Suominen et al 2008), abundance of ants and alter spider community composition (Suominen & Danell 2006, Suominen et al 2008, Lilleeng *et al.* 2018).

1.2.5 Ungulate and insect damage and tree growth

Ungulates can affect tree growth to a large extent, but generally decreases it (Wallgren *et al.* 2014, Edenius *et al.* 1995). The higher the frequency and intensity of browsing the larger the growth reduction (Wallgren *et al.* 2014). Insects can similarly impact growth, with larger affect at higher defoliation levels (Ericsson *et al.* 1980, Lyytikäinen-Saarenmaa 1999). Ungulate herbivory has been demonstrated to both increase and decrease subsequent insect damage levels (Strauss 1991, Schwenk & Strong 2011, Muiruri *et al.* 2015), creating a potential for non-additive effects on plant growth by combined attack by these types of herbivores. The sequence of herbivore attack has been shown to affect plants and subsequent herbivore responses (van Zandt & Agrawal 2004, Erb *et al.* 2011), therefore the sequence of herbivory by ungulates and insects could affect the growth response of the tree.

1.3 Boreal forests and pests

Boreal forests cover large parts of earth's landmass (FAO 2020), and is an important resource in terms of wood production, carbon sequestration and recreation. In Sweden, around 70 % of the land area is boreal forest, of which around 80 % is production forest (Swedish National Forest Inventory 2020). Simplified ecological systems, such as production forests and particularly monocultures, are often more sensitive to stresses and disturbances such as herbivory (Dalin *et al.* 2009, Jactel *et al.* 2017). When the interest of a herbivore coincides with that of humans we refer to them as pests. In boreal forests, herbivorous pests can have large economic effects (Lyytikäinen-Saarenmaa & Tomppo, 2002). Our knowledge on interactions between large and small pest (i.e. ungulates and pest insects) in boreal forests is limited, despite the potentially large consequences for tree growth. Pest problems are expected to increase with global change (Gauthier *et al.* 2015, Hof & Svahlin 2015), providing yet another incentive to study interactions between ungulates and herbivorous insects.

1.3.1 Insect outbreak species

Insect populations are regulated by internal, bottom-up and top-down factors such as competition (Denno *et al.* 1995), plant quality (Larsson *et al.* 2000) and interactions with natural enemies (Berryman 1996). However, sometimes, for reasons not fully understood, populations manages to escape regulation and reach extreme densities (i.e. an outbreak) (Wallner 1987). During outbreaks, these species often become highly problematic killing or causing major growth losses to trees (Walton 2012). Ungulates could alter these regulating factors, potentially influencing population dynamics. Studying if and how ungulates affect e.g. performance of outbreak species is therefore particularly interesting.

2. Aims

The overarching aim of this thesis was to investigate the effects of ungulate herbivory on herbivorous insects in forest ecosystems, at two spatial scales (plant level and habitat level).

2.1 Questions addressed:

The questions addressed in this thesis were:

- Does ungulate herbivory affect the performance of insect herbivores and through which mechanisms (induced responses) do these herbivores interact (**paper I and II**)?

- Do ungulate induced changes to pine trees affect the abundance and diversity of arthropod natural enemies (**paper. II**)?

- Can ungulate herbivory affect population level characteristics of insect herbivores (**paper III**)?

- Is the combined effect of ungulate and insect herbivory on tree growth non-additive (**paper IV**)?

- Do ungulates alter habitat structure and does habitat structure affect abundance and predation pressure of insect herbivores (**paper V**)?

2.2 Underlying hypotheses

Three underlying hypotheses set the foundation for this thesis:

- Presence, abundance and performance of herbivorous insects are affected by ungulate disturbances (such as changes to plant quality, quantity and community composition)

- Interactions between insects and other organisms are affected by ungulate disturbances (such as changes to plant quality, quantity and community composition)

- Combined ungulate and insect herbivory can have antagonistic (1+1<2) or synergistic (1+1>2) effects on tree growth.

3. Study system

The main study system used in this thesis consist of ungulates, Scots pine (*Pinus sylvestris*) and the European pine sawfly (*Neodiprion sertifer*). This study system was selected for several reasons. Both ungulates and sawflies are important pests in boreal production forests in which Scots pine is a dominating tree species. Ungulates and sawflies naturally utilises the same trees (during sapling stage), and these interaction can occur over quite long periods of time. Sawflies are prone to outbreaks and their biology and life cycle are well understood.

3.1 Ungulates

Ungulates are widely distributed over Sweden with local variations in density, and can be viewed as a disturbance factor in boreal forests (Edenius *et al.* 2002). In winter time, a main food source is pine shoots (Bergström & Hjeljord 1987). Winter browsing can affect Scots pine growth and morphology (Wallgren *et al.*, 2014; Edenius *et al.*, 1993), as well as foliage quality (Nykänen & Koricheva, 2004). Large ungulates can also profoundly impact vegetation composition and structure in boreal forests (Kolstad et al 2018a, Kolstad *et al.* 2018b). Moose (*Alces alces*) is the most widespread ungulate browser in Swedish boreal forest, but other cervids can be locally abundant.

3.1.1 Clipping – mimicking ungulate browsing

Clipping is a commonly used way of assessing effects of ungulate browsing on trees (Edenius *et al.* 1993, Edenius *et al.* 1995, Hódar *et al.* 2008). There are both advantages and disadvantages to clipping as a method, which are described in Table 2. In this thesis both clipping and natural browsing is used, depending on the nature of the experiment and the research question. Natural browsing is used in **paper II**, clipping is used in **paper IV** and in **paper I** both natural browsing and clipping is used.

Table 2. Advantages and disadvantages of using clipping to simulate ungulate browsing.

Clipping
Advantages • Can control for timing, frequency, intensity and duration • Trees are not previously selected by browsers (reduces confounding factors) • Can draw more general conclusions on ungulates (not species specific)
Disadvantages • Not species specific • The lack of browser saliva may cause different tree responses • Impossible to study the full effect of browsing (saliva, tree choice, effect on surrounding habitat)

3.1.2 Exclusion experiments

Exclusion experiments are commonly used to study the effect of ungulate browsing and grazing on habitat characteristics (e.g. Faison *et al.* 2016a, Kolstad *et al.* 2018a), such as plant composition, tree height and soil properties. Exclusion of large grazers and browsers is a good way to study the overall impact on habitats, but does not allow for testing the occurrence of specific mechanisms (e.g. distinguishing between DMIIs and TMIIs).

3.2 Scots pine (*Pinus sylvestris*)

Scots pine is a conifer tree, native to Eurasia, common across the globe, and one of the dominating species in Swedish forests (Swedish National Forest Inventory 2020). It is an economically important tree species, and in Swedish forestry one of the main tree species for both wood and pulp production. Scots pine is associated with a suite of herbivores, covering multiple taxa (Fig. 1).

Figure 1. Young Scots pine and some of its associated herbivore fauna. Illustration by Martin Holmer.

3.3 The European pine sawfly (*Neodiprion sertifer*)

The European pine sawfly (*Neodiprion sertifer*, Geoffr.; Hymenoptera, Diprionidae) is a specialist herbivorous insect, using *Pinus* spp. as host plant. It is a univoltine species that overwinters in the egg stage. In late August and early September females oviposit on current year's needles. Eggs are laid in batches, normally ranging between 50 and 120 laid eggs per female (Gur'yanova 2006). In late spring eggs hatch to larvae, which feed gregariously on pine needles for roughly a month. Larvae feed almost exclusively on previous years' needles, avoiding needles on developing shoots. Thereafter larvae spin cocoons, drop to the ground and pupate in the soil (Wallace & Sullivan 1963). Pupae hatch as adults in late summer – early autumn.

In the larval stage sawfly performance is affected by both bottom-up (plant quality) and top-down (predation) processes. Low di-terpene and high nitrogen levels in pine needles has been shown to positively affect developmental time, survival and prospective fecundity (Larsson *et al.* 1986, Björkman *et al.* 1991, Björkman *et al.* 1997). The most important predators of sawfly larvae are ants and spiders (Juutinen 1967, Olofsson 1992, Lindstedt *et al.* 2006, Kaitaniemi *et al.* 2007). In the pupal stage, sawflies experience predation by small mammals (voles, shrews) and survival is density dependent (Holling 1959, Hanski and Parviainen, 1985).

The European pine sawfly is an irregular outbreak species (Pschorn-Walcher 1965, Kolomiets *et al.* 1979), and is considered a major pest in boreal forests of Europe and North America. Up to 38 % reduction in growth of Scots pine has been recorded under severe sawfly defoliation (Lyytikäinen-Saarenmaa & Tomppo 2002). Population dynamics of sawflies can be influenced by plant quality (Larsson *et al.* 2000)

4. Methods

The questions in this thesis were addressed by combining controlled field experiments (**paper I, II and IV**), an observational study (**paper II**), a long-term ungulate exclusion experiment (**paper V**) and modelling (**paper III**).

4.1 Pine field experiment (**paper I, II and IV**)

To be able to study TMIIs between ungulates and sawflies (**paper I and II**) as well as the combined effects on pine growth (**paper IV**) controlled field experiments on two sites dominated by pine trees in Uppland, Sweden were established (site 1: 59 52 01.7N, 18 11 06.4E, site 2: 59 58 00.9N, 18 13 37.0E).

4.1.1 Sawfly performance (**paper I and II**)

To study plant-mediated effects of ungulates (mainly moose) on sawflies I reared sawflies on pine trees that were either browsed or un-browsed. I also measured pine traits that I expected could be the mediating mechanisms. In **paper I** the aim was to study the bottom-up effects on sawfly fecundity and survival. Sawfly larvae were reared on either moose browsed, clipped or un-browsed pine trees, and pine needle C:N ratio and di-terpene content was measured. To be able to study bottom-up effects on fecundity in isolation sawfly larvae were caged on the pines in mesh bags, which excludes predators (Fig. 2). In **paper II** the aim was to study the effect of browsing on top-down influenced sawfly larval survival. Sawfly larvae were reared on pine trees that were either browsed (by moose) or un-browsed, and pine architecture was characterised and needle C:N ratio measured. Since top-down effects on survival was the focus in this study, sawflies were un-caged (exposed to predation).

Figure 2. Sawfly larvae caged on pine trees. To be able to study the indirect effect of ungulate browsing on sawfly performance mediated only through plant responses sawfly larvae were caged in mesh bags to eliminate predation.

4.1.2 Pine growth (**paper IV**)

In **paper IV** the aim was to study the combined effect of ungulate and sawfly herbivory on pine height and radial growth. To do so, pines were exposed to a combination of clipping and sawfly defoliation under two years. The frequency and sequence of herbivory was varied. The first year pines were either exposed to no herbivory, sawfly defoliation, clipping or both. The second year eight different herbivory treatments were used (Table 3). Pine height and radial increment was measured as a response and I assessed if the combined impact of ungulates and sawflies was additive, antagonistic or synergistic and if the sequence and frequency of herbivory affected this.

Table 3. Herbivory treatments in **paper IV** at year two of the study. The type of herbivory (clipping or insects) and the year when the treatment was applied (2016 or 2017) is presented in consecutive order (to demonstrate the sequence and frequency of herbivory).

Treatments year two (sequence of clipping and sawfly herbivory)
Insect 2016
Insects 2016 – Insects 2017
Clipping 2016 – Insects 2017
Clipping 2016 – Insects 2016 – Insects 2017

Clipping 2017 – Insects 2017
Insects 2016 – Clipping 2017 – Insects 2017
Clipping 2016 – Clipping 2017 – Insects 2017
Clipping 2016 – Insects 2016 – Clipping 2017 – Insects 2017

4.1.3 Origin of sawfly populations

The sawflies used for the experiments outlined above were collected from natural, ongoing outbreaks. The sawflies used in **paper I** and **IV** were collected near Oskarshamn in Southern Sweden (57 8 42.4N, 16 17 55.3E), and the sawflies used in **paper II** were collected near Ramnäs in South-central Sweden (59 46 39.98N, 16 05 49.18E).

4.2 Observational study (**paper II**)

To study the community of arthropod predators on browsed and un-browsed pines an observational study was conducted in 14 different pine dominated forest stands. The aim was to assess if browsing affected arthropod predator communities (abundance, diversity and occurrence) and if the level of browsing affected the response. Pines were surveyed for arthropod predators using the beating tray method (Leather 2008) and number of individuals in total and of ants and spiders as well as the number of species was recorded. The intensity of browsing was scored using five damage categories (un-browsed and 25, 50, 75 and 100 % lateral shoots browsed).

4.3 Ungulate exclusion experiment (**paper V**)

In 2012, fenced plots of 7x7m were set up across Sweden in 16 newly regenerated pine stands with Scots pine as the main tree species (Fig. 3). Each fenced plot was coupled with an un-fenced control plot, resulting in 32 plots (16 fenced, 16 control). These plots were initially set up as a long-term vegetation monitoring project, studying the effects of ungulates on habitat characteristics (Widemo & Christoffersson – web page appendices). However, this provides an excellent set up for studying effects of ungulates and habitat characteristics on insect herbivores and predation rate. Such a study was carried out in these plots in 2016 (**paper V**). Additional habitat measures were taken; number and diversity of trees was recorded, along with height and diameter of five haphazardly chosen pines trees (per plot). On those five pines insect abundance and diversity was estimated. I used the beating tray method (Leather 2008) to collect insects on the pines, and the samples were later determined to order or genera. On three out of the five pines, plasticine model larvae (artificial prey) were placed to assess predation rate. The models were left on the trees for two weeks where after they were brought to the lab and the number of marks (attack rate) was counted. Artificial prey is an established and useful way of assessing attack rates in studies comparing different habitats or treatments (Howe *et al.* 2009, Lövei *et al.* 2017). Measuring attack rate on artificial prey does not provide an absolute measure of predation rate, but can be used to determine the relative differences between treatments (Lövei *et al.* 2017).

Figure 3. Map of Sweden with the locations of the fenced and control plots marked. Each dot represents one location (i.e. one pine stand with one fenced and one control plot).Figure is reproduced from paper V.

4.4 Modelling (**paper III**)

I use modelling to explore the potential effects of ungulate browsing on sawfly population dynamics. I altered a model initially developed by Larsson *et al.* 1993 for *Neodiprion sertifer*. The advantage of the model is that it can be used to study how effects on individual performance scale up and influence population characteristics, but at the same time it does not disregard population scale processes such as density dependent cocoon predation. This model has been used several times to explore the effect of altered plant quality on sawfly population characteristics (Larsson *et al.* 2000, Kollberg *et al.* 2015). The model was altered in four ways to study the effect of browsing on sawfly population characteristics: 1) the sawfly population was separated on browsed and un-browsed trees based on the proportion of browsed trees in the landscape, 2) the performance of individual sawflies differed on browsed and un-browsed trees, 3) direct consumption (accidental predation of sawfly eggs by ungulates) was added and 4) sawfly female oviposit choice (preference to oviposit on either browsed or un-browsed trees) was added (Fig. 4). The difference in performance on browsed and un-browsed trees was based on data from **paper I and II**. I used the model to assess how different proportions of browsing could affect sawfly outbreaks and population growth over a range of parameter values for sawfly larval survival and fecundity.

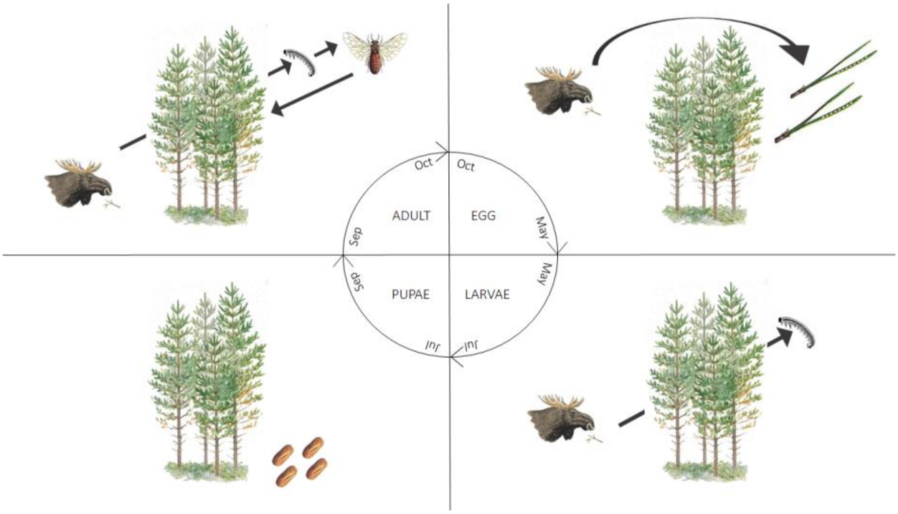

Figure 4. Conceptual figure of the model and the effects of ungulates during the different stages of the sawfly life cycle. During ***adult stage*** *(top-left) fecundity and oviposit-preference are affected by browsing: fecundity depends on if the individual fed on a browsed or on-browsed tree as larvae and female can be modelled to have a preference to oviposit on either browsed or un-browsed trees. During* ***egg stage*** *(top-right) survival is affected by browsing through direct consumption (ungulates accidently ingesting eggs while feeding on pine shoots). During* ***larval stage*** *(bottom-right) survival depends on if the tree is browsed or un-browsed. During* ***cocoon stage*** *(bottom-left) survival is density-dependent (due to small mammal predation) but not affected by browsing. Illustrations by Martin Holmer.*

5. Results and discussion

In this thesis, I show that ungulate browsing can affect insect performance (**Paper I and II**) and arthropod predator communities (**Paper II**), through plant induced responses. However, the underlying mechanisms are still mostly unidentified. I also show that such changes may influence insect population characteristics (**Paper III**). Moreover, I show that combined browsing and insect herbivory can have non-additive effects on tree growth, depending on the sequence and frequency of herbivory (**Paper IV**) and that habitat heterogeneity, influenced by ungulate grazing, can affect insect herbivore abundance and predation rates (**Paper V**). Below these findings will be examined in more detail.

5.1 Insect performance and underlying mechanisms (**Paper I and II**)

In **paper I**, I found that cocoon weight (proxy for fecundity (Gur'yanova 2006)) was higher in sawflies that had been feeding on browsed trees compared to un-browsed trees (Fig. 3). The effect could partly be attributed to lower C:N ratio in needles on browsed trees (i.e. higher nitrogen) (Fig. 3), but not to di-terpene content. The relationship between fecundity and C:N ratio was weak (Fig. 3) and the amount of di-terpenes were neither affected by browsing, nor did it relate to sawfly fecundity. I could also show that bottom-up survival of larvae was not affected by browsing. A potential candidate mechanisms for the effect on fecundity is the amount of tannins, which is related to amount of available nitrogen (Feeny 1986). Browsing can lower the amount of tannins (du Toit *et al.*1990, Hrabar & du Toit, 2014) and plant tannin levels has been shown to affect pupal mass in other insect systems (Kaitaniemi et al 1998, Lindroth *et al.* 1993).

In **paper II**, I found that top-down influenced survival rate of sawfly larvae was lower on browsed trees compared to un-browsed trees. The effect could partly be attributed to browsing induced changes in architecture but not to needle C:N ratio. Based on this, and in combination with the fact that browsing do not alter sawfly bottom-up survival (**paper I**), I still argue that the effect on survival is caused mainly by changes in architecture (altering predator abundance, composition and behaviour and potentially spatial arrangement of alternative prey) and not by changes in plant quality. Browsing did alter pine architecture to a large extent but the main traits that were altered did not affect survival. The response of predators to plant architecture can be very distinctive (Reynolds & Cuddington, 2012a; Reynolds & Cuddington, 2012b) and therefore I suspect that other non-characterised architectural components can be responsible for the difference in survival. Candidate traits to explore would be the amount of edges (caused by moose bites) and the proportion of braches in relation to needles, since this can serve as attachment points and alleviate walking and searching for predators (Reynolds & Cuddington, 2012a; Reynolds & Cuddington, 2012b). Moreover, I did not survey arthropod predators or study predator behaviour on the experimental pine trees. Doing so could have provided an insight to why survival was lower on browsed trees. A different tree architecture could for example alter predator community composition (different predators have different hunting strategies adapted to different types of habitat), which could affect predation of sawflies. Ants are the main arthropod predator of sawfly larvae (Olofsson 1992, Lindstedt *et al.* 2006), thus an architecture suitable for ants could have a strong effect on sawfly survival. I was able to show that ants do respond positively to moderate intensities of browsing (observational study, **paper II**), providing an indication that an increase in ants could be the cause of lower survival on browsed trees. Another additional factor that was not measured in this experiment is the amount, and spatial arrangement, of alternative prey (i.e. other herbivores). Changes in prey numbers (Forkner & Hunter 2000) and arrangement (Bommarco *et al.* 2007) can influence predators and predation rate.

In both **paper I and II** I could show that browsing causes changes to sawfly performance, but failed to identify the major underlying mechanisms. The fail in identifying the mechanisms could be because the measured traits were not the mechanisms responsible for the effect (as discussed above). However, in terms of plant quality traits, one aspect that needs to be considered is within-plant differences. Differences within plants can sometimes be larger than differences among plants (Denno & McClure 1983) and these within-plant differences can be caused or altered by herbivory (Jones *et al.* 1993). Needle samples (for C:N ratio and di-terpene analyses) were taken on a different branch than sawflies were reared on, thus the measured C:N ratio and di-terpene content may not fully correspond to the quality of food that the sawflies experienced. Hence, both C:N ratio and di-terpenes could still be the traits mediating the observed responses.

The positive effect of browsing on fecundity (**paper I**) and the negative effect on survival (**paper II**) is intriguing. This supports the theory that different underlying mechanisms are responsible for the effect (plant quality affects fecundity and plant architecture affects survival). However, the diverging responses could also be caused by within-plant differences in plant quality caused by browsing. Sawflies were reared on un-browsed branches in **paper I** and on browsed branches in **paper II**, which could potentially contribute to the diverging effects, i.e. plant quality could differ between browsed and un-browsed branches (Denno & McClure 1983).

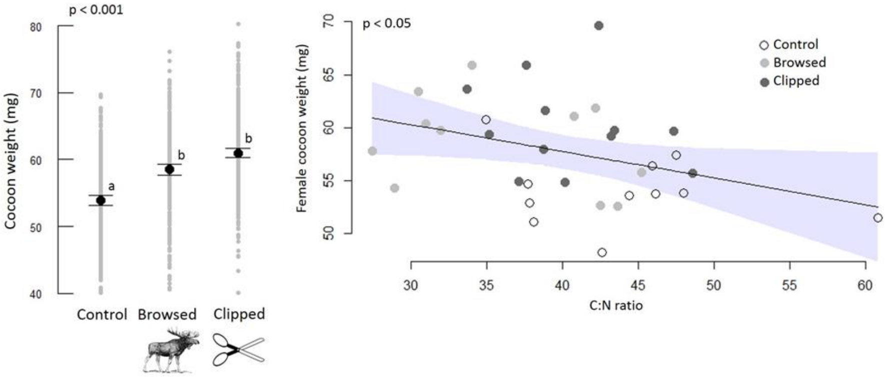

Figure 5. ***Right:*** *Cocoon weight of female sawflies reared on un-browsed (control), browsed or clipped pine trees.* ***Left:*** *Relationship between cocoon weight (pooled per tree) and pine needle C:N ratio. Colour of data points represent the treatment: white = control, grey= browsed and dark grey = clipped. Shaded area represents 95% confidence interval. This figure is adapted from paper I.*

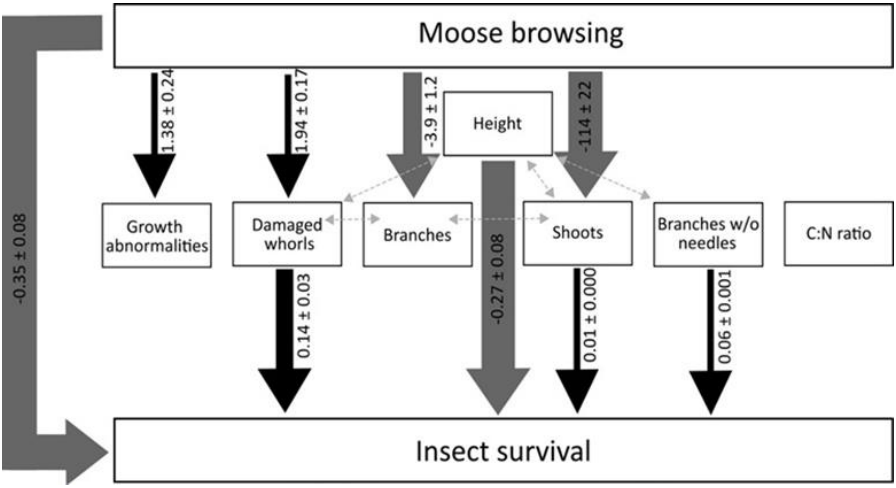

Figure 6. The effect of moose browsing on pine architecture and sawfly survival. The results were obtained using piece-wise structural equation modelling assessing the direct and indirect effects between response and predictor variables as well as the co-variance between predictor variables. The size of the arrows correspond to the importance of the effect. Grey arrows denote negative effects and black arrows positive effects. This figure is adapted from paper II.

5.2 Population responses (**paper III**)

In **paper III** the effect of browsing on population characteristics of the European sawfly was explored. Browsing had a negative effect on population growth rate and the higher the proportion of browsed trees was the fewer parameter combinations resulted in outbreaks. Still, due to the contrasting effects of browsing on fecundity (**paper I**) and larval survival (**paper II**) the overall effect is relatively small and browsing only influences the population in certain parameter ranges. Including direct consumption lowered population growth and caused fewer outbreaks, while including female oviposit choice increased or decreased growth and outbreaks, depending on if the females had a preference for browsed or un-browsed trees. To establish if ungulates could affect sawfly populations in nature, relating occurrences of sawfly outbreaks in the landscape with monitoring of ungulate densities and damage is required.

5.3 Arthropod communities and predation rate (**Paper II and V**)

5.3.1 Tree level (**paper II**)

The proportion of ants was higher on moderately browsed pines, compared to un-browsed and intensively browsed pines (**paper II**). Abundance of ants showed a tendency to the same pattern. This pattern matches previous studies conducted on deciduous trees (Danell & Huss-Danell 1985). Spiders was reversely affected by browsing (trend towards lower proportion and abundance of moderately browsed trees), suggesting negative interference between the two predator groups (Halaj *et al.* 1997, Kaitaniemi *et al.* 2007). Since ants and spiders tend to have different behaviour and hunting strategies, alteration of spider-ant-proportions could shift the type of herbivore prey targeted and potentially affect tree damage levels.

5.3.2 Habitat level (**paper V**)

In **paper V** I investigated the effect of ungulate browsing and grazing on habitat characteristics and the subsequent effect on insect herbivores and predation rate (on tree level). Excluding browsers caused a trend towards changed habitat structure, but did not alter the habitat to a large extent. The only variable that was significantly different between fenced and control plots was tree height. The length of the exclusion experiment (four years at the time of the study) in combination with the locations of the plots (mainly located in Northern Sweden, where growth tends to be slow) as well as the choice of areas with not necessarily high densities of ungulates (Boulanger *et al.* 2018) probably resulted in the small effect. Boulanger *et al.* (2018) showed that habitat structure can be altered by ungulates even in non-overabundance areas, but these effects were recorded after 10 years of exclusion. They also showed that habitat modification was proportional to ungulate density. The trend towards changes in habitat structure combined with results from similar studies (Boulanger *et al.* 2018, Kolstad *et al.* 2018a, Kolstad *et al.* 2018b) allows me to believe that this experiment will generate changes in habitat structure but that more time is required before any major differences can be measured.

Due to the minute effect of ungulates on habitat characteristics, it is difficult to evaluate the indirect effect of browsers on insects and predation. However, this study still provides some insight into how habitat characteristics, which could be affected by ungulates, influence herbivorous insects and predation rate. Insect abundance and diversity as well as predation rate of insect herbivores on pine was affected by the surrounding habitat structure as well as tree traits (**paper V**). The different response variables (abundance, diversity and predation rate) was affected by different habitat and tree variables. The strongest effects were a positive effect of tree height on insect abundance and a negative effect of understory species diversity on insect order diversity. Predation rate was affected negatively by tree height and positively by understory cover and insect herbivore abundance. Understory cover also had a negative effect on insect abundance. The increase in predation rate, with increased herbivore abundance, supports the expectation that increased abundance of prey should increase predator abundance (Suominen *et al.* 2008, Forkner & Hunter 2000) and thus predation rate. The negative effect of understory cover on insect abundance, and the positive effect of understory cover on attack rates, could be caused by an increase in shelter and/or resources for predators (Vanbergen 2006).

5.3.3 Diverging effects of tree height

In **Paper II** taller trees caused lower survival of sawfly larvae indicating higher predation. In **paper V**, attack rates of artificial prey decreased on taller trees. This discrepancy is intriguing and could potentially be caused by the differences between types of prey. Sawflies feed gregariously while plasticine larvae were placed solitary on the pines, thus different types of predators may be attacking these prey, which could be differently affected by tree height. Tree height has been shown to influence insect communities (Campos *et al.* 2006) The difference could also be caused by differences in the surrounding habitat influencing predator communities (Suomimen *et al.* 2008). The effect of habitat structure on prey abundance and predation is rather intricate (**paper V**), and thus differences between understory, tree density, or tree diversity in the field sites used in **paper II** compared with **paper V** could affect within tree predation rates.

5.4 Tree growth (**paper IV**)

In **paper IV** I show that pine height and radial growth is influenced by browsing and sawfly herbivory but that the effect depends on how herbivory is combined over time. In general, browsing had a larger impact on growth than sawfly defoliation. After the first year of the experiment, only radial growth was affected by herbivory and it was only affected by browsing (sawflies did not affect growth, and there was no interaction effect). After the second year, both browsing and sawfly defoliation affected radial growth and there was an interaction effect. Height growth was only affected by browsing. The specific combination of herbivory (sequence and frequency) affected radial growth. In terms of frequency, trees exposed to the highest amount of herbivory (exposed to both clipping and sawflies twice) had the lowest growth, which is in accordance with expectations based on previous studies (Ericsson *et al.* 1980, Lyytikäinen-Saarenmaa 1999), and growth effects were either additive or synergetic (Fig. 5). In terms of sequence, trees exposed to sawfly defoliation prior to clipping grew more than trees exposed to clipping first, and growth effects were either additive or antagonistic (Fig. 5). On trees exposed to clipping first, growth effects were additive (Fig. 5). This pattern could potentially be caused by priming, i.e. when a disturbance renders a plant ready for future attacks (Hilker *et al.* 2016, Mauch-Mani et al 2017) Sawflies feed on pines during active growth stage while clipping occurred during dormancy which could be one reason for why the pines would be primed by sawfly defoliation and not clipping.

It is important to note that in this experiment only one sawfly larval group was added per tree, while in nature more groups per tree is fairly common. Therefore, both the effect of sawfly defoliation on its own and the interaction effect could be even stronger in reality.

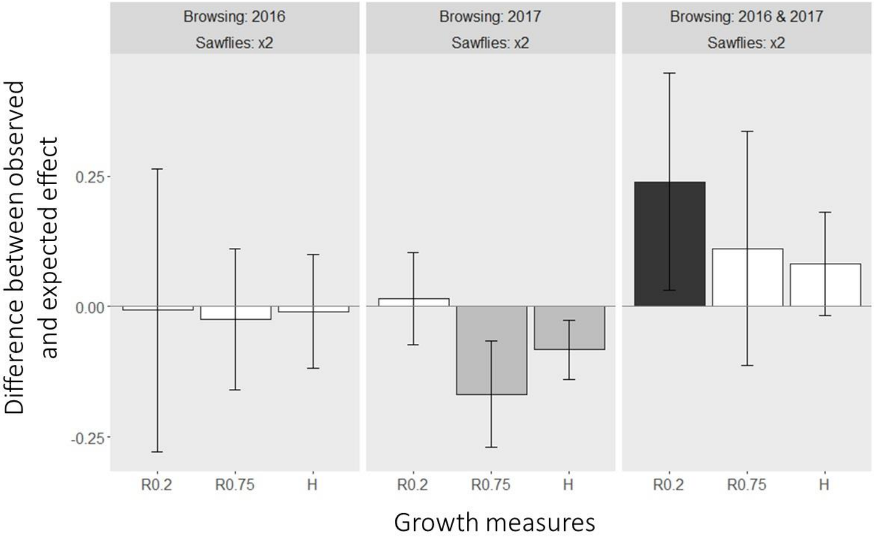

Figure 7. The difference between observed and expected effects of combined ungulate and sawfly herbivory on pine radial and height growth. Bars and errors represent the difference in effect size (mean and 95% confidence intervals). If mean and both ends of the confidence interval are above zero growth effects are considered synergistic. If mean and both ends of the confidence interval is below zero, effects are considered antagonistic. The zero line represents the expected additive effects. Trees in panel one were exposed to clipping in 2016 and sawflies in 2016 and 2017. Trees in panel two were exposed to clipping in 2017 and sawflies in 2016 and 2017. Trees in panel three were exposed to clipping in 2016 and 2017 and sawflies in 2016 and 2017. Dark grey bars represent synergistic effects, light grey bars antagonistic effects and white bars additive effects. This figure is reproduced from paper IV.

5.5 Ungulates and the European pine sawfly

In this thesis I showed that sawfly fecundity and survival in the larval stage was affected by ungulate browsing (**paper I and II**). If other life stages could be affected by ungulates remains un-known. However, to understand if and how ungulates could affect sawfly outbreaks or damage levels, experiments targeting effects in other life stages are necessary.

Egg survival could be affected indirectly by browsing induced responses such as changes in architecture altering predation rates. Egg survival could also be affected directly by direct consumption (explored in **paper III**).

Proposed drivers of the rate of direct consumption is for example the density of the consumer herbivore and of the consumed herbivore (Gish *et al.* 2017).

Cocoon survival could also be affected by ungulates. During cocoon stage the European pine sawfly is subjected to small mammal predation (Hanski & Parviainen 1985), which is affected by habitat characteristics such as ground vegetation and amount of dead wood (Hanski & Parviainen 1985, Bellone *et al.* 2017). Therefore effects of ungulate browsing and grazing on habitat structure could affect cocoon predation rate. Since cocoon predation is likely to have a strong regulating effect on sawfly populations (Hanski 1987, Olofsson 1987), ungulate habitat modification could affect sawfly population dynamics.

6. Conclusions and outlook

In this thesis, I have assessed and explored the effect of ungulate browsing and grazing on insect herbivores. I have shown that browsing and grazing by large ungulates can alter for example insect abundance and performance, and that changes in performance may scale up to influence population growth. The mechanisms underlying these interactions and effects were more intricate than expected, and are still largely unknown. Further studies are needed to establish which mechanisms are responsible for these effects. An important message from this work is that various trait-mediated effects of one herbivore on another can be of different direction. Ungulate browsing had a positive effect on sawfly fecundity but a negative effect on sawfly larval survival, highlighting the complexity of ecological systems. To establish the overall impact of one herbivore on another, multiple response variables need to be measured.

In this thesis, I have also investigated the combined effect of browsing and sawfly herbivory on tree growth. The combined impact of sawfly and ungulate herbivory on pine growth could be both additive, antagonistic and synergistic, depending on the sequence and frequency of herbivory. This also highlights the complexity of ecological system, since the combined impact of two herbivores cannot be expected to have the same effects under different scenarios.

More studies are required if we want to understand both the magnitude of indirect interactions in ecological communities and the effect ungulates can have on arthropod communities and populations. Putting these interactions in a larger context is also vital if we want to understand their strength and importance. Therefore, as next steps within this field of research, I advocate the following five research topics:

i) Controlled field and lab experiments targeting the underlying mechanisms of ungulate-insect TMIIs.

ii) Experiments and observations of indirect effects of ungulates on insects connecting more than two species (aiming to explore indirect interaction webs (Ohgushi 2005)) and determining the strength of different interactions.

iii) Experiments assessing how ungulate herbivory alter within plant variation (spatial and temporal) and the effects on subsequent insect herbivores.

iv) Combined monitoring of larger scale processes, such as insect outbreaks and ungulate damage levels, to assess if the effects on tree and habitat scale could influence landscape scale processes.

v) Long-term studies of how ungulate herbivory affects plant and insect communities under different densities of ungulates coupled with controlled experiments to assess the relative importance of DMIIs and TMIIs.

References

Abrams, P. A. (1995). Implications of dynamically variable traits for identifying, classifying, and measuring direct and indirect effects in ecological communities. *The American Naturalist.* 146(1), 112–134. doi:10.1086/285789

Abrams P.A., Menge B.A., Mittelbach G.G., Spiller D.A., Yodzis P. (1996) The Role of Indirect Effects in Food Webs. In: Polis G.A., Winemiller K.O. (eds) *Food Webs. Springer, Boston,* MA. doi:10.1007/978-1-4615-7007-3_36

Agrawal, A. A. (2000). Specificity of induced resistance in wild radish: causes and consequences for two specialist and two generalist caterpillars. *Oikos.* 89(3), 493 – 500. doi:10.1034/j.1600-0706.2000.890308.x.

Ali, J. G., & Agrawal, A. A. (2014). Asymmetry of plant-mediated interactions between specialist aphids and caterpillars on two milkweeds. Functional *Ecology*. 28(6), 1404–1412. doi:10.1111/1365-2435.12271

Awmack, C. S., & Leather, S. R. (2002). Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology.* 47(1), 817–844. doi:10.1146/annur ev.ento.47.091201.145300

Bailey, J. K., & Whitham, T. G. (2003). Interactions among elk, aspen, galling sawflies and insectivorous birds. *Oikos*, 101(1), 127–134. doi:10.1034/j.1600-0706.2003.12185.x

Belsky, A. J. (1986). Does herbivory benefit plants? A review of the evidence. *American Naturalist*. 127(6), 870–892.

Bergström, R., & Hjeljord, O. (1987). Moose and vegetation interactions in northwestern Europe and Poland. *Swedish Wildlife Research,* Supplement, 1, 213–228.

Berryman, A. A. (1996). What causes population cycles of forest Lepidoptera? *Trends in ecology & evolution*. 11(1), 28-32. doi:10.1016/0169-5347(96)81066-4

Björkman, C., Larsson, S., & Gref, R. (1991). Effects of nitrogen fertilization on pine needle chemistry and sawfly performance. *Oecologia*. 86(2), 202–209. doi:10.1007/BF003 17532

Björkman, C., Larsson, S., & Bommarco, R.(1997). Oviposition preferences in pine sawflies: A trade-off between larval growth and defence against natural enemies. *Oikos*, 79(1), 45–52. doi:10.2307/3546088

Bommarco, R., Firle, S. O., & Ekbom, B. (2007). Outbreak suppression by predators depends on spatial distribution of prey. *Ecological Modelling*. 201(2), 163-170. doi:10.1016/j.ecolmodel.2006.09.012

Boulanger, V., Dupouey, J. L., Archaux, F., Badeau, V., Baltzinger, C., Chevalier, R., Corcket, E., Dumas, Y., Forgeard, F., Mårell, A., Montpied, P., Paillet, Y., Picard, J. F., Saïd, S., & Ulrich, E. (2018). Ungulates increase forest plant species richness to the benefit of non-forest specialists. *Global change biology*. 24(2), e485–e495. doi:10.1111/gcb.13899

Bryant, J. P., Chapin, F. S., & Klein, D. R. (1983). Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos*, 40(3), 357–368. doi:10.2307/3544308

Campos, R. I., Vasconcelos, H. L., Riberio, S. P., Neves, F. S., & Soares, J. P. (2006). Relationship between tree size and insect assemblages associated with *Anadenanthera macrocarpa*. *Ecography*. 29(3), 442-450. doi: 10.1111/j.2006.0906-7590.04520.x

Dalin, P., Kindvall, O., & Björkman, C. (2009). Reduced Population Control of an Insect Pest in Managed Willow Monocultures. *PLoS ONE*. 4(5), e5487. doi:10.1371/journal.pone.0005487

Danell, K., & Huss-Danell, K. (1985). Feeding by Insects and Hares on Birches Earlier Affected by Moose Browsing. *Oikos*, 44(1), 75-81. doi:10.2307/3544046

Danell, K., Bergström, R., & Edenius, L. (1994). Effects of large mammalian browsers on architecture, biomass, and nutrients of woody plants. *Journal of Mammalogy*, 75, 833–844. doi: 10.2307/1382465

Den Herder, M., Virtanen, R., & Roininen, H. (2004). Effects of reindeer browsing on tundra willow and its associated insect herbivores. *Journal of applied ecology*. 41(5), 870-879. doi: 10.1111/j.0021-8901.2004.00952.x

Den Herder, M., Bergström, R., Niemelä, P., Danell, K., & Lindgren, M. (2009). Effects of natural winter browsing and simulated summer browsing by moose on growth and shoot biomass of birch and its associated invertebrate fauna. *Annales Zoologici Fennici*. 46, 63–74. doi:10.5735/086.046.0107

Denno, R. F., & McClure, M. S. (eds) 1983. *Variable plants and herbivores in natural and managed systems*. Academic Press, New York, New York, USA

Denno, R. F., McClure, M. S., & Ott, J. R. (1995). Interspecific interactions in phytophagous insects. *Annual review of entomology*. 40, 297-233. doi:10.1146/annurev.en.40.010195.001501

Du Toit, J. T., Bryant, J. P., & Frisby, K. (1990). Regrowth and palatability of Acacia shoots following pruning by African savanna browsers. *Ecology*. 71(1), 149–154. doi:10.2307/1940255

Edenius, L., Bergman, M., Ericsson, G., & Danell, K. (2002). The role of moose as a disturbance factor in managed boreal forests. *Silva Fennica*. 36(1), 57–67. doi:10.14214/sf.550

Edenius, L., Danell, K., & Bergström, R. (1993). Impact of herbivory and competition on compensatory in growth woody winter plants: on Scots pine browsing by moose. *Oikos,* 66, 286–292. doi: 10.2307/3544816.

Edenius, L., Danell, K. & Nyquist, H. (1995). Effects of simulated moose browsing on growth, mortality, and fecundity in Scots pine: relations to plant productivity. *Canadian journal of forest research*. 25, 529–535. doi: 10.1139/x95-060

Erb, M., Robert, C. A. M., Hibbard, B. E. & Turlings, T. C. J. (2011). Sequence of arrival determines plant-mediated interactions between herbivores. *Journal of Ecology*. 99(1), 7–15.doi:10.1111/j.1365-2745.2010.01757.x

Ericsson, A., Larsson, S., & Tenow, O. (1980). Effects of Early and Late Season Defoliation on Growth and Carbohydrate Dynamics in Scots Pine. *Journal of applied ecology*. 17(3), 747–769. doi:10.2307/2402653

Faison, E. K., DeStefano, S., Foster, D. R., Motzkin, G., & Rapp, J. M. (2016a). Ungulate browsers promote herbaceous layer diversity in logged temperate forests. *Ecology and evolution*. 6(13), 4591-4602. doi: 10.1002/ece3.2223

Faison, E. K.., DeStefano, S., Foster, D. R., Rapp, J. M., & Compton, J. A. (2016b). Multiple Browsers Structure Tree Recruitment in Logged Temperate Forests. *Plos One.* 11(11), e0166783. doi: 10.1371/journal.pone.0166783

FAO. 2020. Global Forest Resources Assessment 2020 – Key findings. Rome. doi:10.4060/ca8753en

Feeny, P. P. (1968). Effect of oak leaf tannins on larval growth of the winter moth *Operophtera brumata*. *Journal of Insect Physiology*. 14(6), 805–817. doi:10.1016/0022-1910(68)90191-1

Forkner, R. E., & Hunter, M. D. (2000). What goes up must come down? Nutrient addition and predation pressure on oak herbivores. *Ecology*. 81(6), 1588–1600. doi:10.1890/0012-9658(2000)081[1588:WGUMCD]2.0.CO;2

Gagic, V., Riggi, L.G.A., Ekbom, B., Malsher, G., Rusch, A., & Bommarco, R. (2016). Interactive effects of pests increase seed yield. *Ecology and Evolution*. 6(7), 2149–2157. doi: 10.1002/ece3.2003.

Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A. Z., & Schepaschenko, D. G. (2015). Boreal forest health and global change. *Science*. 349(6250), 819–822. doi:10.1126/science.aaa9092

Gish, M., Ben-Ari, M., & Inbar, M. (2017). Direct consumptive interactions between mammalian herbivores and plant-dwelling invertebrates: prevalence, significance, and prospectus. *Oecologia* 183, 347–352. doi:10.1007/s00442-016-3775-2.

Gómez, J. M., & González-Megías, A. (2002). Asymmetrical interactions between ungulates and phytophagous insects: Being different matters. *Ecology,* 83(1), 203–211. doi:10.1890/0012-9658(2002)083[0203:AIBUAP]2.0.CO;2

Gómez, J.M., & González-Megías, A. (2007a). Long-term effects of ungulates on phytophagous insects. *Ecological entomology*. 32(2), 229-234. doi: 10.1111/j.1365-2311.2006.00859.x

Gómez, J. M., & González-Megías, A. (2007b). Trait-mediated indirect interactions, density-mediated indirect interactions, and direct interactions between mammalian and insect herbivores. In: Ohgushi T., Craig TP., Price PW. (eds) *Ecological communities: Plant mediation in indirect interaction webs*. Cambridge University Press.

Gur'yanova, T. M. (2006). Fecundity of the European pine sawfly *Neodiprion sertifer* (Hymenoptera, Diprionidae) related to cyclic outbreaks: Invariance effects. *Entomological Review*, 86, 910–921. doi: 10.1134/S0013873806080069

Halaj, J., Ross, D. W., & Moldenke, A. R. (1997). Negative effects of ant foraging on spiders in Douglas-fir canopies. *Oecologia*. 109, 313–322. doi:10.1007/s004420050089

Hanski, I. 1987. Pine sawfly population dynamics: patterns, processes, problems. *Oikos*. 50(3), 327-335. doi:10.2307/3565493

Hanski, I. and Parviainen, P. 1985. Cocoon predation by small mammals, and sawfly population dynamics. *Oikos*. 45(1), 125-136. doi:10.2307/3565230

Hilker, M., Schwachtje, J., Baier, M., Balazadeh, S., Bäurle, I., Geiselhardt, S., Hincha, D. K., Kunze, R., Mueller-Roeber, B., Rillig, M. C., Rolff, J., Romeis, T., Schmülling, T., Steppuhn, A., van Dongen, J., Whitcomb, S. J., Wurst, S., Zuther, E., & Kopka, J. (2016). Priming and memory of stress responses in organisms lacking a nervous system. *Biological reviews*. 91(4), 1118–1133. doi:10.1111/brv.12215

Hobbs, N. (1996). Modification of Ecosystems by Ungulates. *The Journal of Wildlife Management*. 60(4), 695-713. doi:10.2307/3802368

Hódar, J. A., Zamora, R., Castro, J., Gómez, J. M. & García, D. (2008). Biomass allocation and growth responses of Scots pine saplings to simulated herbivory depend on plant age and light availability. *Plant Ecology*. 197, 229–238. doi: 10.1007/s11258-007-9373-y

Hof, A. R., & Svahlin, A. (2015). The potential effect of climate change on the geographical distribution of insect pest species in the Swedish boreal forest. *Scandinavian journal of forest research.* 31(1). doi:10.1080/02827581.2015.1052751

Holling, C. S. (1959). Some characteristics of simple types of predation and parasitism. *Canadian entomologist*. 91, 385-398.

Howe, A., Lövei, G. L., & Nachman, G. (2009). Dummy caterpillars as a simple method to assess predation rates on invertebrates in a tropical agroecosystem. *Entomologia Experimentalis et Applicata*. 131(3), 325-329. doi:10.1111/j.1570-7458.2009.00860.x

Hrabar, H., & Du Toit, J. T. (2014). Interactions between megaherbivores and microherbivores: Elephant browsing reduces host plant quality for caterpillars. *Ecosphere*. 5, 1–6. doi:10.1890/ES13-00173.1

Jactel, H., Bauhus, J., Boberg, J., Bonal, D., Castagneyrol, B., Gardiner, B., Gonzalez-Olabarria, J. R., Koricheva, J., Meurisse, N., & Brockerhoff, E. G. (2017) Tree Diversity Drives Forest Stand Resistance to Natural Disturbances. *Current Forestry Reports*. 3(3), 223-243. doi:10.1007/s40725-017-0064-1

Jactel, H., & Brockerhoff, E. G. (2007). Tree diversity reduces herbivory by forest insects. *Ecology letters*. 10(9), 835-848. doi:10.1111/j.1461-0248.2007.01073.x

Joern, A., & Behmer, S. T. (1997). Importance of dietary nitrogen and carbohydrates to survival, growth, and reproduction in adults of the grasshopper *Ageneotettix deorum* (Orthoptera: Acrididae). *Oecologia*. 112(2), 201–208. doi:10.1007/s0044 20050301

Jones, C. G., Hopper, R. F., Coleman, J. S., & Krischik, V. A. (1993). Control of systemically induced herbivore resistance by plant vascular architecture. *Oecologia*. 93(3), 452–456. doi:10.1007/BF00317892

Juutinen, P. (1967). Zur Bionomie und zum Vorkommen der Roten Kiefernbuschhornblattwespe (*Neodiprion sertifer* Geoffr.) in Finnland in den Jahren 1959-1965. *Comm. Inst. For. Fenn*. 63, 1-129.

Kaitaniemi, P., Riihimäki, J., Koricheva, J., & Vehviläinen, H. (2007). Experimental evidence for associational resistance against the European pine sawfly in mixed tree stands. *Silva Fennica*. 41, 259–268. doi:10.14214/sf.295

Kaitaniemi, P., Ruohomäki, K., Ossipov, V., Haukioja, E., & Pihlaja, K. (1998). Delayed induced resistance in the biochemical compositions of host plant leaves during an insect outbreak. *Oecologia*. 116, 182– 190. doi.org:10.1007/s0044 20050578

Kollberg, I., Bylund, H., Jonsson, T., Schmidt, A., Gershenzon, J., & Björkman, C. (2015). Temperature affects insect outbreak risk through tritrophic interactions mediated by plant secondary compounds. *Ecosphere*. 6, 1–17 doi:10.1890/ES15-000021.1

Kolomiets, N. G., Stadnitskii, G. V., & Vorontzov, A. I. (1979). The European pine sawfly. Amerind Publishing Co., Pvt. Ltd, New Delhi.

Kolstad, A. L., Austrheim, G., Solberg, E. J., Venete, A., M., A., Woodin, S. J., & Speed, J. D. M. (2018a) Cervid Exclusion Alters Boreal Forest Properties with Little Cascading Impacts on Soils. *Ecosystems*. 21(5), 1027–1041. doi:10.1007/s10021-017-0202-4

Kolstad, A.L., Austrheim, G., Solberg, E. J., De Vriendt, L., & Speed, J. D. M. (2018b). Pervasive moose browsing in boreal forests alters successional trajectories by severely suppressing keystone species. *Ecosphere*. 9 (10), e02458. doi: 10.1002/ecs2.2458

Landsman, A. P., Bowman, J. L. (2017). Discordant response of spider communities to forests disturbed by deer herbivory and changes in prey availability. *Ecosphere*. 8(2), e01703. doi: 10.1002/ecs2.1703.

Langellotto, G. A., & Denno, R. F. (2004). Responses of invertebrate natural enemies to complex-structured habitats: A meta-analytical synthesis. *Oecologia*. 139, 1–10. doi:10.1007/s00442-004-1497-3

Larsson, S., Björkman, C., & Gref, R. (1986). Responses of *Neodiprion sertifer* (Hym., Diprionidae) larvae to variation in needle resin acid concentration in Scots pine. *Oecologia*. 70(1), 77-84. doi:10.1007/BF00377113

Larsson, S., Björkman, C., & Kidd, N. A. C. (1993). Outbreaks in diprionid sawflies: why some species and not others? – In: Wagner, M. R. and Raffa, K. F. (eds), *Sawfly life history adaptations to woody plants*. Academic Press. 453–483.

Larsson, S., Ekbom, B., & Björkman, C. (2000). Influence of plant quality on pine sawfly population dynamics. *Oikos*. 89(3), 440–450. doi:10.1034/j.1600-0706.2000.890303.x

Lawton, J. H. (1983). Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology*. 28, 23–39. doi:10.1016/B978-0-12-374144-8.00000-0

Leather, S. R. 2008. *Insect Sampling in forest ecosystems*. Blackwell Science Ltd, Blackwell Publishing.

Lilleeng M. S., Rydgren K., Halvorsen R., Moe S. R., & Hegland S. J. (2018) Red deer structure the ground-dwelling beetle community in boreal forest. *Biodiversity and conservation*. 27, 2507-2525. doi:10.1007/s10531-018-1550-x

Lindroth, R. L., Kinney, K. K., & Platz, C. L. (1993). Responses of deciduous trees to elevated atmospheric CO2: Productivity, phytochemistry, and insect performance. *Ecology*. 74(3), 763–777. doi:10.2307/1940804

Lindstedt, C., Mappes, J., Päivinen, J., & Varama, M. (2006). Effects of group size and pine defence chemicals on Diprionid sawfly survival against ant predation. *Oecologia*. 150, 519–526. doi:10.1007/s00442-006-0518-9

Lyytikäinen-Saarenmaa, P. (1999). The responses of scots pine, *Pinus sylvestris*, to natural and artificial defoliation stress. *Ecological applications*. 9(2), 469–474 (1999). doi:10.1890/1051-0761(1999)009[0469:TROSPP]2.0.CO;2

Lyytikäinen-Saarenmaa, P., & Tomppo, E. (2002) Impact of sawfly defoliation on growth of Scots pine *Pinus sylvestris* (Pinaceae) and associated economic losses. Bulletin of Entomological Research. 92(2), 137–140. doi:10.1079/BER2002154

Lövei, G. L., & Ferrante, M. (2017). A review of the sentinel prey method as a way of quantifying invertebrate predation under field conditions. *Insect Science.* 24(4), 528-542. doi:10.1111/1744-7917.12405

Martin J-L., Stockton S. A., Allombert S., Gaston A. J. (2010) Top-down and bottom-up consequences of unchecked ungulate browsing on plant and animal diversity in temperate forests: lessons from a deer introduction. *Biological invasions*. 12(2), 353-371. doi:10.1007/s10530-009-9628-8

Mattson, W. J. (1980). Herbivory in relation to plant nitrogen content. *Annual Review of Ecology, Evolution, and Systematics*. 11(1), 119–161. doi:10.1146/annur ev.es.11.110180.001003

Mauch-Mani, B., Baccelli, I., Luna, E., & Flors, V. (2017). Defense Priming: An Adaptive Part of Induced Resistance. *Annual review of plant biology*. 68, 485–512. doi:10.1146/annurev-arplant-042916-041132

McInnes, P.F., Naiman, R.J., Pastor, J., Cohen, Y. (1992) Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. *Ecology*. 73(6), 2059-2075.doi:10.2307/1941455

Muiruri, E. W., Milligan, H. T., Morath, S., & Koricheva, J. (2015). Moose browsing alters tree diversity effects on birch growth and insect herbivory. *Functional Ecology*. 29(5), 724–735. doi:10.1111/1365-2435.12407

Nykänen, H., & Koricheva, J. (2004). Damage-induced changes in woody plants and their effects on insect herbivore performance: A meta-analysis. *Oikos*, 104(2), 247–268. doi:10.1111/j.0030-1299.2004.12768.x

Ohgushi, T. (2005). Indirect interaction webs: Herbivore-induced effects through trait change in plants. *Annual Review of Ecology, Evolution, and Systematics*. 36, 81–105. doi:10.1146/annur ev.ecolsys.36.091704.175523

Olofsson, E. (1987). Mortality factors in a population of *Neodiprion sertifer* (Hymenoptera: Diprionidae). *Oikos*. 48(3). 297-303. doi:10.2307/3565517

Olofsson, E. (1992). Predation by *Formica polyctena* Förster (Hym., Formicidae) on newly emerged larvae of *Neodiprion sertifer* (Geoffroy) (Hym., Diprionidae). *Journal of Applied Entomology*. 114, 315–319. doi:10.1111/j.1439-0418.1992.tb01132.x

Poelman, E. H., van Dam, N. M., van Loon, J. J. A., Vet, L. E. M., & Dicke, M. (2009). Chemical diversity in *Brassica oleracea* affects biodiversity of insect herbivores. *Ecology*. 90(7). doi:10.1890/08-0977.1

Pschorn-Walcher, H. (1965). The ecology of *Neodiprion sertifer* (Geoffr.) (Hymenoptera: Diprionidae) and a review of its parasite complex in Europe. *Commonwealth Inst Biol Cont Tech Bull*. 5, 33-97.

Reynolds, P.G., & Cuddington, K. (2012a). Effects of plant gross morphology on predator consumption rates. *Environmental entomology* 41, 508-515. doi:10.1603/EN11178

Reynolds, P.G., & Cuddington, K. (2012b). Effects of plant gross morphology on predator searching behaviour. *Environmental entomology* 41, 516-522. doi:10.1603/EN11179

Schwenk, W. S., & Strong, A. M. (2011). Contrasting patterns and combined effects of moose and insect herbivory on striped maple (Acer pensylvanicum). *Basic and Applied Ecology*. 12(1), 64–71. doi:10.1016/j.baae.2010.10.002

Stephens, A. E. A., Srivastava, D. S. & Myers, J. H. (2013). Strength in numbers? Effects of multiple natural enemy species on plant performance. *Proceedings of the Royal Society B Biological Sciences.* 280(1760). doi:10.1098/rspb.2012.2756

Stolter, C. (2008). Intra-individual plant response to moose browsing: Feedback loops and impacts on multiple consumers. *Ecological Monographs*. 78(2), 167–183. doi:10.1890/07-0401.1

Strauss, S. Y. (1991). Direct , Indirect, and Cumulative Effects of Three Native Herbivores on a Shared Host Plant. *Ecology*. 72(2), 543–558. doi:10.2307/2937195.

Suominen, O., Danell, K. (2006). Effects of large herbivores on other fauna. In: Pastor J, Danell K, Duncan P, Bergström R, editors. *Large Herbivore Ecology, Ecosystem Dynamics and Conservation*. Cambridge: Cambridge University Press. pp. 383-412

Suominen O, Persson IL, Danell K, Bergström R, Pastor J (2008) Impact of simulated moose densities on abundance and richness of vegetation, herbivorous and predatory arthropods along a productivity gradient. *Ecography*. 31(5), 636-645. doi:10.1111/j.0906-7590.2008.05480.x

Swedish National Forest Inventory. (2020). Skogsdata 2020. Forest statistics 2020 Official Statistics of Sweden, Swedish University of Agricultural Sciences. Institutionen för skoglig resurshushållning, Umeå.

Tabuchi, K., Ueda, A., & Ozaki, K. (2010). Contrasting effects of deer browsing on oviposition preference, neonate survival and potential fecundity of a galling insect. *Écoscience*. 17(4), 379–386. doi:10.2980/17-4-3354

Vanbergen, A. J., Hails, R. S., Watt, A. D., & Jones, T. H. (2006) Consequences for host-parasitoid interactions of grazing-dependent habitat heterogeneity. *Journal of Animal Ecology*. 75(3), 789-801. doi:10.1111/j.1365-2656.2006.01099.x

Van Zandt, P.A., & Agrawal, A. A. (2004). Community-wide impacts of herbivore induced plant responses in milkweek (*Asclepias syriaca*). *Ecology*. 85(9): 2616-2629. doi:10.1890/03-0622

Wallace, D. R., & Sullivan, C. R. (1963). Laboratory and Field Investigations of the Effect of Temperature on the Development of *Neodiprion sertifer* (Geoff.) in the Cocoon. *The Canadian entomologist.* 95(10), 1051-1066 doi:10.4039/Ent951051-10

Wallgren, M., Bergquist, J., Bergström, R., & Eriksson, S. (2014). Effects of timing, duration, and intensity of simulated browsing on Scots pine growth and stem quality. *Scandinavian Journal of Forest Research*. 29(8), 734–746. doi:10.1080/02827 581.2014.960896

Wallner, W. (1987). Factors affecting insect population dynamics: Differences between outbreak and non-outbreak species. *Annual review of entomology*. 21(1), 109-133.

Walton, A. (2012). Provincial-Level Projection of the Current Mountain Pine Beetle Outbreak: Update of the infestation projection based on the Provincial Aerial Overview Surveys of Forest Health conducted from 1999 through 2011 and the BCMPB model (year 9). BC Forest Service.

Werner, E., E., & Peacor, S., D. (2003). A review of trait-mediated indirect interactions in ecological communities. *Ecology*. 84(5), 1083-1100. doi: 10.1890/0012-9658(2003)084[1083:AROTII]2.0.CO;2

Widemo, F., Christoffersson, P. SLU och Holmen Skog i samarbete om uppföljning av effekter av klövviltbetning i ungskog. Umeå: SLU. Web page: https://www.slu.se/institutioner/vilt-fisk-miljo/miljoanalys/slu-och-holmen-skog-i-samarbete-om-uppfoljning-av-effekter-av-klovviltbetning-i-ungskog/

Popular science summary

Plants occur in almost all ecosystems on earth and where there are plants, there are herbivores – animals that feed on plants. When attacked by herbivores plants respond in various ways to prevent further attack and to counteract the negative effects caused by the damage. This is referred to as ‘induced responses’. When plants respond to damage by one herbivore, the resulting induced responses can affect subsequent herbivores feeding on the same plant – this is known as an indirect interaction. Even though indirect interactions have been explored in many systems, it has not been explored to a large extent between mammalian and insect herbivores. Indirect interactions between mammals and insects could be of great importance in for example forest ecosystems where ungulate browsers (such as moose) and pest insects are common and often utilise the same trees as food plants. Ungulates affect trees in various ways, changing nutrient composition, plant defences and tree architecture. These ungulate induced responses could potentially affect insect performance, communities and populations. Moreover, combined ungulate and insect herbivory could potentially affect tree growth non-independently. This means that the combined impact of the two herbivores on growth is either larger or smaller than what would be expected from their independent effects. In this thesis, I study the indirect interaction between ungulates and forest insects, and explore the consequences of such interactions for tree growth and insect population dynamics. I focused my research on Scots pine (*Pinus sylvestris*) and the European pine sawfly (*Neodiprion sertifer*). I found that ungulates can *(i)* affect sawfly survival and egg laying capacity, *(ii)* influence sawfly population characteristics, *(iii)* affect insect communities and interactions and that *(iv)* combined ungulate and sawfly herbivory can reduce pine growth non-additively. Overall, my findings suggest that interactions between ungulates and insects cannot be disregarded in ecological systems, and can affect tree growth. This thesis contributes to a larger understanding of ecological communities and interactions between plants and herbivores.

Populärvetenskaplig sammanfattning

Växter finns i nästintill alla ekosystem på jorden, och där det finns växter finns det växtätare. Växter är anpassningsbara och reagerar på skador från växtätare, både för att skydda sig mot vidare skador och för att reparera skadorna. Dessa reaktioner omfattar bland annat produktion av försvarsämnen, förändrat näringsinnehåll och förändrad tillväxt. När en växt reagerar på skador från en växtätare kan det påverka kommande växtätare – detta kallas för en indirekt interaktion. Två växtätare interagerar alltså med varandra – men indirekt – genom växtens reaktioner. Indirekta interaktioner mellan växtätare har främst studerats mellan sinsemellan lika arter (till exempel mellan insekter). Interaktioner mellan väldigt olika arter, så som däggdjur och insekter har studeras i betydligt mindre grad. Indirekta interaktioner mellan däggdjur och insekter skulle kunna ha stor betydelse i skogsekosystem, där arter så som klövvilt och skadeinsekter är vanligt förekommande och dessutom ofta utnyttjar samma träd. Klövvilt påverkar träd på flertalet olika sätt, och dessa förändringar kan komma att påverka till exempel överlevnad och förekomst av skadeinsekter. I den här avhandlingen har jag studerat hur bete från klövvilt påverkar insekter på tall. Jag har främst fokuserat på röd tallstekel (*Neodiprion sertifer*), som är en skadeinsekt som kan orsaka stor skada på tallskog. I denna avhandling visar jag att: klövviltsbete kan påverka tallsteklars överlevnad och äggläggningskapacitet och därmed eventuellt påverka deras populationstillväxt. Jag visar också att klövviltsbete kan förändra sammansättningen av insektssamhällen på tallar. Dessutom visar jag att kombinerat bete från klövvilt och tallsteklar kan ha icke-additiva effekter på tillväxt hos tall, det vill säga att tillväxten hos tallar kan bli både större och mindre än vad som kan förväntas rent teoretiskt av de individuella tillväxteffekterna från de båda växtätarna. Resultaten i denna avhandling bidrar till en ökad förståelse för indirekta interaktioner samt belyser komplexiteten i ekologiska system.

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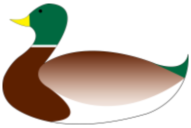

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Herbivores that share a host plant can directly and indirectly affect each other in several ways, with consequences for plant damage and growth. Interactions between taxonomically distant herbivores has been poorly studied. This thesis examines the effects of ungulate browsing and grazing on performance, abundance and diversity of herbivorous insects and their predators, and explores how such changes can influence insect population dynamics. It also examines the combined effect of ungulate and insect herbivory on tree growth.

Michelle Nordkvist received her PhD education at the department of Ecology, SLU and obtained her Master of Science in Biology from Uppsala University.

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